Land Use and Sedimentation Impacts on Coral Reefs in the Eastern Caribbean

by

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Abstract

Human activities are leading to increased stress on coastal ecosystems worldwide. On coral reefs, sediment runoff has been recognized as an important stressor for several decades. Manipulative experiments have repeatedly shown that sediment negatively affects coral and have highlighted the organism-scale consequences of artificially increasing sediment levels. However, little quantitative data exist on changes in sediment accumulation rates that have occurred over coral reefs concurrently with coastal development, and clear links between enhanced sediment load and changes in natural reef communities have been difficult to establish. In this thesis, I apply new methods to assess terrestrial sediment stress to coral reefs, quantify changes in sedimentation rates over reefs, and identify areas in upstream watersheds that contribute disproportionately to the coastal sediment yield. Using reef sediment composition as a proxy for terrestrial influence to a reef, I show associations between terrigenous sediment load and several metrics of reef health across two spatial scales: at multiple sites on the island of Saint Lucia and across multiple islands along the eastern Caribbean chain. The proportion of terrigenous material in surface reef sediment was a better predictor of both current coral cover and decadal change in coral cover than protection afforded by well-enforced marine protected areas. The proportion of terrigenous sediment increased over time on reefs located near obvious sources of sediment but not at sites with no such input, indicating that temporal increases are caused by local anthropogenic activities and are not likely the result of long-distance transport of sediment. Sediment accumulation rate, as estimated by short-lived radioisotope analyses, has at least doubled over coral reefs downstream of two watersheds in Saint Lucia during the past six to seven decades. Unpaved roads appear to be the most important contributing factor to downstream coastal sediment yield, and in particular a small number of steep road segments. These findings highlight that substantial changes have recently occurred in the sedimentary regime of several eastern Caribbean coral reefs, and show that increased runoff is likely an important driver of changes in coral reef communities in this region.

Keywords: coral; sediment accumulation rate; runoff; species assemblages; sediment composition; marine protected areas

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Chapter 1.

General Introduction

Human population growth, with associated increases in resource exploitation and waste production, is causing growing stress on ecosystems around the globe (Foley et al. 2005, Bargagli 2008, Mora 2008). In the marine environment, human impacts have been especially important in the coastal zone (Halpern et al. 2008), where habitat degradation has dramatically accelerated in the last 150-300 years (Lotze et al. 2006). Coral reef ecosystems in particular have exhibited dramatic changes worldwide in the past several decades, with substantial declines in coral cover due in large part to anthropogenic factors such as overfishing, global climate change and runoff (Hughes 1994, Gardner et al. 2003, Bruno and Selig 2007, Burke et al. 2011). Reduced herbivory caused by overfishing and disease can allow increases in macroalgal biomass, which in turn suppresses coral growth, fecundity and recruitment (Mumby and Steneck 2008). Increased sea surface temperatures are associated with coral bleaching, the loss of symbiotic zooxanthellae (Hoegh-Guldberg 1999). While corals can recover from mild bleaching, extended episodes such as those recorded in 1998 and 2005 can lead to extensive coral mortality (Glynn et al. 2001, Graham et al. 2008, Eakin et al. 2010) and increase coral vulnerability to disease (Miller et al. 2009). Agricultural activities and coastal development can decrease water quality and contribute to coral declines, through the discharge of sediment, nutrients and pollutants (Pastorok and Bilyard 1985, Tomascik and Sander 1987, Rawlins et al. 1998, Van Woesik et al. 1999, Fabricius and

De'Ath 2004, Fabricius et al. 2005, Richmond et al. 2007, Alvarado et al. 2009). Live coral plays a crucial role in the structure and functioning of coral reef ecosystems, and loss of coral cover can affect the ecosystem through both biological interactions (Jones et al. 2004, Munday 2004, Coker et al. 2009, Stella et al. 2011) and the loss of habitat caused by the erosion of the reef structure (Alvarez-Filip et al. 2009).

Marine protected areas (MPAs), the main tool used in the conservation of coral reefs, may be effective in restoring top-down control of macroalgae by increasing herbivore biomass (e.g. Hawkins et al. 2006, Francini-Filho and de Moura 2008, Guarderas et al. 2011) and thereby aid in the recovery of corals. However, their effectiveness is destined to be limited if they do not control the threats that originate outside MPAs (Jameson et al. 2002, Aronson and Precht 2006). Recent evidence shows that marine protected areas in the Caribbean have indeed had little impact on the trajectories of coral cover inside their boundaries (Aronson and Precht 2006, Hawkins et al. 2006, Coelho and Manfrino 2007, Mora 2008). Of the many threats to corals that are external to MPAs, those that originate locally (e.g. runoff) should be much easier to manage than global threats (e.g. climate change), and should be a priority for local conservation efforts.

This thesis focuses on one such local threat, sediment runoff, in the eastern Caribbean. Limited data exist on the coral reefs of this region compared to the rest of the Caribbean, but the available information suggests that eastern Caribbean reefs are especially threatened by human impacts (Halpern et al. 2008, Burke et al. 2011). Increased sedimentation may play a particularly important role in the trajectory of corals in this region since steep topography, high rainfall and rapid development on nearby islands all lead to high levels of erosion (MacDonald et al. 1997, Ramos-Scharrón and MacDonald

2007), while the limited extent of wetlands means that much of the sediment produced on the islands reaches the coastal zone (Brooks et al. 2007, Ryan et al. 2008).

The mechanisms by which sediment can negatively impact coral are generally well understood (Rogers 1990, Fabricius et al. 2005), however there is still surprisingly little information on how sediment accumulation rates have changed over time near coral reefs along with anthropogenic development. There is therefore a general knowledge gap on the actual effects of sediment runoff on corals in the wild. One of the limitations in understanding the effect of sediment on corals is the way the term “sedimentation” is used in the coral reef literature. Coral reef ecologists have generally used sediment traps to measure sedimentation rates (Hodgson 1989, Edinger et al. 1998, Nemeth and Nowlis 2001, Torres 2001, Torres et al. 2001, Nugues and Roberts 2003, Mallela et al. 2004, Wielgus et al. 2004, Wilson 2005, Dikou and van Woesik 2006, Dutra et al. 2006, Done et al. 2007, Fisher 2007, Fisher et al. 2008, Smith et al. 2008), but such traps have been shown repeatedly to have serious limitations (Bloesch and Burns 1980, Gardner 1980), especially in the high energy environment of coral reefs (Storlazzi et al. 2011). Sediment traps on coral reefs greatly overestimate sediment accumulation rate, as they measure both runoff from land (i.e., terrigenous sediment, which includes organic and non-calcareous inorganic particles) as well as sediment which is resuspended by waves during storm events. The latter includes terrigenous sediment deposited on the reef as well as reef-produced organic and calcareous particles (Bothner et al. 2006). Since increased runoff from land, rather than sediment resuspended by storms, is the issue of greater concern in coral reef conservation, alternative methods must be used to quantify it.

