

Full Length Research Paper

Effects of river sediments on coral recruitment, algal abundance benthic community structure on Kenyan coral reefs

Shaaban A. Mwachireya^{1*}, Tim R. McClanahan², Brian E. Hartwick³, Isabelle M. Cote³ and Lance Lesack⁴

¹Kenya Marine and Fisheries Research Institute, P. O. BOX 81651, Mombasa 80100, Kenya.

²Wildlife Conservation Society, Marine Programs, Bronx, NY. 10460, USA.

³Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6 Canada.

⁴Department of Geography, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6 Canada.

Received 12 January, 2015; Accepted 14 July, 2014

The effects of sediment concentration and season on coral recruitment algal abundance and benthic community structure were studied in Kenyan coral reef lagoons to determine their potential influence on coral recovery. Nutrient levels and recruit numbers were higher during the southeast monsoon (SEM) than during the northeast monsoon (NEM) season and in sediment-exposed compared to non-sediment exposed reefs. Mean algal biomass also exhibited the same seasonal trend (except at one site), but was higher in the non-sediment exposed reef compared to the other reefs. Corals in the sediment exposed reef exhibited morphological differences relative to the other reefs: fewer corymbose and plate-like but more branching, massive and solitary forms and increased colony and corallite sizes. However, sediments did not suppress coral recruitment rates. These morphological changes coupled with the interaction between biological and physico-chemical characteristics have important ecological and geological implications: by potentially modifying calcium carbonate production and ameliorating the adverse effects of climate induced stress events, this may minimize coral mortality and enhance reef recovery.

Key words: Algal biomass, coral recruitment, hydrodynamics, coral morphology, seasonality, sediments.

INTRODUCTION

Recent coral reef studies have highlighted the declining trends in coral abundance worldwide (Bellwood et al., 2004; Lirman and Fong, 2007; Pandolfi et al., 2011; De'ath et al.,

2012; Darling et al., 2013) due to global climate change (McClanahan et al., 2005; Hoegh-Guldberg et al., 2007; Selig et al., 2012; Doropoulos et al., 2012; Logan et al.,

*Corresponding author. E-mail: mwachireya@yahoo.com. Tel 254 (41) 475154; Fax 254 (41) 475157.

2014; McClanahan et al., 2012; Palumbi et al., 2014) and anthropogenic disturbances, especially increases in human activities and associated development (West and Woessik, 2001; Wolanski et al., 2009; Hughes et al., 2010). In many cases, these declines have been linked to human induced perturbations that influence gradients of water quality and levels of exploitation that lead to increased sea surface temperature (SST) and atmospheric CO₂ (Fabricius, 2005; Pandolfi et al., 2005; Fabricius and McCorry, 2006; Richmond et al., 2007; Doropoulos et al., 2012; Logan et al., 2014). Recently, local and regional risk assessments have ranked the degree of vulnerability of reefs to anthropogenic stressors based primarily on potential land-based sources of disturbances (Burke and Maidens, 2004; Nyström et al., 2000; Wolanski et al., 2009). Further, the 1997/1998 worldwide bleaching event was unprecedented in its global impact on coral reefs with reports of about 50 to 90% coral mortality in some areas (Goreau et al., 2000; McClanahan et al., 2005; McClanahan, 2014). The interaction of anthropogenic and natural disturbances is therefore of great concern to the future existence and the persistence of coral reefs worldwide. In order to develop management strategies that improve coral survival and recovery, a greater understanding of life history processes and terrestrial impacts on coral recruitment and settlement is needed (Fabricius, 2005; Nozawa and Harrison, 2008; Maina et al., 2011; Darling et al., 2012).

Reproduction, recruitment and settlement are important processes in the maintenance and replenishment of coral reef populations (Hariri et al., 2002; Glassom et al., 2004; Gilmore et al., 2013), but water quality is considered a major factor influencing the above three population parameters (Nzali et al., 1998; Miller et al., 2000; Belleveau and Paul, 2002; Harrington et al., 2004; Glassom et al., 2004). In particular, water quality through its sediment and nutrient components has been reported to affect early coral life history processes by (1) the influence of nutrients and sediments on coral disease dynamics (Kuta and Richardson, 2002; Bruno et al., 2003), (2) altering the structural strength and density of reef substrate by influencing rates of bioerosion (Tribollet and Golubic, 2011; Carreiro-Silva et al., 2012), (3) modifying predation and herbivory rates on coral reefs through changes in grazing populations (McClanahan et al., 2011; Baker et al., 2013), (4) modifying heterotrophic filter feeding populations and therefore, net carbonate production (Dunn et al., 2012; Godinot et al., 2012), (5) influence of sediments on coral settlement through changes in substrate composition (Fabricius et al., 2005; Birrell et al., 2005, 2008; Diaz-Pulido et al., 2010) and (6) the action of sediments in reducing the competitive success of corals for space against algae (Nugues and Roberts, 2003a; McClanahan et al., 2012).

Recent increases in human activities such as farming, coastal development and deforestation have elevated the amount of soil transported by rivers into the marine environment with subsequent increases in turbidity and sediment in coral reef areas (Rotmann and Thomas, 2012). Increased terrestrial sediments into marine and coastal

habitats have been identified as a major cause of distribution, diversity, community structure changes and degradation in coral reefs (Rodgers, 1999; and Roberts, 2003a; Fabricius, 2005). At the individual level, sediments have been linked to modification of light, thus affecting coral photosynthesis, overpower the sediment cleansing mechanisms and generally interfere with coral physiology leading mortality (Rodgers, 1990; Nugues; Fabricius, 2005). Moreover, Rodgers (1990) put forward seven characteristics of coral reefs effected by sediments: (1) low species diversity and absence of some species, (2) reduced percent coral cover, (3) high abundance of forms and species resistant to smothering and low light intensity (4) generally smaller colonies or, (5) generally larger colonies depending on coral sediment-tolerance/adaptive capabilities, (6) upward shift in depth zone and (7) a greater abundance of branching forms. Despite many reports on these potential influences, studies on the effects of sediments on benthic algae (and consequently coral recruitment) have produced inconsistent results, with elevated as well as reduced algal abundance reported in areas with high sediment levels (Hughes and Tanner, 2000; Irving and Connell, 2000; Gorgula and Connell, 2004). Resolving these conflicting and inconsistent findings is a major priority for coral reef management. Consequently, we assessed the effect of increased sediment levels on the coral community structure and coral recruit-algal density relationship in four protected reef lagoons in Kenya.

MATERIALS AND METHODS

Study sites

Field studies were carried out in four Kenyan coral reef lagoons: (1) Malindi near the Sabaki river mouth (2) Watamu close to the mangrove-fringed Mida creek, (3) Mombasa, and (4) the offshore Kisite (Shimoni) reef on the extreme southern end of Kenya's fringing reef (Figure. 1). All four reefs are marine protected areas (MPAs) with more than 15 years of protection from fishing, coral and shell collection, and all forms of harvesting. The study reefs have been described fully in previous reports (Katwijk et al., 1993; McClanahan et al., 1994; Watson and Ormond, 1994; Mangubhai et al., 2007). These four shallow water reefs are found at 0.3 to 2 m deep at low tide with Kenya having a 4 m tidal range. Study reefs were chosen due to their accessibility, the type of exploitation and the influence of river discharge. The Malindi reefs experience a strong pulse of land-derived sediments during the short rain (northeast monsoon, NEM) season from the Sabaki River as a result of the reversed monsoon driven currents (Kayanne et al., 2006; Fleitmann et al., 2007). Watamu reef is a fringing reef adjacent to the highly ramified, groundwater sustained Mida mangrove creek that is devoid of any external freshwater input. Mombasa reef is a stretch of lagoonal fringing reef about 6 km long and 1 km from the shore, situated about 5 km from the city of Mombasa. This reef is moderately influenced by local rainfall and is adjacent to two mangrove creeks, Tudor and Mtwapa. Shimoni is a remotely located reef in the Kisite MPA on the seaward side of Wasini Island offshore from Shimoni town. Minimal terrestrial anthropogenic influence was expected from this reef due to its remote location. Three study sites were selected in Malindi and Shimoni reefs, and two sites were used in Watamu and Mombasa reefs. Sampling was conducted during the northeast (NEM) and the

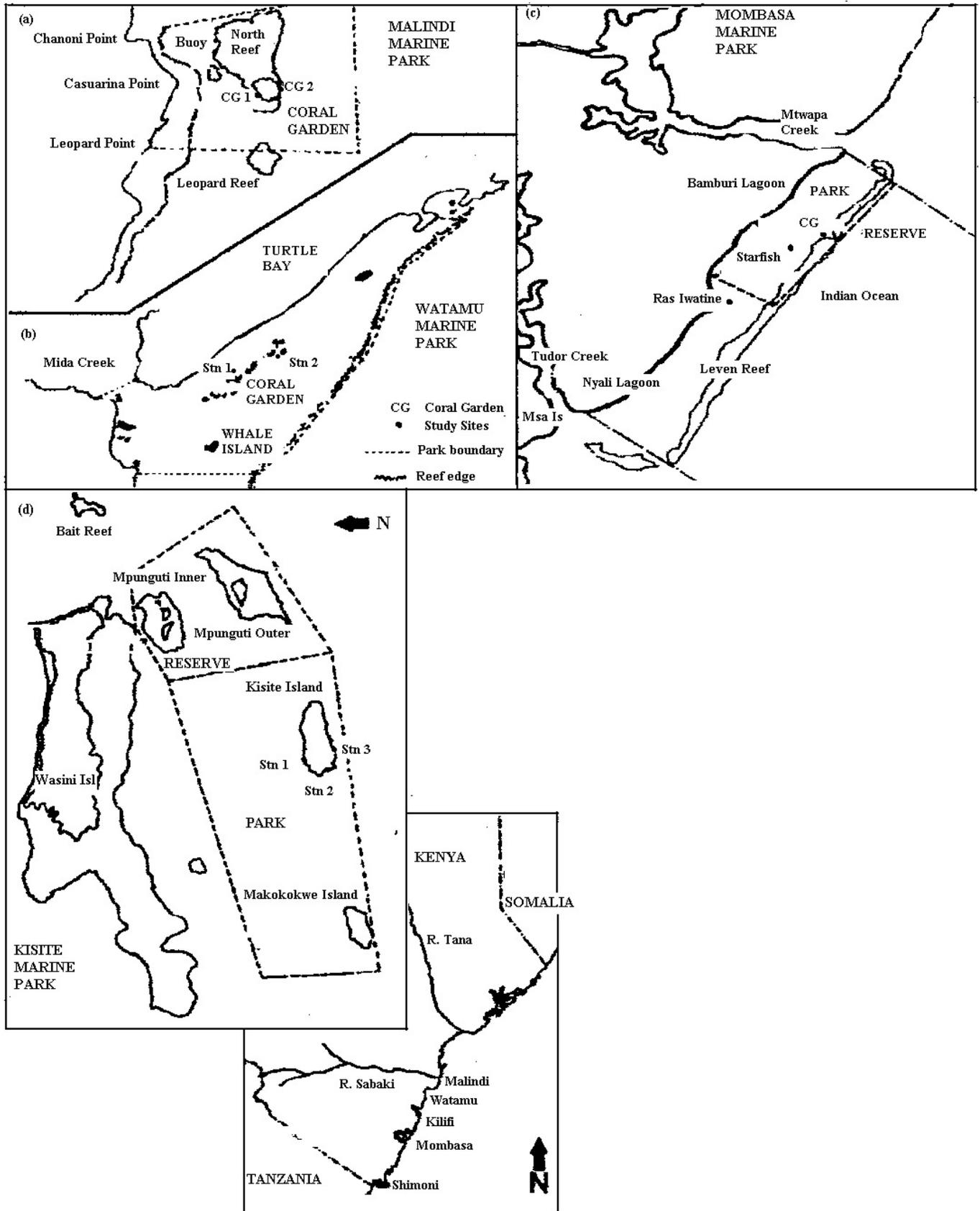


Figure 1. Map of the Kenyan coastline showing location of Malindi, Watamu, Mombasa and Shimoni protected reefs and study sites.

southeast (SEM) seasons in order to capture the effects of changing oceanographic conditions (McClanahan, 1988).

Measurement of environmental parameters

Environmental sampling was conducted twice per month for three months during each of the NEM and SEM seasons. 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 after filtration of 1 L water samples through 0.45 μM pore size glass filters and spectrophotometric analysis of the filtrate. Total suspended sediment (TSS) concentration was determined by filtering 1 L water samples through pre-weighed 0.45 μM pore size glass filters. The filters were then oven dried overnight at 60°C and weighed again for gravimetric determination of suspended sediment concentration. Sedimentation rates were measured using sediment traps consisting of a set of four plastic cups attached to PVC pipe driven firmly into the substrate at each site with cup mouths approximately 50 cm above the sea bottom. Accumulated sediments were collected biweekly and after collection, sediments were washed with freshwater, small animals and plants were removed and the sediment was oven dried at 60°C overnight. Further, at each reef, samples of bottom sediment were randomly collected monthly using a cylindrical corer (50 cm high and 2 cm in diameter). Sediment samples were dried at 60°C to constant weight after washing with distilled water to remove salts. Replicate 100 g samples were then sieved through 710, 500, 355, 180, 125 and 63 μM using an automatic sieve shaker. Differences in sediment quality were inferred from the average weight of coarse (> 180 μM) and fine (\leq 180 μM) sediment fractions. Number of samples varied between eight and sixteen cores per reef. Sediment organic matter (as an indicator of terrestrial influence) was determined as loss in weight after combusting samples in a furnace at 500°C for 4 h.

Coral spat settlement studies

Twenty to forty ceramic tiles (15 x 15 cm) with the unglazed surface facing up were randomly deployed in each site. Tiles were attached to the substrate with cable ties and left in the field for four to six months during each of the two East African monsoon seasons over a three year period. After collection, tiles were thoroughly washed with sea and freshwater to remove sediments and salts, packed individually with old newspapers to avoid damage, sun dried at the laboratory and later bleached to reveal the coral recruits. The tiles were examined at low magnification, recruits were counted and their diameters were measured (to the nearest mm) under a microscope equipped with an ocular scale.

Algal settlement and substrate studies

Ten to fifteen tiles from each reef per season were preserved in formalin after collection and transported to the laboratory. Tiles were thoroughly washed with freshwater to remove formalin and marine sediments, and algae samples were scrapped from five areas of 2 x 2 cm from the 4 corners and the centre of each tile. Algae samples were dried overnight in an oven at 100°C for determination of dry algal biomass. At each of the sites, benthic cover was studied by completing nine to twelve 10 m benthic line transects randomly placed on the substrate for description of the benthic cover (McClanahan and Shafir, 1990). The length of benthic categories > 3 cm were and classified according to the following categories: hard and soft coral, coralline, calcareous and fleshy algae, sponge, seagrass and sand. Hard corals were identified to the genus level, their percent cover was estimated and colony diameters were measured. Hard corals were further

classified into eight coral growth forms: massive, branching, foliose, plate, digitate, corymbose, solitary and encrusting. Substrate complexity (rugosity) was estimated using the procedure described in McClanahan and Shafir (1990). Diversity was assessed using species richness, Pielou's *J* evenness index and Shannon's *H* diversity (Shannon and Weaver, 1949).

Statistical analysis

A one way-analysis of variance (ANOVA) was employed to test for differences in substrate cover, coral genera and colony size between reefs, and a 2-way ANOVA was used to test for differences in algal biomass and environmental factors between reefs and seasons. A 3-way ANOVA test was used to test for differences in sediment quality (reef x season x gain size) and coral recruit density (reef x season x surface). Bartlett's and Shapiro-Wilk tests were used to test for homoscedasticity and normality of variance, respectively. Where differences were detected, comparisons were done using Tukey HSD test to determine which means were significantly different. Sediment and algal data were log (*x*+1) transformed in order to conform to the assumptions of ANOVA. Pearson's correlation coefficients were used to examine the degree of association between biological and oceanographic parameters. The statistical programs STATISTICA 6.0 for Windows and JMP 7.0 were used for the above analyses while PRIMER (Plymouth Routines in Multivariate Ecological Research) was used in the analysis of diversity indices.

RESULTS

Environmental parameters

Mean seasonal environmental variables showed that Malindi had higher nutrient and sedimentation concentrations compared to the other reefs with a general decline in nutrients and sediments toward Shimoni in the south (Figures 2 and 3). Current velocity did not differ between seasons but was high in Malindi relative to the other reefs (Figure 2a). Mean temperature and salinity values for all study sites were significantly lower during the SEM compared to the NEM period (except salinity in Malindi, Figure 2b and c). Water column chlorophyll-*a* concentration exhibited a unique pattern: being higher in Malindi and Watamu compared to Mombasa and Shimoni during the SEM but generally lower and more similar during the NEM (Figure 2d). Mean phosphate concentrations did not differ between reefs during the NEM season; however, during the SEM, phosphate concentrations were found to be significantly lower in Shimoni and higher in Watamu compared to the other study reefs (Figure 2e). No significant difference in nitrate concentration was detected between seasons, but nitrate concentration was higher in Malindi and declined to the south toward Shimoni reef (Figure 2f).

Total suspended sediment concentration (TSS) and TSS organic content exhibited little spatial variation but were higher in the SEM compared to the NEM for all sites, except Mombasa (Figures 3a and b). Sedimentation (sediment deposition) rates were found to be high during the SEM compared to the NEM for all studied

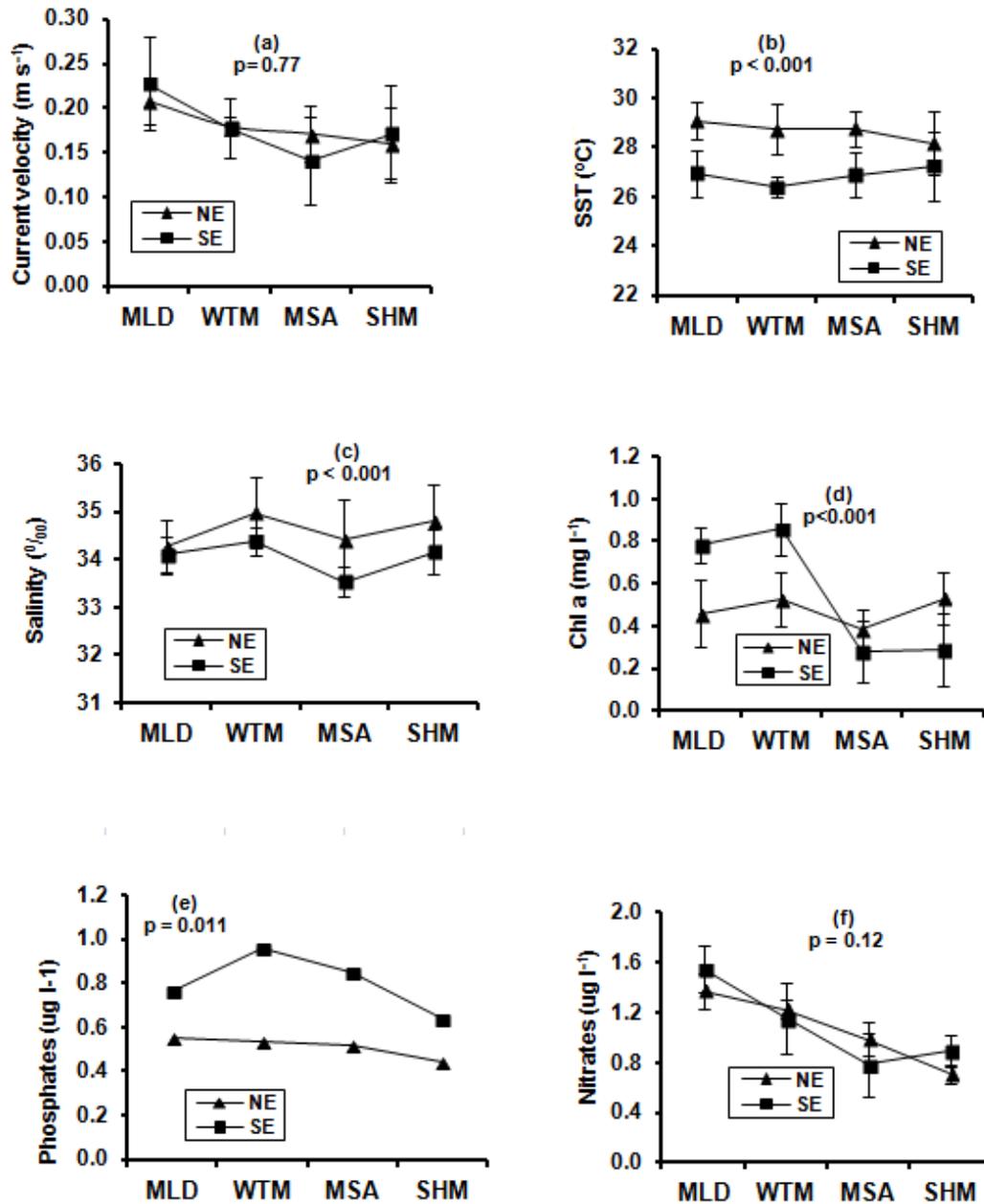


Figure 2. Seasonal means of environmental factors (means \pm SD) in study reefs, Malindi (MLD), Watamu (WTM), Mombasa (MSA) and Shimoni (SHM). Sample size for each mean: current velocity, SST and salinity, $11 < n < 24$, chlorophyll a, phosphates and nitrates, $10 < n < 33$. Significant tests are for reef \times season interaction term.

reefs, in addition to being higher in Malindi relative to the other study reefs (Figures 3c).