This thesis explores the causes and consequences of changes in sediment accumulation rates over coral reefs. Specific objectives are to 1) quantify the effects of land-derived sediment on coral reef communities in the field, 2) analyze geographic patterns of recent changes in sedimentation regimes in the eastern Caribbean and 3) model the effects of land use change in a watershed on sediment yield to downstream reefs. I begin, in Chapter 2, with a systematic review of field studies that have measured both sedimentation rate (mostly derived from traps) and coral cover. This review highlights considerable knowledge gaps and the limitations of sediment traps in coral reefs environments. Chapters 3 and 4 are based on field data collected throughout the eastern Caribbean. Chapter 3 explores the relationship between coral reef community structure and the composition of surface sediment, used as a proxy for terrestrial influence on a reef. Chapter 4 provides evidence of changes in sediment composition over time in sediment cores from multiple reefs located in close proximity to clear sources of sediment and shows that short-lived radioisotopes can be used successfully to date coral reef-associated sediment. Chapters 5 and 6 focus on the island of Saint Lucia, where enhanced sedimentation has been identified as an important problem for corals (Sladek Nowlis et al. 1997, Hawkins et al. 2006) and where well-enforced MPAs have been established to protect coral reef ecosystems. Chapter 5 examines the effects of spatial protection and terrigenous sediment input on the coral reefs of Saint Lucia. Finally, Chapter 6 uses a simple GIS-based sediment budget model to estimate changes in sediment yield in relation to land use changes over a 15-year period in two Saint Lucian watersheds, and identify those land uses that are most important in causing increased terrigenous sediment accumulation rates measured on the reefs. In my final chapter I synthesize the findings of previous chapters, suggest future research directions and outline the management implications of this work.

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Chapter 2.

Effects of sedimentation on corals: A systematic review of field studies with emphasis on the Caribbean

Abstract

Excess sedimentation is known to be detrimental to corals in small-scale experiments, yet we still have a limited understanding of effects of sediment on coral at regional scales. I conducted a systematic search of unmanipulated field studies that focused on the effects of sedimentation on corals. Only 10 studies provided spatially replicated data that could be included in a meta-analysis of the relationship between sedimentation rate and coral cover at a global scale. The overall effect size r was small (r = -0.11) and not significantly different from zero. Re-analyses of Caribbean studies suggest that shifts in coral community composition may occur with increased sedimentation in the absence of changes in total coral cover. Sediment characteristics and issues with field measurements of deposition rates may obscure coral responses to sedimentation. This study identifies research priorities to allow an assessment of the importance of increasing sedimentation as a regional cause of ecological change on coral reefs.

Introduction

Coral reef ecosystems around the world have experienced tremendous declines in the past decades (Bellwood et al. 2004, Bruno et al. 2007). This change is especially apparent in the Caribbean region (Gardner et al. 2003), where a steady decrease in coral cover has occurred concurrently, on some reefs, with an increase in macroalgae (Côté et al. 2006, Bruno et al. 2009). The causes of coral decline are numerous and include disease, overfishing of herbivores, storms, thermally induced bleaching episodes, and lower water quality (Aronson and Precht 2006).

One of the most important tools for protecting reefs is the use of Marine Protected Areas (MPAs; Mumby and Steneck 2008), which regulate extractive activities within their boundaries. The establishment of MPAs has, in many cases, resulted in increases in fish biomass and size (Mosqueira et al. 2000, Halpern 2003); however, MPAs have been shown repeatedly to have little effect on corals themselves (Aronson and Precht 2006, Hawkins et al. 2006, Coelho and Manfrino 2007, Mora 2008). With the continuing degradation of coral reefs and accompanying erosion of the reef structure (Alvarez-Filip et al. 2009) on which fish and invertebrates depend, the long-term preservation of many reef-dwelling populations is also compromised (Jones et al. 2004, Paddack et al. 2009).

The two most likely causes for the lack of effect of MPAs on corals are global climate change which, through increased sea surface temperatures, leads to coral bleaching both in and out of reserves (Aronson and Precht 2006), and decreased water quality from land-based sources of sediment and pollution, which are currently outside the jurisdiction of most MPAs (Stoms et al. 2005, Richmond et al. 2007). Climate change needs to be addressed at a global level, but water quality can realistically be controlled by local regulatory agencies to improve the effectiveness of MPAs in protecting corals, provided that we understand the link between the terrestrial and marine environments. Our understanding of this link, particularly with respect to coral reefs, is still limited. Fabricius (2005) provided a thorough review of the effects of terrestrial runoff on corals and described potential mechanisms by which increases in inorganic nutrients, particulate organic matter, turbidity and sedimentation affect corals. However, this review was qualitative and did not provide an understanding of the magnitude of the effect of each of these elements of runoff on corals.

Of the four elements of terrestrial runoff mentioned above, sedimentation is widely held to be an important problem for Caribbean coral reefs (Sladek Nowlis et al. 1997, Hawkins et al. 2006, Ramos-Scharrón and MacDonald 2007). Yet, after several decades of research on the effects of sedimentation on corals (Aller and Dodge 1974, Rogers 1983, Cortés and Risk 1985, Hodgson 1989, 1990), our understanding of the relationship between the two at a regional scale is still poor. While the effect of increased sediment on corals is relatively easy to test and is well understood at a very small, reef or sub-reef scale (Rogers 1983, Babcock and Davies 1991, Nemeth and Nowlis 2001, Weber et al. 2006), large-scale relationships between increased sedimentation (and other elements of terrestrial runoff) and reef degradation have been difficult to establish, possibly because of confounding factors and natural variation in reef communities (Fabricius et al. 2005). These impediments have made it difficult to gauge the importance of increasing sedimentation as a regional cause of ecological change on coral reefs.