Higher proportions of organic matter in trapped (deposited) and bottom sediments were measured in Malindi during the NEM compared to the SEM, but sediment organic content did not differ between seasons in the other study reefs (except bottom sediment organic content in Mombasa). Bottom sediment organic content was found to be higher in Mombasa and Shimoni

compared to Malindi and Watamu (Figures 3d and e). A higher proportion of fine sediment particles ($< 180 \mu\text{m}$) was observed in Watamu and Shimoni relative to Mombasa and Malindi during the SEM season. During the NEM season, a higher proportion of fine particles was found in the Watamu reef compared to all other reefs, however Malindi sediment-exposed reef exhibited a higher proportion relative to Shimoni and Mombasa reefs (Figure 3f, Table 1).

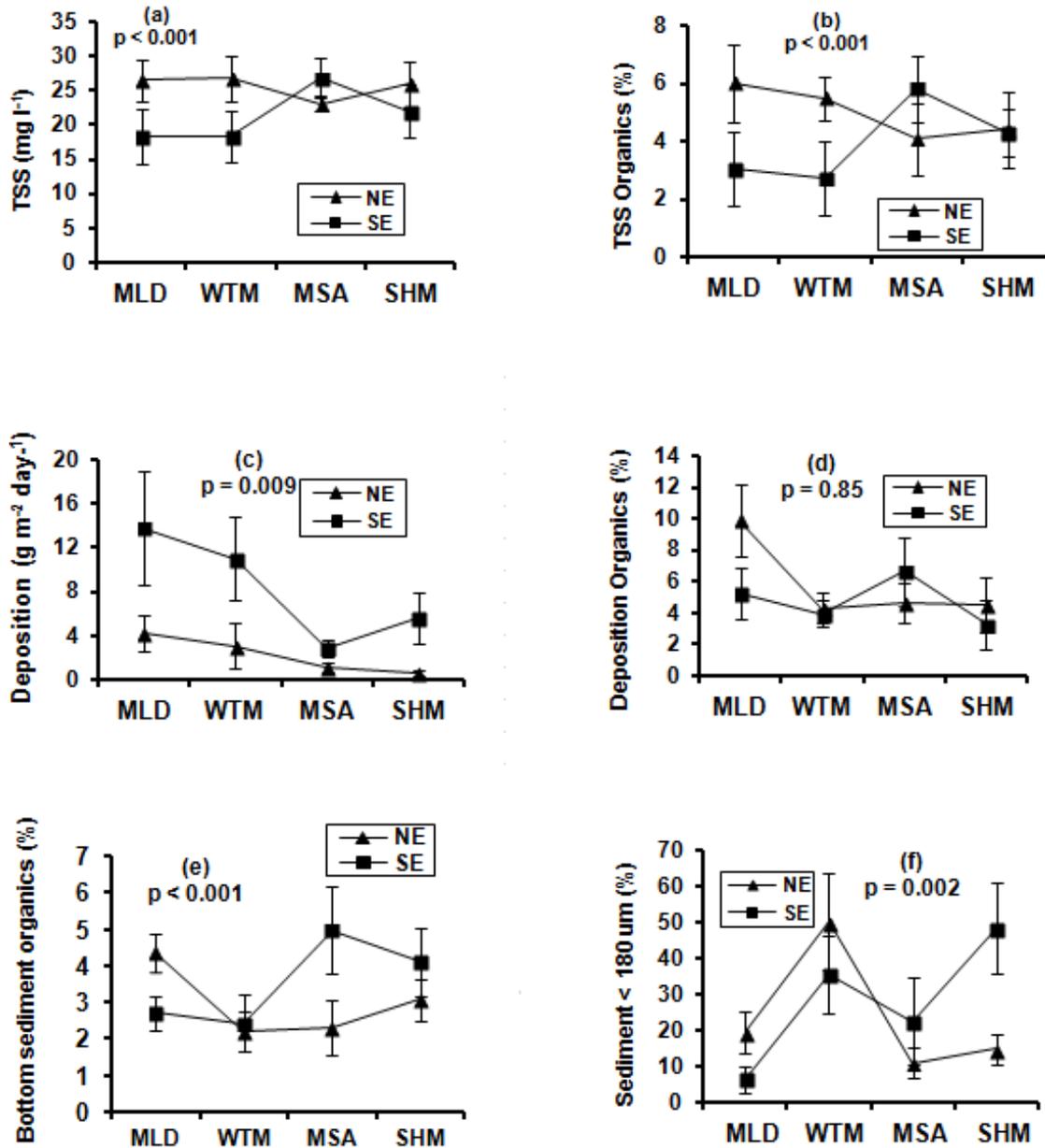


Figure 3. Sediment and sediment organic content (means ± SD) in relation to season and reefs, Malindi (MLD), Watamu (WTM), Mombasa (MSA) and Shimoni (SHM). Sample size; TSS and organics, 20 < n < 23, sediment deposition rates and organics, 12 < n < 18 traps, bottom sediment organics and percent particle size < 180 μm, 8 > n < 16 cores. Significant tests are for reef x season interaction term

Coral recruitment studies

Overall, recruit density did not differ between seasons and all reefs showed similar seasonal patterns in number of coral recruits (Figures 4 and 5; Table 2). Average recruit density (mean of 2 seasons) in the sediment exposed reefs of Malindi (21.4 recruits per tile) was significantly higher compared to all other study reefs, with more recruits being counted during the NEM compared to SEM season in all sites. Further, significant high numbers of recruits were

observed on the underside (lower surface) of tiles relative to the up-facing surface except for the Shimoni reef. Recruit size studies showed truncated size-frequency distributions with the 2.1-4.0 mm size-class constituting the majority of recruits in all reefs (Figure 5).

Algal settlement and substrate studies

Bare surface comprised 28.9, 52.0, 48.26 and 53.85% of

Table 1. Analyses of variance testing the effect of reef, season and grain size (coarse and fine) on bottom sediments of Kenyan coral reef closures (ns = not significant, * =significant at $\alpha = 0.05$).

Source	SS	df	MS	F	p
Grain size					
Reef	1.97	3	0.66	0.35	ns
Season	11.97	1	11.97	654	*
Grain	270.59	1	270.4	147.42	*
Reef*Season	0.76	3	0.35	0.14	ns
Season*Grain	16.39	1	16.39	8.93	*
Grain*Reef	79.29	3	26.43	14.40	*
Reef*Season*Grain	44.99	3	14.99	8.17	*
Error	519.34	283	1.84		
Fine sediments					
Reef	30.91	3	10.30	7.29	*
Season	1.97	1	1.97	1.39	ns
Reef*Season	20.29	3	6.76	4.79	*
Error	161.15	114	1.41		

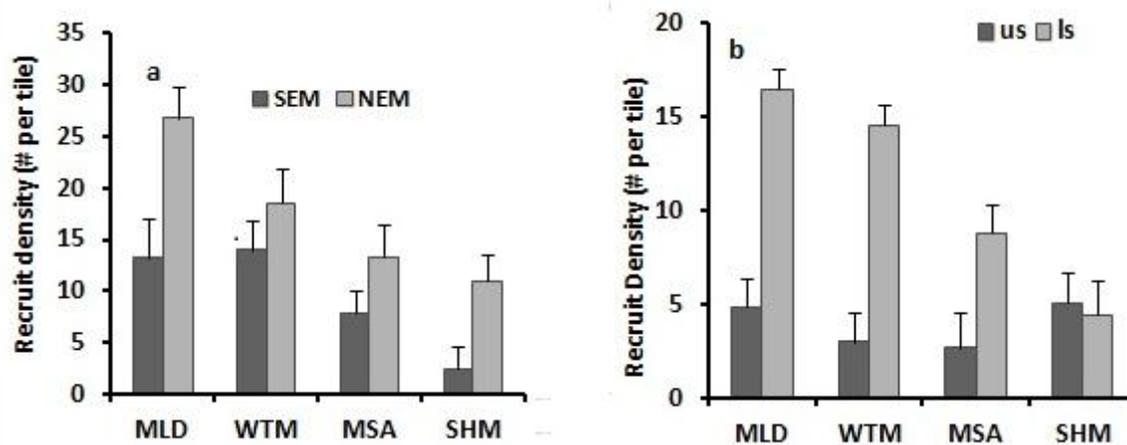


Figure 4. Density of coral recruits (# per tile, mean \pm SD) changes in study reefs, Malindi (MLD), Watamu (WTM), Mombasa (MSA) and Shimoni (SHM) (a) season and (b) surface orientation of tiles; us = upper surface, ls = lower surface. Sample size for each mean: $20 < n < 90$.

Table 2. Analyses of variance testing the effect of reef, season and tile surface on coral spat density on Kenyan protected coral reef lagoons (ns = not significant, * =significant at $\alpha = 0.05$).