Here, I tackle this gap in knowledge by providing a quantitative synthesis of literature on the effect of sediment on corals. More specifically, I ask whether the negative relationship between sedimentation rate and coral cover that characterizes small-scale experiments and observations is detectable at a large scale in natural coral reef ecosystems. Using a meta-analysis, I assess the global evidence available of effects of sedimentation on coral cover. I explore the importance of specific sediment characteristics, size and source, in determining coral community structure on Caribbean reefs. Finally, I highlight four areas with marked deficiencies in data and their implications for coral reef conservation.

Methods

I conducted a systematic review of field studies that examined the link between sedimentation levels and coral cover. Studies were identified through searches of ISI Web of Science (1900-2008) and Aquatic Science and Fisheries Abstracts (1960-2008) databases with the following key words: (coral OR reef) AND (sediment* OR silt* OR water quality OR turbid* OR clarity OR runoff OR resuspen*). Eight experts were also contacted personally, which produced one unpublished manuscript and one unpublished thesis.

I assessed the papers for relevance by reading the title and abstract. This assessment was conservative and the paper was retained if there was any indication of useful data. I then read the full text of the retained papers and kept all those that provided data on the effect of sedimentation or turbidity on some measure of coral health (e.g., growth, %

cover, abundance, recruitment), regardless of geographic location. I also searched all studies cited in the reference section of papers providing data. The three criteria for acceptance were that the study had to be (1) observational (i.e., on unmanipulated reefs), (2) spatially replicated, and (3) carried out in the field. Studies that were replicated in time were not used since there were too few of them (n = 3) for analysis.

The information extracted from each paper that met the acceptance criteria included: location of study site, depth, sampling design (e.g. sampling method, number of replicates), measures of coral cover (overall percentage and/or percentage by species), coral growth rate and/or juvenile coral abundance, as well as all measures of sedimentation presented. When the number of studies reporting the same measures of sedimentation and coral responses allowed it, meta-analysis was used to combine results across studies. When too few studies were available on specific measures of sedimentation or coral responses, a qualitative review was performed. I also re-analyzed data from studies reporting changes in species-specific coral cover to examine the effects of sedimentation from a coral community perspective.

Meta-analysis

Meta-analysis allows the quantitative synthesis of the results of separate studies on a similar topic. It entails the calculation of an ‘‘effect size’’ for each study, i.e., a common currency by which to measure the magnitude of the response of interest within each study. Effect sizes are then combined into an overall effect size across studies. Heterogeneity among studies, Q_T, is tested against a χ^2 distribution with n-1 degrees of freedom. A significant Q_T means that the variance among effect sizes is greater than expected by sampling error, and hence there is variation in magnitude or direction of effects sizes across studies (Rosenberg et al. 2000). Total heterogeneity, Q_T, can be partitioned into variation in effect size explained by the model (Q_M) and residual variation (Q_E). A significant Q_M implies significant differences in mean effect sizes among groups or a significant relationship between effect size and a continuous moderator variable (Rosenberg et al. 2000).

I used the correlation between coral cover and sedimentation rate across all sites in a given study (Pearson product-moment correlation coefficient, *r*) as a measure of effect size in my analysis. This metric is suitable for continuous data structure and has the advantage that data from primary research studies need not contain all summary data (i.e. means, standard deviations and sample sizes), thereby allowing us to include a greater proportion of studies in the meta-analysis (Rosenberg et al. 2000, Boreinsten 2009). If *r* was not provided in a study, it was calculated with SPSS 16, using the reported data for coral cover and sedimentation rate. When data were only presented in figures, the graphs were enlarged and digitized using Grab it Graph Digitizer software (www.datatrendsoftware.com). If multiple depths were sampled at some sites, I used only the depth for which the most sites could be included. In the single study where sampling was repeated over time to assess changes in coral cover with an increase in sedimentation rate (Nemeth and Nowlis 2001), I only used data for spatial comparisons from the initial assessment.

All data were analyzed using MetaWin software version 2.1.4. Individual correlation coefficients were z-transformed to stabilize variances (Shadish and Haddock 2009) and then combined across studies using a random-effects model. I used bias-corrected 95% bootstrap confidence intervals (Adams et al. 1997) of the mean z-transformed correlation coefficients to determine the significance of each effect size. The confidence intervals were generated from 999 iterations. An effect size was considered significant if its confidence interval did not include zero.

A wide variety of measurements of sedimentation as well as coral responses were reported in the available literature. I therefore subdivided studies into groups of comparable sediment measures and coral responses. There were enough studies to conduct a meta-analysis only on the relationship between total coral cover and sedimentation rate. To account for the potential influence of sediment trap design and deployment time on the measurement of sedimentation rates, and hence on the relationship between coral cover and sedimentation rate, I also conducted meta-analyses using trap height, diameter, height above the substrate, height:diameter ratio and deployment period as continuous moderators.

Analysis of coral species composition

Sedimentation could affect coral species composition in addition to, or instead of, coral cover. We therefore also examined studies reporting changes in coral species composition changes under different sedimentation regimes. Because of data limitation, this analysis could be performed only for the Caribbean region.

Four studies reported cover of individual coral species in relation to sedimentation. One (Mallela et al. 2004) reported sedimentation rate, while the other three, all conducted in Puerto Rico (Acevedo et al. 1989, Torres 1998, Torres and Morelock 2002), reported sediment composition and size. I carried out multivariate coral species composition analyses (which were not carried out in the original Puerto Rican studies) using the software PRIMER (version 6.1.9; PRIMER 2006). For both sediment composition and size, I separated sites into “low” and “high” categories based on natural breaks in the combined data. Fortuitously, this produced contrasting groups of roughly equal sizes. In the case of sediment composition, “low” sites had between 2-35% terrigenous (non-calcareous) sediment and “high” sites, between 45-80%. For sediment size, “low” sites had 2-52% fine (<0.063 μm) sediment, and “high” sites, 70-90%. To compare coral communities between sites, I performed an analysis of similarity (ANOSIM) based on percent of cover of coral species using Bray-Curtis similarity coefficients (Clarke and Warwick 1994). ANOSIM generates an R statistic, which can vary between 0 (similarities are comparable within and between groups) and 1 (all samples within group are more similar to each other than to any sample across groups). The significance of R (i.e. difference from zero) is tested with a permutation test (n max in this study = 999 permutations). To identify which coral species contributed most to the dissimilarity between groups, I used a similarity percentage analysis (SIMPER). Differences in coral community structure between sites were visualized using multidimensional scaling (MDS) plots.