Source	SS	df	MS	F	p
Reef	1892.33	3	630	4.18	*
Season	35.24	1	35.24	0.23	ns
Surface	3231.03	1	3231.03	21.39	*
Reef*Season	2082.15	3	694.05	4.59	*
Reef*Surface	1821.62	3	607.21	4.19	*
Season*Surface	1944.71	1	1944.71	12.87	*
Reef*Season*Surface	1047.81	3	349.27	2.31	ns
Error	51667.03	342	151.07		

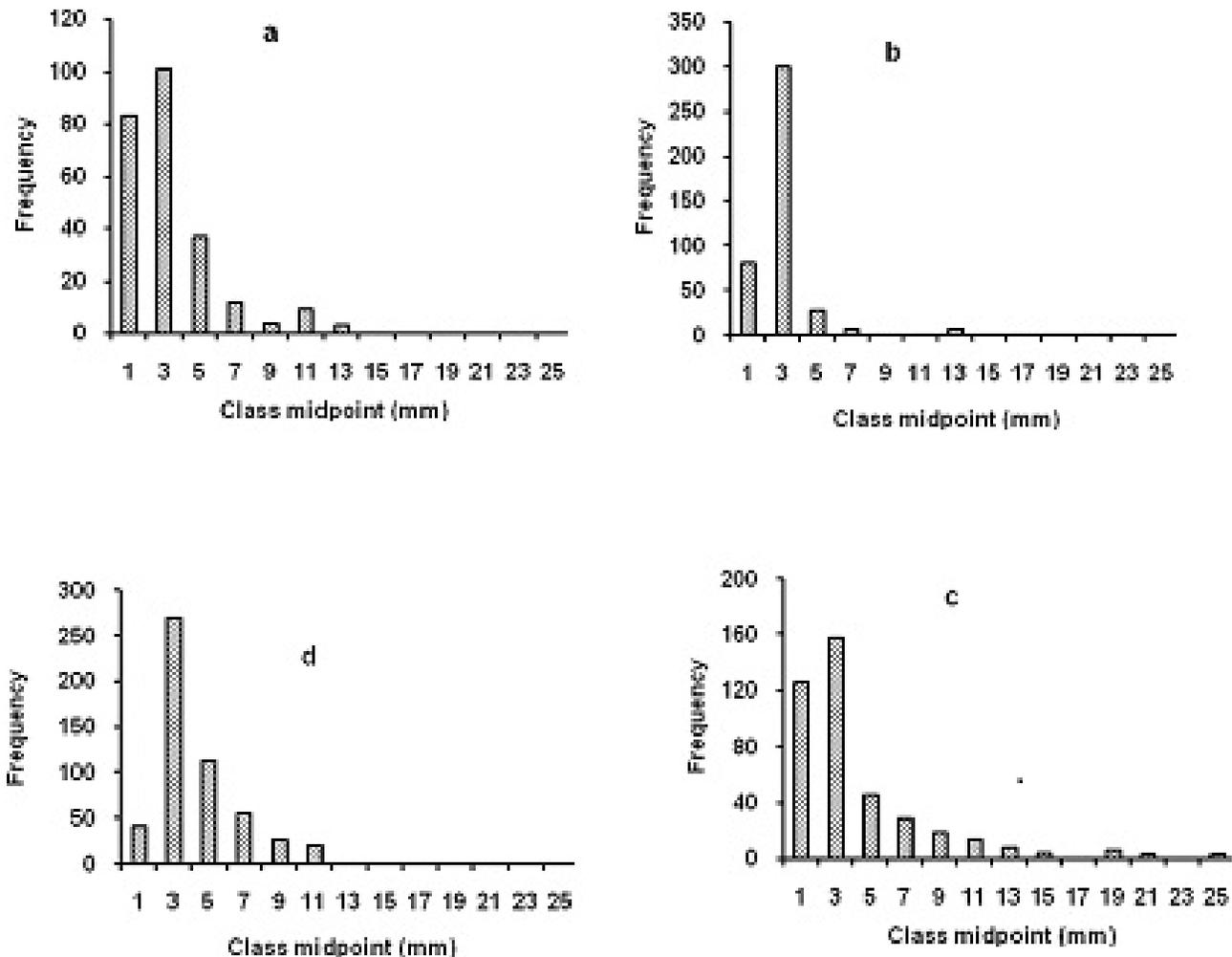


Figure 5. Size frequency distribution diagram for coral recruits from study reefs. Sample size for each reef: Malindi, $n=40$ tiles (856 recruits), Watamu $n=50$ tiles (750 recruits), Mombasa, $n=41$ tiles (472 recruits) and Shimoni, $n=58$ tiles (294 recruits).

Table 3. Analyses of variance test for the effect of reef and season on algal biomass from tiles deployed in Kenyan protected coral reef lagoons (ns = not significant, * = significant at $\alpha = 0.05$).

Source	SS	df	MS	F	p
Reef	238.28	3	79.43	8.26	*
Season	10.79	1	10.79	1.12	ns
Reef*Season	180.88	3	60.29	6.27	*
Error	1202.02	125	9.62		

tile surfaces in Malindi, Watamu, Mombasa and Shimoni, respectively. Mean algal biomass did not exceed 10 g cm^{-2} , did not differ between seasons. Algal biomass in all reefs was higher during the NEM compared to the SEM except in the sediment-exposed Malindi reef (Table 3 and Figure 6). Mean biomass for Malindi was significantly lower than Shimoni reef but not different from Mombasa and Watamu

reefs. In all sites, colonization was mostly by lower canopy algae. *Halimeda* and turf algae were found to be the dominant algal categories in Malindi. Coral cover in the Shimoni reef was significantly higher than the other reefs with the sediment-exposed Malindi reef showing higher cover than Watamu reef but lower than Mombasa (Table 4). No significant difference in turf algae cover was detected between Shimoni and Malindi reefs, however, higher turf algae cover was measured in Mombasa and Watamu compared to the other two reefs. Malindi reef had higher soft coral, calcareous and coralline algae cover whereas high sponge cover was measured in Mombasa compared to all other reefs. Rugosity did not differ between reefs.

The relative abundance of plate-like and corymbose growth forms was higher in Shimoni compared to the other reefs (Figure 7). Solitary and branching forms dominated Malindi reef relative to all other reefs. Massive forms constituted the largest proportion of corals in all sites,

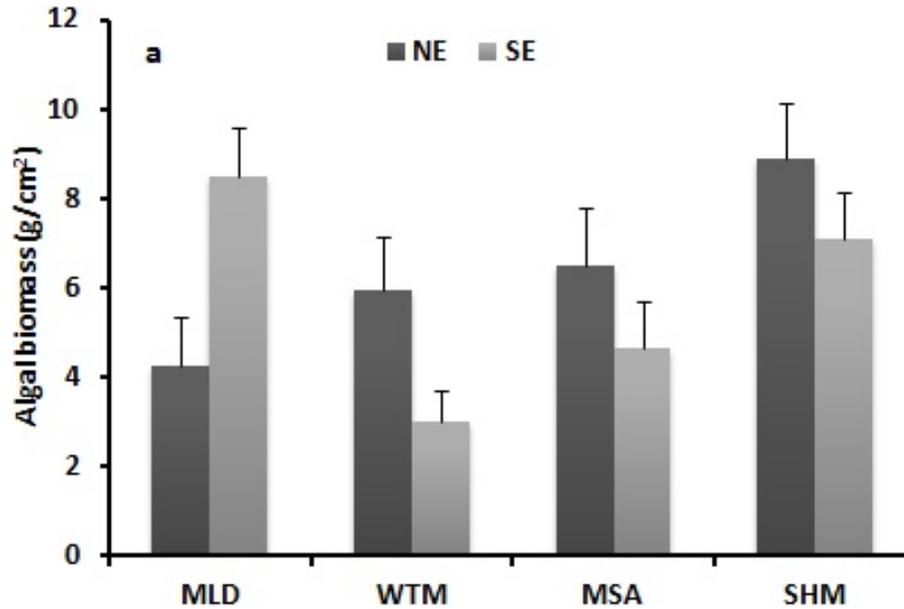


Figure 6. Seasonal algal biomass (g cm^{-2} dry wt) values (mean \pm SE) on settlement tiles from Malindi (MLD), Watamu (WTM), Mombasa (MSA) and Shimoni (SHM). Error bars indicate standard deviations. Sample size for each mean: $15 < n < 30$ tiles.

Table 4. Mean bottom cover (natural substrate) and standard deviations, rugosity and sphericity from four Kenyan protected reefs with their comparison tests (ns = not significant, * = significant at $\alpha = 0.05$, nt = not tested).

Substrate	Malindi	Watamu	Mombasa	Shimoni	p
Hard Coral	21.7 \pm 3.90	14.7 \pm 3.89	24.5 \pm 4.51	28.9 \pm 1.74	*
Algal turf	23.5 \pm 10.2	41.7 \pm 15.8	36.7 \pm 3.23	19.7 \pm 9.50	*
Calcareous algae	16.3 \pm 9.14	12.2 \pm 10.2	0.12 \pm 0.43	13.5 \pm 6.4	*
Macroalgae	2.39 \pm 6.21	4.25 \pm 6.67	9.23 \pm 6.03	7.93 \pm 7.35	*
Coralline algae	24.1 \pm 6.96	23.9 \pm 11.7	4.75 \pm .94	27.6 \pm 29.02	*
Seagrass	0.97 \pm 2.36	0.00 \pm 0.00	6.82 \pm 5.77	1.22 \pm 2.87	*
Soft coral	4.64 \pm 3.94	0.54 \pm 0.96	1.09 \pm 0.71	2.56 \pm 2.65	*
Sand	6.09 \pm 7.00	2.03 \pm 2.83	12.6 \pm 4.61	4.68 \pm 10.51	*
Sponge	0.00 \pm 0.00	0.59 \pm 0.89	1.55 \pm 0.60	0.31 \pm 0.93	*
Rugosity	1.30 \pm 0.10	1.24 \pm 0.05	1.26 \pm 0.15	1.33 \pm 0.07	ns

contributing > 60% of coral cover at Watamu, Mombasa and Shimoni, and slightly over 40% at Malindi (Table 5). The abundance of digitate forms did not differ between reefs. Malindi reef had higher cover of *Acropora*, *Galaxea*, *Platygyra*, and branching and massive *Porites* compared to all other reefs (Figure 8). Watamu reef was dominated by *Montipora* whereas *Favia* and massive *Porites* were dominant in Mombasa reef. Branching *Porites* and *Acropora* were the dominant genera in the Shimoni reef. Size structure data revealed that Malindi reef had larger colonies of *Echinopora*, *Galaxea*, *Goniastrea*, *Favites*, *Millepora* and *Pocillopora* compared to the other reefs (Figure 9). Although not statistically tested, Shimoni reef

exhibited higher species diversity and richness indices compared to the sediment-exposed Malindi reef, but both were lower than values measured in the Watamu reef. All reefs exhibited similar evenness.

DISCUSSION

Recruitment and settlement are vital processes in the development of coral populations and are essential in community recovery after disturbance. In post-disturbance periods, the settlement of coral larvae is a key ecological process in the resilience and persistence of coral reefs

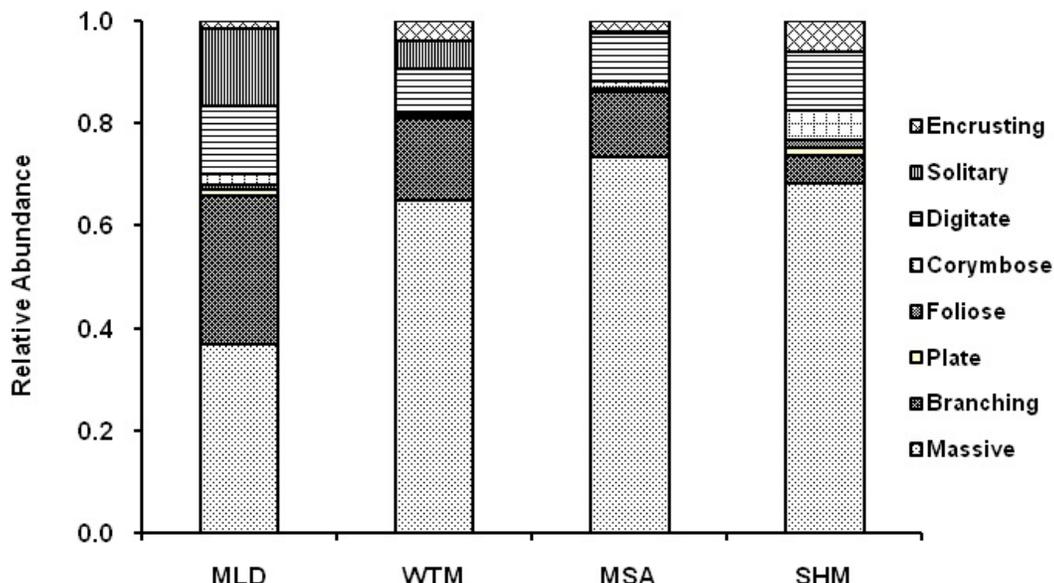


Figure 7. Relative abundance of coral growth forms from the four Kenya study reef, Malindi (MLD), Watamu (WTM), Mombasa (MSA) and Shimoni (SHM). Data are percentages of a minimum of 53 and maximum of 1363 colonies per reef.

Table 5. Average lengths (in cm) of live coral cover (\pm SE) found beneath line transect for major genera in Malindi, Shimoni and Watamu and statistical comparisons (ns = not significant * = significant at $\alpha = 0.05$; nt = not tested, transect = 1000 cm)

Genera	Malindi	Watamu	Shimoni	F	p
Acropora	30.4 \pm 3.80	17.7 \pm 2.70	27.9 \pm 2.9	3.16	*
Echinopora	1.64 \pm 0.80	2.90 \pm 1.80	8.18 \pm 3.03	2.45	ns
Favites	0.27 \pm 0.20	1.22 \pm 0.72	1.11 \pm 0.75	0.60	ns
Galaxea	14.6 \pm 2.46	2.31 \pm 0.68	9.22 \pm 2.39	5.86	*
Goniastrea	0.59 \pm 0.33	0	1.14 \pm 0.79	0.77	ns
Goniopora	0	0.34 \pm 0.25	0.98 \pm 0.97	0.56	ns
Hydnophora	0	4.43 \pm 2.68	0.81 \pm 0.72	3.21	*
Millepora	0.40 \pm 0.32	2.00 \pm 0.71	1.88 \pm 1.01	1.22	ns
Montipora	11.2 \pm 3.00	51.9 \pm 11.5	0.60 \pm 0.60	27.4	*
Pavona	0	0.22 \pm 0.23	0.10 \pm 0.11	0.77	ns
Platygyra	5.32 \pm 1.50	4.32 \pm 1.60	0.00	7.04	*
Pocillopora	2.36 \pm 0.79	3.91 \pm 0.83	1.72 \pm 1.19	1.13	ns
Porites (branching)	4.78 \pm 1.94	2.90 \pm 0.91	2.96 \pm 1.09	0.53	ns
Porites (massive)	8.59 \pm 3.00	18.7 \pm 4.38	1.87 \pm 1.15	8.89	*
Diversity indices					
Richness	3.42	5.37	4.27		nt
Evenness	0.903	0.910	0.918		nt
Diversity	2.17	2.63	2.42		nt

(Arnold et al., 2010; Venera-Ponton et al., 2011; Doropoulos et al., 2012). Likewise, optimal habitat characteristics are critical in the post-settlement survival

of benthic larvae (Kendrick, 1991; Airoldi and Virgilio, 1998; Harrington et al., 2004), and benthic algae and sediments offer both inductive and inhibitive settlement

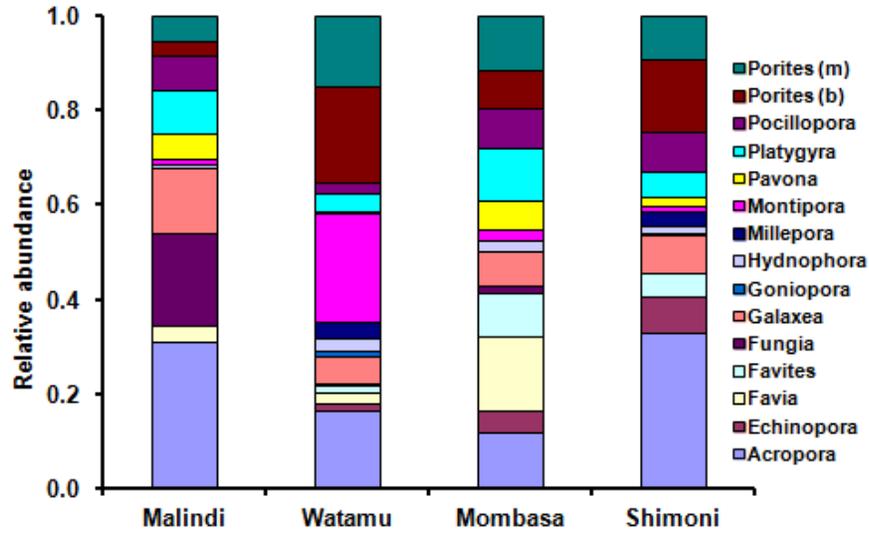


Figure 8. Relative abundance of some common coral genera from the four Kenyan study reefs. Data are percentages of a minimum of 9 and a maximum of 12 line transects per reef.

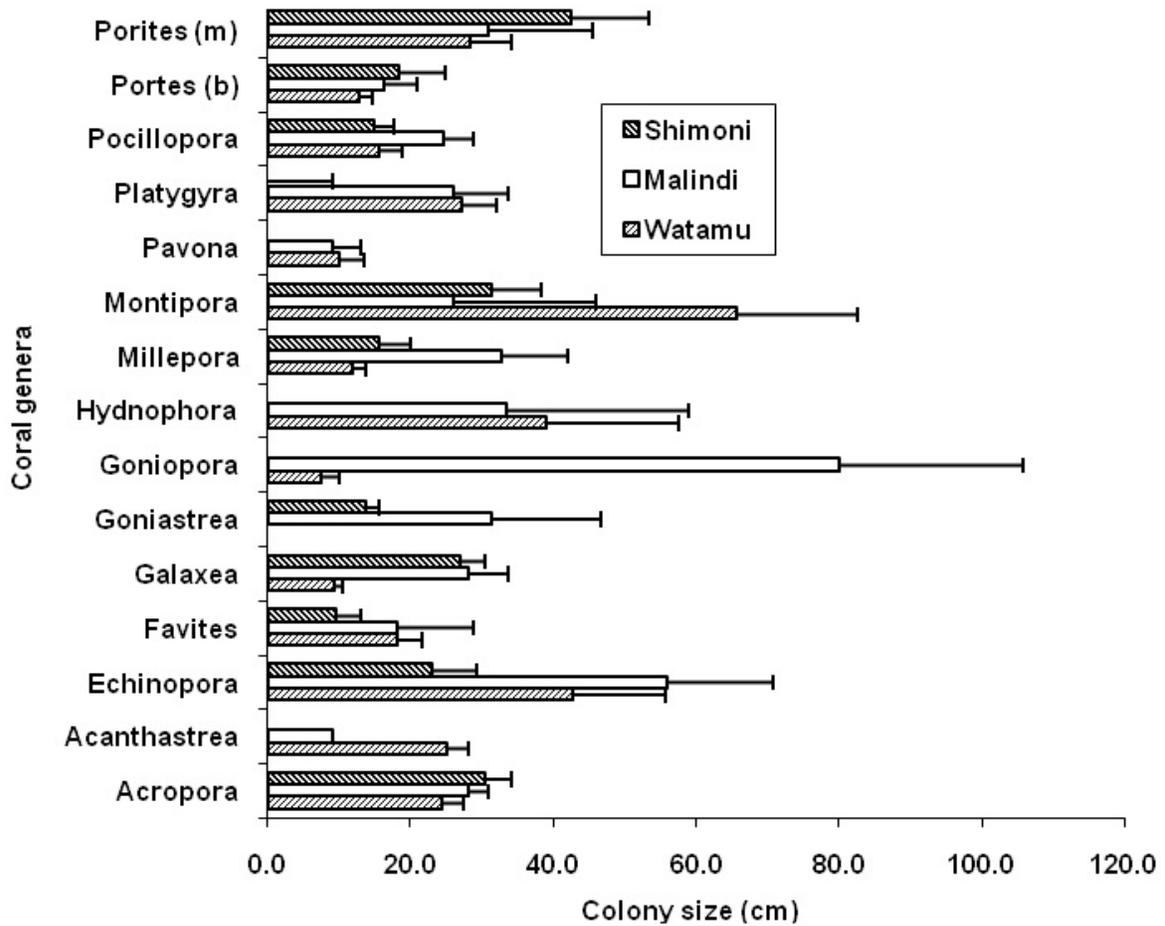


Figure 9. Average colony sizes (mean \pm SD) of common coral genera from three Kenyan protected reefs. Data are means from 9 > n < 12 lines transects per reef.

cues for planktonic larvae (Kuffner et al., 2006; Thomsen and McGlathery, 2006; Diaz-Pulido et al., 2010). Past studies have indicated that coral larvae often search for appropriate substrate that is devoid of fleshy algae, silt and shifting sediments for successful settlement (Thomsen and McGlathery, 2006; Doropoulos et al., 2012). Competition for space in reef communities means that organisms that colonize new and open substrates and factors that facilitate or inhibit coral settlement play critical roles in influencing the structure and resilience of reef communities (Casey et al., 2015).

Environmental parameters

This study reveals high sedimentation rates on Malindi reef during the SEM period despite the northerly direction of winds and local currents away from the Sabaki River (Brakel, 1984; Katwijk et al., 1993; Obura, 1995; McClanahan and Obura, 1997). The reason for the higher sedimentation rates during the SEM is due to resuspension of sediments by increased hydrodynamic energy (Brakel, 1984; Kayanne et al., 2006; Fleitmann et al., 2007), and this is pronounced in Malindi where large amounts of sediments from the River Sabaki are deposited during the NEM and are available for re-suspension over the SEM season. The calmer conditions in Malindi during NEM resulted in transportation and accumulation of fine sediments and sediments of higher silt fraction through suspended and saltation that may later be re-suspended during the rougher SEM sea conditions. The importance of sediment quality in coral ecology has previously been discussed (Rodgers, 1990; Fabricius, 2005). High hydrodynamic energy and runoff are prevalent during the SEM in East African coastal areas (McClanahan, 1988; Kitheka et al., 2003). Despite the southward plume and river discharge movement during the NEM, salinity and SST values from Malindi were not different from those measured from the other study reefs. This is likely due to complete mixing of marine and fresh waters and/or low discharge volume unable to cause any significant changes in salinity and SST (Kitheka et al., 2003).