Results

Variation in measures of sedimentation

Sedimentation was measured in a variety of ways, including sedimentation rate, turbidity, % terrigenous sediment, and % clay-size sediment (Table 2.1). Sedimentation rate was the commonest measure of sedimentation, although there was extensive variation in the specific manner in which it was measured (Table 2.1).

Table 2.1. Studies relating various aspects of sedimentation to coral cover on tropical reefs. Brief details of the sedimentation measurement methods are included. H: sediment trap height; D: sediment trap diameter; HB: sediment trap height above bottom; T: deployment period of traps; ?: not reported

Study	Sedimentation rate	Other sedimentation measure	Region
Acevedo 1989		% silt, % terrigenous	Caribbean
Adjeroud 1997		Turbidity (Nephelometric Turbidity Units (NTU); Bioblock M ESD 01 turbidimeter)	Indo-Pacific
Dikou and van Woesik 2006	Sediment traps Design: H 13cm; D 6 cm; HB 20 cm; T 1 month		Indo-Pacific
Done et al. 2007	Sediment traps with baffles Design: H 30 cm; D 6.6 cm; HB ?; T ?		Indo-Pacific
Dutra et al. 2006	Sediment traps Design: H 26 cm; D 6 cm		Caribbean
Edinger et al. 1998	Sediment traps Design: H 30 cm; D 5 cm; HB 25-75 cm; T 1-2 weeks		Indo-Pacific
Fabricius et al 2005		Suspended solids (average 2 years; mg/L)	Indo-Pacific
Fisher 2007	Sediment traps Design: H 61 cm; D 5.1 cm; HB ?; T 1-5 months	Turbidity (NTU; Portable turbidimeter)	Caribbean

Hodgson 1989	Sediment traps Design: H:D 2:1 to 3:1; HB 150 cm; T 1 month		Indo-Pacific
Loya 1976	Method unreported		Caribbean
Sladek Nowlis et al. 1997		Thickness of the fine clay-like mud layer in hollows on reef (2 months after tropical storm)	
Mallela et al. 2004	Sediment traps Design: H 19.9 cm; D 5.1 cm; HB 50 cm; T 2-3 weeks	Noted if sediment is present, in at least 10 'hollows' per site	Caribbean
McClanahan & Obura 1997	Sediment accumulation on 15 cm x 15 cm tiles; T 7-30 days; results scaled to be comparable to standard tubular traps		Indo-Pacific
Nemeth and Nowlis 2001	Sediment traps Design: H 20.8 cm; D 5.2 cm; HB 20-40 cm; T 1-2 months	Turbidity (NTU; Hach 21 OOP turbidimeter)	Caribbean
Smith et al. 2008	Sediment traps Design: H 20.8 cm; D 5.2 cm; HB 50 cm; T 1-2 months		Caribbean
Torres 1998		% silt, % terrigenous	Caribbean
Torres and Morelock 2001		% silt, % terrigenous	Caribbean
Torres et al. 2001	Sediment traps Design: H 22.9 cm; D 7.6 cm; HB ?; T 20-40 days		Caribbean
Weil et al., unpublished	Sediment accumulation plates (Astroturf); T 3 days		Caribbean
Wielgus et al. 2004	Sediment traps Design: H 16 cm; D 7 cm; HB ?; T 2 weeks		Indo-Pacific
Wilson 2005	Sediment traps Design: H 11.5 cm; D 5 cm; HB ?; T 4 weeks		Indo-Pacific

Effects on coral cover: global meta-analysis

Fifteen studies reported field measures of percent coral cover as well as sedimentation rate (mg*cm^{-2}*day^{-1}) at multiple sites. For illustrative purposes, all data are shown in Figure 2.1. In both Caribbean and Indo-Pacific studies, coral cover varied widely at low sedimentation rates and less at higher sediment loads, with coral cover generally being lower in the Caribbean (Figure 2.1).

Ten studies had enough sites (i.e., four or more) to generate correlation coefficients for meta-analysis (Table 2.2). Only two studies reported a significant correlation between coral cover and sedimentation rate (Hodgson 1989, Fisher 2007; Table 2.2), and in both cases, the relationship was positive. Seven out of 10 studies showed a negative correlation but none was significant. The overall effect size of all studies was slightly negative ($z = -0.11$) though non-significant since the confidence interval overlapped zero (bootstrap 95% CI: -0.53 to 0.40). An effect size of this magnitude is considered small (Cohen, 1988). The overall heterogeneity in effect sizes among studies was not significant ($Q_T = 9.23$, $n = 10$, $P = 0.42$), indicating that studies did not vary greatly in magnitude and direction of observed effect sizes. Mean effect sizes did not differ between studies from the Caribbean ($z = -0.037$; bootstrap 95% CI: -0.43 to 0.42; $n = 6$) and the Indo-Pacific ($z = -0.054$; bootstrap 95% CI: -0.63 to 0.75; $n = 4$) ($Q_M = 0.0024$, $n = 10$, $P = 0.96$), and neither regional effect size was significant (since the CIs encompass zero). Study-specific effect sizes did not vary with any of the elements of trap design tested (trap height, diameter, height:diameter ratio, height over the substrate) or with measures of deployment time (average, shortest and longest) ($P > 0.05$ in all cases).