Spatial and temporal distribution of nutrient loads associated with high levels of human activities in both freshwater and coastal watersheds are controlled by seasonal hydrodynamic changes (Christiansen et al., 1996; Madsen et al., 2001). Elevated nutrient levels observed during the SEM relative to the NEM season and in Malindi compared to the other reefs were probably due to several reasons. Firstly, the proximity of Malindi to the Sabaki River compared to the other reefs and the high discharge volume ($\sim 400\text{-}650\text{ m}^3\text{s}^{-1}$) during the SEM likely increase nutrient loads relative to the NEM period (low discharge volume, $60\text{-}80\text{ m}^3\text{s}^{-1}$; McClanahan, 1988; Kitheka et al., 2003). Secondly, phosphates are continuously trapped by bottom sediments (Ohowa, 1996; Xie et al., 2003), and are eventually released into

the water column through disturbances in the sea bottom during high hydrodynamic events, conditions that are prevalent during the SEM period. The high levels of chlorophyll a concentration observed during the SEM result from heavy rains, high river discharge and runoff (relative to the NEM), and affirm the effects of River Sabaki and the Mida mangrove creek in Malindi and Watamu, respectively. Further, reported upwelling conditions off the southern Somali and northern Kenya coast during the SEM season (McClanahan, 1988) may also be a contributing factor to the observed (elevated nutrient levels) findings in the current study.

Coral recruitment patterns

Coral recruit density varied with reef, seasons and surface orientation in accordance with findings from other studies (Obura, 1995; McClanahan and Obura, 1997; Glassom et al., 2004; Obura et al., 2005; Karisa et al., 2008). Consistent with other studies, coral larvae showed high affinity for underside surfaces, which is considered a strategy to escape from algae competition (Kuffner et al., 2006; Arnold et al., 2010; Venera-Ponton et al., 2011), sedimentation and light stress on upper surfaces (Thomason et al., 2002; Birrell et al., 2005). We could not ascertain reasons for the no effect of surface orientation on recruit numbers in Shimoni, however un-interfered light penetration may be a likely candidate. High coral recruit densities found in the sediment-exposed Malindi reef may be attributed to several factors. The presence of swift-currents, moderate (wave action) tidal amplitude ($\sim 4\text{ m}$ in East Africa) and a deep-water channel likely enhanced flushing rates, thereby preventing the accumulation of sediment to chronic levels and thus increasing available space for coral settlement. However, increased hydrodynamics have been shown to sweep away larvae from substrates before attachment (Reidenbach et al., 2009) but this probably varies with organisms or substrate types, thus explaining the findings in the present study. Control of macroalgae by herbivorous fish populations may also be an important contributing factor in promoting increased coral settlement through increased substrate availability (Edmunds and Carpenter, 2001; Casey et al., 2015). In addition, the observed high coral recruit densities observed during the NEM period coincide with the period of warmest sea temperatures and the timing of gamete release by a number of coral species in the Western Indian Ocean region (Mangubhai et al., 2007). Therefore, the interplay and interaction of oceanographic and biological factors may play a significant role in the maintenance of coral populations in disturbed reefs such as the Malindi reef.

Recruit densities measured in the current study are similar to those measured in Sodwana Bay, South Africa (Glassom et al., 2006) but different from density patterns

measured along the Australian coast (Harriot and Banks, 1995) though recruitment is generally known to decline with increasing latitude. This is attributed the relative position of Kenya and South Africa towards the extreme ends of two opposite flowing currents, the northerly flowing East African Coastal Current and the south flowing Mozambique Current that split from the South Equatorial Current near the Tanzania-Mozambique border (Mangubhai et al, 2007). This dispersal pattern differs from that observed along the eastern and western coasts of Australia (Harriott and Banks, 1995) that are both bathed by southerly flowing currents, the East Australian Current and Leeuwin Current, respectively (Harrison and Booth 2007).

Algal settlement and diversity studies

The high coral recruit density measured in the Malindi reef relative to the other reefs differed from the results of earlier studies on the settlement of sessile organisms where sediments were shown to negatively impact coral settlement (Kendrick, 1991; Bobcock and Smith, 2000; Fabricius and De'ath, 2001; Birrell et al., 2005; Thomsen and McGlathery, 2006). However, the interaction of high sedimentation and hydrodynamics, high herbivory and reduced algal biomass may have played a significant role in our findings. Previous studies have shown that benthic algae compete with corals through a variety of mechanisms, including the promotion of bacterial growth that cause high juvenile coral mortality (McCook et al., 2001, Nugues et al., 2004; Diaz-Pulido et al., 2010; Venera-Ponton et al., 2011; O'Leary et al., 2012). In addition, Connell and Karlson (2000) reported that sediments negatively affect algal abundance and biomass through reduction in growth and reproductive success, potentially causing enhanced coral settlement in sediment-exposed reefs. These findings suggest that although algae may have a substantial impact on coral recruitment, sedimentation may indirectly modify coral recruitment by influencing algal abundance and biomass. Consequently, high coral recruitment rates were found on Malindi reef despite the suspected detrimental effects of Sabaki river sediments flowing into the Malindi reef system, possibly due to the presence of an optimal breeding population of sediment tolerant coral species, in addition to the aforementioned factors.

Benthic and coral community composition

Larger coral colonies were found in the sediment-exposed reefs relative to other reefs, which is consistent with previous findings (Obura, 1995; McClanahan and Obura, 1997; Nugues and Roberts, 2003b; McClanahan, 2014). Further, in a separate study conducted in the same reefs, dominant coral genera in sediment exposed

reefs showed larger corallite diameters compared to non-sediment impacted reefs (Mwachireya et al., 2015), suggesting this to be a strategy to survive exposure to high sediment levels. Similar findings of larger diameters in sediment influenced reefs have previously been reported by other workers (Todd, 2001; Todd et al., 2008). Increased corallite size has been associated with enhanced sediment rejection capability (Todd et al., 2008) and large colony sizes have been linked to reduced susceptibility of corals to high sediment levels as well as increasing reproductive success relative to smaller colonies (McClanahan and Obura, 1997). Sediments have also been reported to cause partial mortality and reduced coral size (Nugues and Roberts, 2003b) and this may cause reduced coral recruitment and increased frequency of small-sized colonies in sediment intolerant species (McClanahan and Obura, 1997; Hughes and Tanner, 2000; Nugues and Roberts, 2003b). The effects of high sediment levels in Malindi corals is further reinforced by the presence of high relative abundance of sediment-tolerant branching, digitate and solitary but low relative abundance of sediment-intolerant (encrusting, corymbose and plate-like) growth forms.

It can therefore be concluded that coral community characteristics observed in the sediment-exposed reef in this study are a reflection of (1) high recruitment rates and low macroalgal cover, (2) sediment rejection characteristics such as colony and corallite morphology (3) hydrodynamic influences on growth forms, sediment and larval dispersal, and (4) the effects of grazing activities of herbivorous fish on algae freeing space for coral settlement. Consistent with Rodgers (1990), we found that reef communities in the sediment exposed reef exhibited low species diversity, reduced coral cover, high abundance of sediment tolerant species, generally smaller or larger colonies depending on sediment tolerance and greater abundance of branching corals. The dominance of sediment-tolerant corals as well as high levels of coral recruitment may contribute to the thriving coral community in Malindi reef despite exposure to high levels of sediments from the Sabaki River. This has important ecological and geological implications by potentially influencing rates and patterns of calcium carbonate accretion in sediment disturbed coral reefs (Perry and Larcombe, 2003).

Biological and physicochemical parameters

Sedimentation rates were positively correlated with recruit density similar to current velocity but were negatively correlated with fleshy algal cover. Sediment organic content was negatively related to recruit density but not algal biomass. Interestingly, all nutrient types and chlorophyll a concentrations were positively correlated with recruit density but negatively correlated with algal biomass and

cover, contrary to general perceived views (Belleveau and Paul, 2002; Fabricius, 2005; Venera-Ponton et al., 2011). Previous studies on the relationship between algae and nutrient concentrations have also provided conflicting results (Diaz-Pulido and Garzón-Ferreira, 2002; Diaz-Pulido and McCook, 2003; Fabricius, 2005), which may be due to the many interacting biological and physico-chemical factors known to modify the algae-nutrient interaction. The negative association between algae and sedimentation rate is similar to findings of Gorgula and Connell (2004) but different from those of Irving and Connell (2002) and Nugues and Roberts (2003b). Sediment quality, site hydrodynamics and microhabitat differences and their interactions may be the likely factors responsible for the observed differences between studies (Arnold et al., 2010; Nakamura et al., 2011). Further, our results suggest that the organic fraction of sediment has a greater negative influence on recruit density compared to the actual sedimentation rate values.

The positive relationship between sediments and coral recruitment is likely due to (a) increased sediment accumulation reducing the recruitment, attachment and survival of new algal recruits onto substrates (Umar et al., 1998; Birrell et al., 2005), (b) elevated sediment concentrations smothering short fronds and also preventing the vegetative regeneration of fleshy algae (Umar et al., 1998), (c) positive sediment effects on calcareous and coralline algae facilitating the recruitment and settlement of coral recruits (Kendrick, 1991; Airoidi and Virgilio, 1998; Harrington et al., 2004) and (d) protective management increasing the abundance of herbivorous fish that free substrate space through their grazing activities on algae (Venera-Ponton et al., 2011). The present results therefore suggest that high coral recruitment levels can occur in reefs with moderate sedimentation rates and that the effects of sedimentation on algae in coral reefs are much more complex than previously considered. It would seem that algae are merely opportunistic beneficiaries of sediment-associated factors rather than being favoured by high sediment loads. Therefore, attention should also be directed toward the effects of other water quality characteristics such as nutrients, toxins (pesticides, heavy metals) and organic material on a wide range of life history parameters in reef organisms (Rodgers, 1990; Richmond et al., 2007) that can tip the balance toward algal proliferation and reduced coral recruitment, which may lead to the decline of coral reefs.

This study provides evidence that increased sediment influx from Sabaki River has a significant impact on Malindi coral communities based on the dominance of sediment-adapted coral morphologies and reduced coral cover despite high or comparable recruitment rates relative to reefs unaffected by sedimentation. The existence of river discharge around the Malindi area since the formation of the Rift Valley (~39 million years ago) and the presence of coral reefs at sufficient distance from the Sabaki estuary suggests that the combination of

biological and oceanographic characteristics of sediment-exposed reefs probably help to modify the potential impacts of sediments to below critical levels necessary to cause severe coral reef decline. Moderate sedimentation rates and high current speeds may enhance coral recruitment by inhibiting substrate colonization and overgrowth by competing algae and this has important implication for the recovery of coral reefs in areas affected by terrestrial sediment influx.