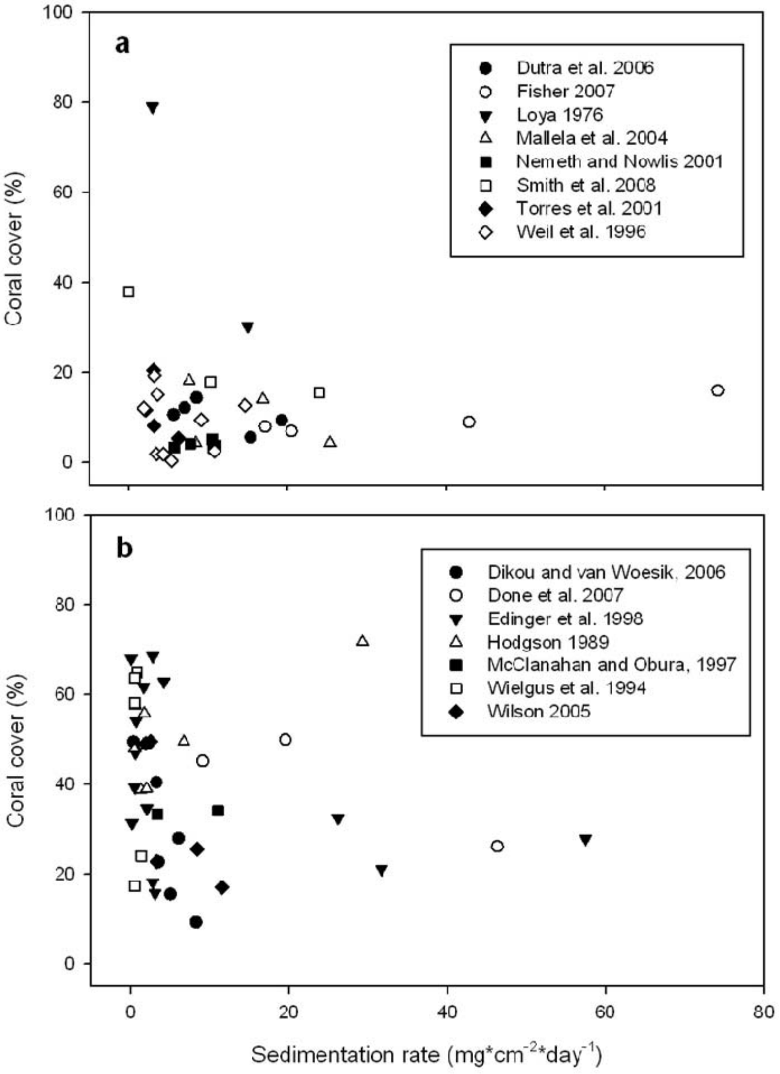

Figure 2.1. Total hard coral cover (%) as a function of sedimentation rate (mg*cm^{-2}*day^{-1}) as reported in 15 published studies. (Indo-Pacific: n = 7 studies; Caribbean n = 8 studies). Studies include those listed in Table 2.2, in addition to Loya 1976, McClanahan and Obura 1997, Wielgus et al. 2004, Done et al. 2007, Smith et al. 2008.

Table 2.2. Summary of studies included in the meta-analysis of effect of sedimentation rate on coral cover. For each study, the Pearson correlation coefficient (r) was calculated for the relationship between coral cover and sedimentation rate across sites; P refers to the significance of this correlation. The sample size represents the number of sites at which coral cover and sedimentation rate were measured.

Study	*r*	P	Sample size	Range of sedimentation rate (mg*cm^{-2}*day^{-1})	Location
Dikou and van Woesik 2006	-0.63	0.19	6	0.4 – 8.3	Singapore
Dutra et al. 2006	-0.62	0.27	5	5.5 – 11.8	Brazil
Edinger et al. 1998	-0.39	0.16	14	0.02 – 83.7	Indonesia
Fisher 2007	0.95	0.05	4	17.2 – 74.4	Florida
Hodgson 1989	0.76	0.03	8	0.5 – 29.3	Indo-Pacific
Mallela et al. 2004	-0.42	0.58	4	7.6 – 25.4	Jamaica
Nemeth and Nowlis 2001	0.29	0.64	5	5.7 – 10.9	St. Thomas
Torres et al. 2001	-0.54	0.46	4	2.1 – 6.3	Dominican Republic
Weil et al. 1996	-0.07	0.87	9	1.9 – 14.7	Florida
Wilson 2005	-0.78	0.12	5	1.9 – 11.5	India

Effects on Caribbean coral species composition

Four studies investigated species-specific changes in coral cover with changes in sedimentation rate on Caribbean reefs (Acevedo et al. 1989, Torres 1998, Torres and Morelock 2002, Mallela et al. 2004). Mallela et al. (2004) showed that across eight sites in one Jamaican bay, *Diploria strigosa* and *Siderastrea siderea* were associated with the highest overall sedimentation rates whereas *Agaricia agaricites* was limited to the clearer sites.

Three studies from Puerto Rico (Acevedo et al. 1989, Torres 1998, Torres and Morelock 2002) allowed a quantitative examination of the effects of sediment composition and size on coral community structure. There was a clear distinction in coral species composition between sites receiving low (2-35%) or high (45-80%) proportions of terrigenous sediment (Figure 2.2a). The multi-dimensional scaling plot had a relatively low stress value (0.13), suggesting that Figure 2.2a is a reasonably accurate representation of community composition differences among sites. The ANOSIM confirms the visual separation of sites based on terrigenous fraction (R = 0.841, P = 0.005). *Montastrea annularis* was the species contributing the most (>60%) to the dissimilarity between sites with low and high terrigenous sediment input: this species was more abundant at sites with a smaller proportion of terrigenous sediment (Table 2.3). *Agaricia* spp. and *Montastrea cavernosa*, which together accounted for over 20% of the differences between sites, had opposite patterns of abundance: the cover of *Agaricia* spp. was higher at sites with low terrigenous input, whereas that of *M. cavernosa* was lower.

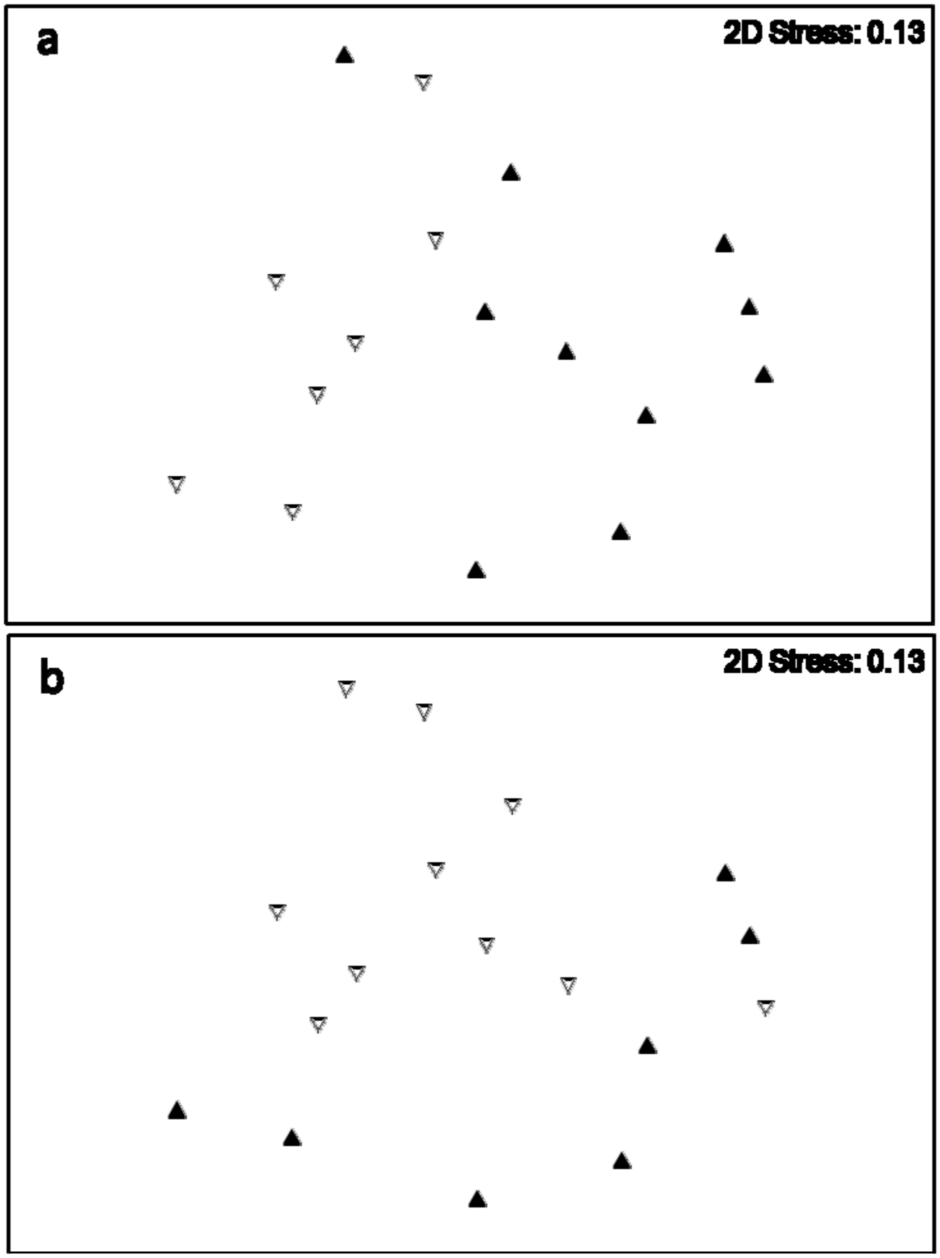

Figure 2.2. Non-metric multidimensional scaling plots of coral community composition (% cover) for all coral reef sites in Acevedo et al. (1989), Torres (1998) and Torres and Morelock (2002). Sites were categorized based on (a) sediment source: low (2-35%; open triangles) vs high (45-80%; solid triangles) proportion of terrigenous sediment, and (b) sediment size: low (2-52%; open triangles) vs high (70-90%; solid triangles) proportion of fine sediment (<0.063 µm).

Table 2.3. Summary of results from a Similarity Percentage (SIMPER) analysis of cover of Caribbean coral species at sites in Puerto Rico with low (2-35%) or high (45-80%) proportions of terrigenous sediment. The five coral species contributing the most to dissimilarities in coral community composition between the two groups are shown. Standard deviations are given in parentheses. Data from Acevedo (1989), Torres (1998) and Torres and Morelock (2002).

Species	Mean cover (%) Low terrigenous input	Mean cover (%) High terrigenous input	% contribution to dissimilarity between groups	% cumulative contribution
Montastrea annularis	15.45 (8.99)	1.01 (1.23)	60.36	60.36
Agaricia spp.	2.50 (2.05)	0.37 (1.34)	11.83	72.19
Montastrea cavernosa	0.64 (0.98)	2.34 (1.31)	9.52	81.71
Colpophyllia natans	1.46 (0.67)	0.38 (0.93)	6.46	88.17
Diploria strigosa	0.98 (1.39)	0.23 (0.36)	3.55	91.72

Coral communities also differed between sites with a high (70-90%) or low (2-52%) proportion of fine sediment (R = 0.315, P = 0.006; Figure 2.2b). *Montastrea annularis* was again the species contributing the most (~45%) to differences between sites with high or low fine sediment fraction, with a higher cover of *M. annularis* at sites with a higher proportion of fine-grained sediment (Table 2.4). *Agaricia* spp. and *M. cavernosa* also contributed substantially to differences between groups (14.96% and 14.23%, respectively), with a higher mean cover of both at sites with low proportion of fine-grained sediment. Note that there was no association between the proportion of silt-sized and terrigenous sediment across sites (*r* = 0.19, n = 17, P = 0.44), or between group membership (high vs low) across both analyses (2 X 2 contingency table: χ^2_1 = 0.15, P = 0.70).

Table 2.4. Summary of results from a Similarity Percentage (SIMPER) analysis of cover of Caribbean coral species at sites in Puerto Rico with low (2-52%) or high (70-90%) proportion of fine sediment. The six coral species contributing the most to dissimilarities in coral community composition between the two groups are shown. Standard deviations are given in parentheses. Data from Acevedo (1989), Torres (1998) and Torres and Morelock (2002).

Species	Mean cover (%) Low terrigenous input	Mean cover (%) High terrigenous input	% contribution to dissimilarity between groups	% cumulative contribution
Montastrea annularis	7.28 (10.84)	6.05 (7.17)	44.62	44.62
Agaricia spp.	0.39 (0.55)	2.48 (2.11)	14.96	59.58
Montastrea cavernosa	1.32 (1.42)	2.18 (1.69)	14.23	73.81
Colpophyllia natans	0.70 (0.92)	0.98 (1.16)	7.18	80.99
Siderastrea siderea	0.62 (0.60)	0.30 (0.32)	5.09	86.08

Effects on growth of Caribbean corals

There were too few field studies to allow a quantitative synthesis of the effects of sediment on coral growth. Most of the studies (5 out of 7) pertained to Caribbean reefs. In the Caribbean, increased sedimentation rate has been shown repeatedly and in several locations to be associated with a decrease in the growth of *M. annularis* (Dodge et al. 1974, Cortés and Risk 1985, Torres and Morelock 2002, Cruz-Piñón et al. 2003). Growth rates of *Porites astreoides* and *Siderastrea siderea* remained unchanged at all levels of terrigenous fraction in Puerto Rico, despite decreases in the cover of *P. astreoides* over the same gradient of terrigenous input (Torres and Morelock 2002). In St. Lucia, radial extension rates of *Colpophyllia natans* decreased along a gradient of increasing sedimentation, whereas *S. siderea* was not affected (Nugues and Roberts 2003).