Conflict of interests

The authors did not declare any conflict of interest.

ACKNOWLEDGEMENTS

This research was supported by grants from the British Ecological Society (BES), the World Wildlife Fund (WWF) and the International Development Research Centre (IDRC) Doctoral Research Award and the Simon Fraser University (SFU) President's Award to the first author. Logistic support was provided by KWS rangers and laboratory and field assistance from the staff of Kenya Marine and Fisheries Research Institute (KMFRI). Excellent fieldwork assistance was provided by Masudi J. Zamu and Anthony M. Nzioka. We also greatly appreciate the reviewers' comments that helped in improving this manuscript.

REFERENCES

- Airoidi L, Virgilio M (1998). Responses of turf-forming algae to spatial variations in deposition of sediments. *Mar. Ecol. Prog. Ser.* 165:271-282. <http://dx.doi.org/10.3354/meps165271>
- Arnold SN, Steneck RS, Mumby PJ (2010). Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Mar. Ecol. Prog. Ser.* 414:91-105. <http://dx.doi.org/10.3354/meps08724>
- Baker AC, McClanahan TR, Starger CJ, Boonstra RK (2013). Long-term monitoring of algal symbiont communities in corals reveals stability is taxon dependent and driven by site-specific thermal regime. *Mar. Ecol. Prog. Ser.* 479:85-97. <http://dx.doi.org/10.3354/meps10102>
- Belleveau SA, Paul VJ (2002). Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. *Mar. Ecol. Prog. Ser.* 232:105-111. <http://dx.doi.org/10.3354/meps232105>
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004). Confronting the coral reef crisis. *Nature* 429:827-833.
- Birrell CL, McCook LJ, Willis BL, Diaz-Pulido GA (2008). Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanogr. Mar. Biol.: Ann. Rev.* 46:25-63. <http://dx.doi.org/10.1201/9781420065756.ch2>
- Birrell, CL, McCook LJ, Willis BL (2005). Effects of algal turfs and sediment on coral settlement. *Mar. Pollut. Bull.* 51:408-414. <http://dx.doi.org/10.1016/j.marpolbul.2004.10.022>
- Bobcock RC, Smith L (2002). Effects of sedimentation on coral settlement and survivorship. *Proc. 9th Int. Coral Reef Symp.* 1:245-248.
- 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](http://dx.doi.org/10.1016/0034-4257(84)90060-9)
- Bruno JF, Petes L, Drew E, Harvell C, Hettinger A (2003). Nutrient

- enrichment can increase the severity of coral diseases. *Ecol. Lett.* 6(12):1056-1061. <http://dx.doi.org/10.1046/j.1461-0248.2003.00544.x>
- Burke L, Maidens J (2004). *Reefs at Risk*, World Resource Institute, Washington DC, 81 p.
- Carreiro-Silva M, Kiene WE, Golubic S, McClanahan TR (2012). Phosphorus and nitrogen effects on microbial euendolithic communities and their bioerosion rates. *Mar. Pollut. Bull.* 64:602-613. <http://dx.doi.org/10.1016/j.marpolbul.2011.12.013>
- Casey JM, Choat JH, Connolly SR (2015). Coupled dynamics of territorial damselfishes and juvenile corals on the reef crest. *Coral Reefs* 34(1):1-11. <http://dx.doi.org/10.1007/s00338-014-1221-7>
- Christiansen C, Gertz FM, Laima JC, Lund-Hansen LC, Vang T, Jørgensen C (1996). Nutrient (P, N) dynamics in the southwestern Kattegat, Scandinavia: sedimentation and resuspension effects. *Environ. Geol.* 29:66-77. <http://dx.doi.org/10.1007/s002540050105>
- Cornell HV, Karlson RH (2000). Coral species richness; ecological versus biogeographical influences. *Coral Reefs* 19:37-49. <http://dx.doi.org/10.1007/s003380050224>
- Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Cote IM (2012). Evaluating life history strategies of reef corals from species traits. *Ecol. Lett.* 15:1378-1386. <http://dx.doi.org/10.1111/j.1461-0248.2012.01861.x>
- Darling ES, McClanahan TR, Corte IM (2013). Life histories predict coral community disassembly under multiple stressors. *Glob. Chang. Biol.* 19:1930-1940. <http://dx.doi.org/10.1111/gcb.12191>
- De'ath, Fabricius KE, Sweatman H, Puotinen M (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc. Nat. Acad. Sci. USA*, 109:17995-17999. <http://dx.doi.org/10.1073/pnas.1208909109>
- Devlin MJ, Fabricius KE (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Mar. Pollut. Bull.* 50:125-14. <http://dx.doi.org/10.1016/j.marpolbul.2004.11.028>
- Diaz-Pulido G, Garzón-Ferreira J (2002). Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. *Bot. Marina* 45:284-292.
- Diaz-Pulido G, Gouezo M, Tilbrook B, Dove S, Anthony KRN (2011). High CO₂ enhances the competitive strength of seaweeds over corals. *Ecol. Lett.* 14:156-162. <http://dx.doi.org/10.1111/j.1461-0248.2010.01565.x>
- Diaz-Pulido G, Harii S, McCook LJ, Hoegh-Guldberg O (2010). The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs*, 29(1):203-208. <http://dx.doi.org/10.1007/s00338-009-0573-x>
- Diaz-Pulido G, McCook LJ (2003). Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology* 84:2026-2033. <http://dx.doi.org/10.1890/01-3127>
- Doropoulos C, Ward S, Diaz-Pulido D, Hoegh-Guldberg O, Mumby P J (2012). Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecol. Lett.* 15: 338-346. <http://dx.doi.org/10.1111/j.1461-0248.2012.01743.x>
- Dunn JG, Sammarco PW, LaFleur Jr G (2012). Effects of phosphate on growth and skeletal density in the scleractinian coral *Acropora muricata*: A controlled experimental approach. *J. Exp. Mar. Biol. Eco.* 41: 34-44. <http://dx.doi.org/10.1016/j.jembe.2011.10.013>
- Edmunds PJ, Carpenter RC (2001). Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proc. Nat. Acad. Sci.* 98(9): 5067-5071. <http://dx.doi.org/10.1073/pnas.071524598>
- 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>
- Fabricius KE, De'ath G (2001). Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19: 303-309. <http://dx.doi.org/10.1007/s003380000120>
- Fabricius KE, McCorry D (2006). Changes in octocoral communities and benthic cover along a water quality gradient in the reefs of Hong Kong. *Mar. Pollut. Bull.* 52:22-33. <http://dx.doi.org/10.1016/j.marpolbul.2005.08.004>
- Fleitmann D, Dunbar RB, McCulloch M, Mudelsee M, Vuille M, McClanahan TR, Cole JE, Eggins E (2007) East Africa soil erosion recorded in a 300 year old coral colony from Kenya. *Geophys. Res. Lett.* 34:L04401, doi:10.1029/2006GLO028525.
- Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013). Recovery of an isolated coral reef system following severe disturbance. *Science* 340:69-71. <http://dx.doi.org/10.1126/science.1232310>
- Glassom D, Celliers M, Schleyer MH (2006) Coral recruitment patterns at Sodwana Bay, South Africa. *Coral Reefs* 25:485-492. <http://dx.doi.org/10.1007/s00338-006-0117-6>
- Glassom D, Zakai D, Chadwick-Furman NE (2004). Coral recruitment: Spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar. Biol.* 144:641-651. <http://dx.doi.org/10.1007/s00227-003-1243-0>
- Godinot C, Tribollet A, Grove R, Ferrier-Pagès C (2012) Bioerosion by euendolith decreases in phosphate-enriched skeletons of living corals. *Biogeosci. Disc.* 9:2424-2444
- Goreau T, McClanahan TR, Hayes R, Strong A (2000). Conservation of coral reefs after the 1998 global bleaching event. *Conserv. Biol.* 14: 5-15. <http://dx.doi.org/10.1046/j.1523-1739.2000.00011.x>
- Gorgula SK, Connell SD (2004). Expansive covers of turf-forming algae on human-dominated coasts: the relative effects of increasing nutrients and sediment loads. *Mar. Biol.* 145:613-619. <http://dx.doi.org/10.1007/s00227-004-1335-5>
- Harrington L, Fabricius FH, De'ath G, Negri A (2004). Recognition and selection of settlement substrata determines post-settlement survival in corals. *Ecology* 85:3428-3437. <http://dx.doi.org/10.1890/04-0298>
- Harii S, Kayanne H, Takigawa H, Hayashibara T, Yamamoto M (2002). Larval survivorship, competency periods and settlement of two brooding corals, *Heliopora coerulea* and *Pocillopora damicornis*. *Mar. Biol.* 141:39-46. <http://dx.doi.org/10.1007/s00227-002-0812-y>
- Harriot VJ, Banks SA (1995). Recruitment of scleractinian corals in Solitary Islands Marine Reserve, a high latitude coral-dominated community in Eastern Australia. *Mar. Ecol. Prog. Ser.* 123: 155-161. <http://dx.doi.org/10.3354/meps123155>
- Harrison PL, Booth DJ (2007). Coral reefs: naturally dynamic and increasingly disturbed ecosystems. *Mar. Ecol. Chapter 13: 316-377.*
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards A J, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioi ME (2007). Coral Reefs under rapid climatic change and ocean acidification. *Science* 318: 1737-1742. <http://dx.doi.org/10.1126/science.1152509>
- Hughes TP, Graham NA, Jackson JB, Mumby PJ, Steneck RS (2010). Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25(11):633-642. <http://dx.doi.org/10.1016/j.tree.2010.07.011>
- Hughes TP, Tanner JE (2000). Recruitment failure, life histories and long term decline of Caribbean coral reefs. *Ecology* 81: 2250-2263. [http://dx.doi.org/10.1890/0012-9658\(2000\)081\[2250:RFLHAL\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)081[2250:RFLHAL]2.0.CO;2)
- Irving AD, Connell SD (2002) Interactive effects of sediment and microtopography on the abundance of sub-tidal turf-forming algae. *Phycologia* 41:517-522. <http://dx.doi.org/10.2216/10031-8884-41-5-517.1>
- Karisa JF, Kaunda-Arara B, Obura DO (2008). Spatial and temporal variation in coral recruitment and mortality in coastal Kenya. In Obura DO, Tamelander J, Lindahl O (eds.) *Coastal Ocean Research and Development in the Indian Ocean (CORDIO)*.
- 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>
- Kayanne H, Iijima H, Nakamura N, McClanahan TR, Behera S, Yamagata Y (2006). Indian Ocean Dipole index recorded in Kenyan coral annual density bands. *Geophys. Res. Lett.* 33. <http://dx.doi.org/10.1029/2006gl027168>
- Kendrick GA (1991). Recruitment of coralline crusts and filamentous turf algae in Galapagos archipelago: effects of sediment scour, erosion and accretion. *J. Exp. Mar. Biol. Ecol.* 147: 47-63. [http://dx.doi.org/10.1016/0022-0981\(91\)90036-v](http://dx.doi.org/10.1016/0022-0981(91)90036-v)
- Kitheka JU, Nthenge P, Obiero M (2003). Sabaki estuary sediment transport dynamics and resultant sediment fluxes in the monsoon-