Effects on recruitment of Caribbean corals

Only two studies estimated the abundance of juvenile corals in the field across a wide range of sedimentation rates (from ~2 to ~19mg*cm^{-2}*day^{-1}) (Weil et al. 1996, Dutra et al. 2006), and neither showed a clear trend in juvenile coral abundance with sedimentation rate.

Discussion

Overall trends and summary

There is a general agreement that increased sedimentation is detrimental to corals, yet many studies that suggest such a link do not quantify the relationship (e.g. Chansang et al. 1981, Marszalek 1981, Ayling and Ayling 1987, Brown et al. 1990, Cook et al. 1993, Carricart-Ganivet and Merino 2001, Frank and Jell 2006, Bouchon et al. 2008, Golbuu et al. 2008, Horta-Puga and Carriquiry 2008). The meta-analysis of available field data presented here showed that overall, the association between sedimentation rate – the most commonly reported measure of sediment load – and total coral cover is weak, at best.

There are four possible explanations for this unexpected result.

First, the power of the analysis was low because there are currently too few studies with enough replicates that investigate the association between coral cover and sedimentation rate. My meta-analysis included 10 field studies that used comparable sedimentation measurements and coral responses; five more studies were available but with spatial replication that was too limited for inclusion. The limited yield of my exhaustive search was surprising and emphasizes the need for both increased research effort and standardization. A higher power would increase the likelihood of detecting an overall effect of sediment on coral cover despite possible confounding factors (e.g. freshwater input, nutrient levels) that may covary with sediment load or characteristics.

Second, increased sedimentation rate may result in changes other than total cover. The multivariate re-analysis of published data from studies in Puerto Rico revealed significant differences in coral species composition between sites that receive varying levels of terrigenous and fine-grained sediment (Acevedo et al. 1989, Torres 1998). These community differences may be linked to species-specific differences in susceptibility to sedimentation, as evidenced by the variable effects of sediment on growth rates of different Caribbean corals. Species-specific effects on recruitment could also occur, although these have yet to be shown in the field in the Caribbean.

A third possibility is that the highest sedimentation rates experienced by corals in nature do not yet exceed harmful thresholds. It is notable that the range of sedimentation rates in the observational field studies considered here was wide (0.02 – 83.7 mg*cm^{-2}*day^{-1}; but generally below 30 mg*cm^{-2}*day^{-1}), but markedly lower than the levels that appear to be detrimental to corals in laboratory or field experiments (e.g., 200 – 3,800 mg*cm^{-2} (Rogers 1983); 33 – 160 mg*cm^{-2} (Weber et al. 2006)). The mismatch between small- and larger-scale apparent effects of sedimentation may therefore be due to the use of unnaturally high sedimentation rates in many experiments.

Finally, there may in fact be a strong association between sedimentation rates and coral cover but sediment traps widely used (Table 2.1; Torres and Morelock 2002, Wilson 2005, Smith et al. 2008) do not yield accurate estimates of sedimentation rate in high-energy coral reef environments (Storlazzi et al. 2011). Sediment traps tend to overestimate sedimentation rates as they accumulate both sediment from runoff as well as that resuspended by storms (Bothner et al. 2006), yet little sediment gets resuspended and escapes once in the trap (Bloesch and Burns 1980, Storlazzi et al. 2011). Extended deployment time increases the risk of overflow and fouling, and variations in trap height and design may make comparisons between studies difficult (Meesters et al. 1998, Bothner et al. 2006), even though these features were unrelated to the strength of relationship observed in my analysis between sedimentation rate and coral cover in individual studies.

Gaps identified: setting a research agenda

In this review, I found a general deficiency in quantitative data in published literature on sedimentation levels and how it impacts coral reefs in the field. Few studies report measurements of sedimentation or turbidity and those that do often have low spatial replication. I have identified four major gaps in our understanding of the impacts of sedimentation on corals, which I discuss in turn below.

Species-specific effects of sedimentation. Studies from Puerto Rico and elsewhere clearly show that the effects of sediment vary among coral species (Acevedo et al. 1989, Torres 1998, Torres and Morelock 2002, Mallela et al. 2004, Dikou and van Woesik 2006, Rogers 2009); however, the majority of studies focus on total percent cover. It is important to establish how individual coral species respond to changes in sedimentation to increase our ability both to predict shifts in coral community structure and to infer from community structure the extent of sediment stress in areas where no information on sedimentation is available. In the Caribbean, a shift in dominance from *Montastrea annularis* to more sediment-tolerant species, for example, might be a better indicator of sediment stress than total percent cover. However, an understanding of coral species susceptibility to co-occurring anthropogenic stressors (e.g. thermally induced bleaching) will also be necessary for reliable inferences to be made from coral species composition.

Other coral responses to sedimentation. Field studies to date have focused on percent cover, with a few studies examining growth and recruitment. Laboratory and field experiments have shown that sediments reduce settlement (Babcock and Davies 1991, Gilmour 1999, Birrell et al. 2005) and increase mortality (Gilmour 1999, Fabricius et al. 2003) of Indo-Pacific acroporid recruits; similar results have been shown for *Pocillopora damicornis* recruits (Hodgson 1990, Te 1992). However, too few studies are available to examine whether these trends are general and whether they occur under natural conditions. Corals may also exhibit other reactions to sedimentation. For example, Smith et al. (2008) found a strong correlation between sedimentation rate and the incidence of bleaching, partial mortality and coral health impairment. This suggests again that percent cover alone may not be a good indicator of sediment stress, and that monitoring programs should also assess coral bleaching and health.