- driven Malindi Bay, Kenya. LOICZ-START AFRICAT Project Report-II-Sabaki p 1-57.
- Kuffner IB, Walters LJ, Becerro MA., Paul VJ, Ritson-Williams R, Beach KS (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Mar. Ecol. Prog. Ser.* 323:107-117. <http://dx.doi.org/10.3354/meps323107>
- Kuta K, Richardson L (2002). Ecological aspects of black band disease of corals: relationships between disease incidence and environmental factors. *Coral Reefs* 21(4):393-398.
- Lirman D, Fong P (2007). Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Mar. Pollut. Bull.* 54:779-791. <http://dx.doi.org/10.1016/j.marpolbul.2006.12.014>
- Logan CA, Dunne JP, Eakin CM, Donner SD (2014). Incorporating adaptive responses into future projections of coral bleaching. *Glob. Chang. Biol.* 20:125-139. <http://dx.doi.org/10.1111/gcb.12390>
- 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: e23064. <http://dx.doi.org/10.1371/journal.pone.0023064>
- Mangubhai S, Harrison PL, Obura DO (2007). Patterns of larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. *Mar. Ecol. Prog. Ser.* 348:149-159. <http://dx.doi.org/10.3354/meps07090>
- Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF (2001). The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444:71-84. <http://dx.doi.org/10.1023/A:1017520800568>
- McClanahan TR (2014). Decadal coral community reassembly on an African fringing reef. *Coral Reefs* 33:939-950. <http://dx.doi.org/10.1007/s00338-014-1178-6>
- 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](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>
- McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E., Mumby PJ, Paddock M, Selig ER, van Woeseik R. (2012). Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* 7: e42884. <http://dx.doi.org/10.1371/journal.pone.0042884>
- McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005). Detriments to post-bleaching recovery of corals. *Coral Reefs* 24: 230-246. <http://dx.doi.org/10.1007/s00338-004-0471-1>
- McClanahan TR, Maina JM, Muthiga NA (2011). Associations between climate stress and coral reef diversity in the Western Indian Ocean. *Glob. Chang. Biol.* 17: 2023-2032. <http://dx.doi.org/10.1111/j.1365-2486.2011.02395.x>
- McClanahan TR, Nugues M, Mwachireya S (1994). Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *J. Exp. Mar. Biol. Ecol.* 184:237-254. [http://dx.doi.org/10.1016/0022-0981\(94\)90007-8](http://dx.doi.org/10.1016/0022-0981(94)90007-8)
- McClanahan TR, Shafir SH (1990). Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* 83:362-370. <http://dx.doi.org/10.1007/BF00317561>
- McCook LJ, Jompa J, Diaz-Pulido G (2001). Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19: 400-417. <http://dx.doi.org/10.1007/s003380000129>
- Miller MW, Weil E, Szmant AM (2000). Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. *Coral Reefs* 19: 115-123. <http://dx.doi.org/10.1007/s003380000079>
- Nakamura M, Ohki S, Suzuki A, Sakai K (2011). Coral larvae under ocean acidification: survival, metabolism, and metamorphosis. *PLoS ONE*, 6:e14521. <http://dx.doi.org/10.1371/journal.pone.0014521>
- Novak V, Santodomingo N, Rösler A, Di Martino E, Braga JC, Taylor PD, Johnson KG, Renema W (2013). Environmental reconstruction of a late Burdigalian (Miocene) patch reef in deltaic deposits (East Kalimantan, Indonesia). *Palaeogeogr. Palaeoclimat. Palaeoecol.* 374:110-122. <http://dx.doi.org/10.1016/j.palaeo.2013.01.009>
- Nozawa Y, Harrison PL (2008). Temporal patterns of larval settlement and survivorship of two broadcast-spawning acroporid corals. *Mar. Biol.* 155: 347-351. <http://dx.doi.org/10.1007/s00227-008-1034-8>
- Nugues MM, Roberts CM (2003a). Partial mortality in massive reef corals as an indicator of sediment stress on coral reefs. *Mar. Poll. Bull.* 46:314-323. [http://dx.doi.org/10.1016/S0025-326X\(02\)00402-2](http://dx.doi.org/10.1016/S0025-326X(02)00402-2)
- Nugues MM, Roberts CM (2003b). Coral mortality and interaction with algae in relation to sedimentation. *Coral reefs* 22(4): 507-516. <http://dx.doi.org/10.1007/s00338-003-0338-x>
- Nugues MM, Smith GW, van Hooidonk RJ, Seabra MI, Bak RPM (2004). Algal contact as a trigger for coral disease. *Ecol. Lett.* 7:919-923. <http://dx.doi.org/10.1111/j.1461-0248.2004.00651.x>
- Nyström M, Folke C, Morberg F (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trend Ecol. Evol.* 15: 413-417. [http://dx.doi.org/10.1016/S0169-5347\(00\)01948-0](http://dx.doi.org/10.1016/S0169-5347(00)01948-0)
- Nzali LM, Johnstone RW, Mgaya YD (1998). Factors affecting scleractinian coral recruitment on a nearshore reef in Tanzania. *Ambio* 25: 717-721.
- O'Leary J, Potts D, Braga J, McClanahan T R (2012). Indirect consequences of fishing: reduction of coralline algae suppresses juvenile coral abundance. *Coral Reefs* 31: 547-559. <http://dx.doi.org/10.1007/s00338-012-0872-5>
- 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 p326.
- Obura DO, Furaha J, Mwaura J (2005). Coral settlement patterns in the Mombasa Marine Park. *Coral Reef Degradation in the Indian Ocean (CORDIO) Status Report 2005*, 167-173.
- Ohwa BO (1996) Seasonal variations of nutrient fluxes in the Indian Ocean from the Sabaki River, Kenya. *Discov. Innov.* 8:265-274.
- Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014). Mechanisms of reef coral resistance to future climate change. *Science* 344:895-898. <http://dx.doi.org/10.1126/science.1251336>
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011). Projecting coral reef futures under global warming and ocean acidification. *Science*, 333(6041):418-422. <http://dx.doi.org/10.1126/science.1204794>
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden, JC, Possingham HP, Sala E (2005). Are US coral reefs on the slippery slope to slime? *Science* 307: 1725-1726. <http://dx.doi.org/10.1126/science.1104258>
- Perry CT, Larcombe P (2003). Marginal and non-reef building coral environments. *Coral Reefs* 22:427-432. <http://dx.doi.org/10.1007/s00338-003-0330-5>
- Richmond RH, Rongo T, Golbuu Y, Victor S, Idechong N, Davis G, Kosta W, Neth S, Hamnett M, Wolanski E (2007). Watersheds and coral reefs: Conservation Science, Policy and Implementation. *BioScience* 57:598-607. <http://dx.doi.org/10.1641/B570710>
- 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>
- Santodomingo N, Novak V, Pretkovic V, Marshall N, Di Martino E, Capelli ELG, Johnson KG (2015). A diverse patch reef from turbid habitats in the middle Miocene (East Kalimantan, Indonesia). *Palaios*, 30(1):128-149. <http://dx.doi.org/10.2110/palo.2013.047>
- Selig ER, Casey KS, Bruno JF (2012). Temperature-driven coral decline: the role of marine protected areas. *Glob. Chang. Biol.*, 18: 1561-1570. <http://dx.doi.org/10.1111/j.1365-2486.2012.02658.x>
- Shannon CE, Weaver W (1949). *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, IL, 125 pp.
- Thomason JC, LeTissier MDA, Thomason PO, Filed SN (2002). Optimizing settlement tiles: the effect of surface texture and energy, orientation and deployment duration upon the fouling community. *Biofouling* 18:293-304. <http://dx.doi.org/10.1080/0892701021000034409>
- Thomsen, MS., McGlathery K (2006). Effects of accumulations of sediments and drift algae on recruitment of sessile organisms associated with oyster reefs. *J. Exp Mar Biol. Ecol.* 328: 22- 34. <http://dx.doi.org/10.1016/j.jembe.2005.06.016>
- Todd PA (2008). Morphological plasticity in scleractinian 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 scleractinian coral *Favia speciosa* (Dana) around Singapore. *Hydrobiologia* 444:227-235. <http://dx.doi.org/10.1023/A:1017570100029>
- Tribollet A, Golubic S (2011). Reef Bioerosion: Agents and Processes In Z. Dubinsky and N. Stambler (eds) *Coral Reefs: An Ecosystem in Transition*, Springer Science + Business Media BV. http://dx.doi.org/10.1007/978-94-007-0114-4_25
- Umar MJ, McCook LJ, Price IR (1998). Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs* 17:169-177. <http://dx.doi.org/10.1007/s003380050111>
- Venera-Ponton DE, Diaz-Pulido G, McCook LJ, Rangel-Campo A (2011). Macroalgae reduce growth of juvenile corals but protect them from parrotfish damage. *Mar. Ecol. Prog. Ser.* 421: 109-115. <http://dx.doi.org/10.3354/meps08869>
- Watson M, Ormond RFG (1994). Effects of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar. Ecol. Prog. Ser.* 109: 115-129. <http://dx.doi.org/10.3354/meps109115>
- West K, van Woesik R (2001). Spatial and temporal variance of river discharge on Okinawa (Japan): inferring the temporal impact on adjacent coral reefs. *Mar. Pollut. Bull.* 42:864-872. [http://dx.doi.org/10.1016/S0025-326X\(01\)00040-6](http://dx.doi.org/10.1016/S0025-326X(01)00040-6)
- Wolanski E, Martinez JA, Richmond RH (2009). Quantifying the impact of watershed urbanization on a coral reef: Maunaloa Bay, Hawaii. *Estuar Coast Shelf Sci* 84: 259-268. <http://dx.doi.org/10.1016/j.ecss.2009.06.029>
- Xie LQ, Xie P, Tang HJ (2003). Enhancement of dissolved phosphorus release from sediment to lake water by *Microcystis* blooms—an enclosure experiment in a hyper-eutrophic, subtropical Chinese lake. *Environ. Pollut.* 122:391-399. [http://dx.doi.org/10.1016/S0269-7491\(02\)00305-6](http://dx.doi.org/10.1016/S0269-7491(02)00305-6)