Effects of sediment grain size and composition. The focus of studies to date has largely been on one aspect of sedimentation, i.e. rate. Yet, there is recent evidence that other sediment characteristics are important. Weber (2006), for example, found that silt-sized and nutrient-rich sediments induced higher physiological stress to *Montipora peltiformis* than other types of sediment at the same concentration. However, these relationships may vary among species. Similarly, accumulation of non-calcareous sediment may affect corals more than overall sedimentation. Yet, sediment composition is rarely reported. Differences in sediment composition could explain why some studies from Florida – a low-lying carbonate platform – fail to show a negative correlation between coral cover and sedimentation rate (Weil et al. 1996, Fisher 2007) or show higher coral cover and growth inshore (Lirman and Fong 2007), whereas similar studies near tall volcanic islands show a negative relationship between sediment load and coral cover (Acevedo et al. 1989, Torres and Morelock 2002, Smith et al. 2008).

There may also be important differences in how species respond to changes in composition and size of sediment. The analysis presented here for Puerto Rican reefs (based on Acevedo 1989, Torres 1998 and Torres and Morelock 2002) shows that *M. annularis* cover decreases with an increasing proportion of terrigenous sediment, yet cover of the same species increases with increasing proportion of fine sediment. The latter result is contrary to what would be expected from recent laboratory (Weber et al. 2006) and field (Smith et al. 2008) studies.

Accurate measurement of sediment input. Sediment traps, which are widely used to measure sedimentation rates on coral reefs (Table 1), have several recognized flaws in their use in this environment, which need to be kept in mind when interpreting data (Storlazzi et al. 2011). If deployed for extended periods of time, traps may overflow, be subjected to disturbance by organisms seeking refuge in them (Bloesch and Burns 1980) or their opening may become partially overgrown by fouling organisms. Storms and heavy swell re-suspend sediment back into traps, blurring the estimation of sediment delivery from land. Trap height above the bottom directly influences how much re-suspended sediment accumulates in the trap (Meesters et al. 1998, Bothner et al. 2006), and traps tend to overestimate the amount of fine-grained and non-calcareous material compared to sediment accumulating on the nearby reef (Storlazzi et al. 2011). Despite these limitations, sediment traps continue to be the most widespread method to measure sedimentation on coral reefs, perhaps because of a lack of satisfactory alternatives. At the very least, standardization of sediment trap design and deployment time across studies would increase comparability.

Implications for Caribbean coral reef management

Increased sedimentation is considered to be an important management concern for coral reefs, particularly in the western Atlantic (Cortés and Risk 1985, Hawkins et al. 2006, Ramos-Scharrón and MacDonald 2007, Rogers et al. 2008), yet the reported relationship between sedimentation rate and coral cover in the field varies widely between studies in in this region. For example, Smith et al. (2008) reported an inverse relationship between coral cover and sedimentation rate for the US Virgin Islands while Fisher (2007) found a positive relationship between the two variables in Florida. This could be due to natural variation in coral cover and difficulties in accurately measuring sedimentation, but it could also be due to inherent differences in the vulnerability of different reefs to increased sedimentation. In areas that experience strong currents, for example, increases in terrigenous sediment may not be detrimental as the sediment is quickly carried offshore. Coral reefs that are located near low-lying, limestone land masses such as Florida or Barbados, are likely to receive sediment with a high proportion of calcium carbonate, which appears to be less detrimental to corals than non-carbonate sediment (Torres and Morelock 2002). Fringing reefs, by their proximity to sources of sediments, may generally be at greater risk than barrier reefs.

My review suggests that current knowledge does not allow broad generalizations regarding the threshold levels at which sediment becomes detrimental to corals. Disturbances in small to medium mountainous watersheds feeding directly to the coast cause the most rapid increases in sediment flux worldwide (Milliman and Syvitski 1992, Dearing and Jones 2003). Coral reefs that fringe tall, volcanic islands may therefore be particularly vulnerable to increased sedimentation from human activities (Larsen and Webb 2009). Many island-states in this region are engaging in ambitious and potentially unsustainable development programs, which will likely increase sedimentation levels on nearby reefs (Rojas et al. 1988, Cox et al. 2006, Larsen and Webb 2009). A better understanding of unacceptable levels of sedimentation for Caribbean coral reefs and identification of potential changes in coral communities under heavy sediment loads should be management priorities in this region.

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Chapter 3.

Variation in benthic communities of eastern Caribbean coral reefs in relation to surface sediment composition

Abstract

The detrimental effects of sedimentation on coral reefs are commonly studied at a local scale but patterns at larger scales have been elusive, making it difficult to determine the role of sedimentation in contributing to regional ecological patterns in these ecosystems. The relationships between characteristics of reef-associated surface sediment and the benthic composition of 22 reefs around 11 islands of the eastern Caribbean were examined. The percent cover of live coral, macroalgae and turf algae decreased with higher terrigenous fraction of surface sediment, while the cover of sponges increased. Significant differences in coral species assemblages were observed between sites exhibiting sediment with high and low terrigenous fraction. In particular, the cover of corals in the *Montastrea annularis* complex decreased significantly across sites with increasing terrigenous sediment fraction. The proportion of terrigenous sediment near reefs increased with proximity to a clear source of sediment input. The proportion of fine-grained sediment had no effect on benthic composition. These results suggest that sedimentation may play a role in shaping coral reef communities at a regional scale.

Introduction

Human activities have the potential to greatly affect the input of terrestrial sediment into coastal zones (Neil et al. 2002). Worldwide, the largest recent increases in sediment flux have occurred in the tropics (Syvitski et al. 2005), owing particularly to disturbances (e.g., deforestation and development) in small to medium-sized mountainous drainage basins feeding directly to the coast (Milliman and Syvitski 1992; Dearing and Jones 2003). Enhanced sediment delivery can increase the potential for burial of pollutants, alter nutrient fluxes, and influence the benthic composition of coastal habitats.

At tropical latitudes, coral reefs are one of the main ecosystems negatively affected by increased development and sedimentation (Rogers 1990; Sladek Nowlis et al. 1997; Hawkins et al. 2006; Richmond et al. 2007; Wolanski et al. 2009). Numerous laboratory and small-scale field experiments have shown that increased sedimentation leads to reduced growth rates (Dodge et al. 1974), reduced settlement rates (Hodgson 1990; Babcock and Davies 1991) and increased mortality of corals (Rogers 1983; Piniak and Brown 2008). However, patterns at larger scales have been elusive (Van Woesik et al. 1999, McLaughlin et al. 2003; Fabricius et al. 2005), making it difficult to determine whether sedimentation may be an important driver of regional ecological changes on coral reefs through its predictable but ubiquitous local-scale effects. Arguing against this possibility is the fact that across geographically distant locations, coral cover varies inconsistently with sedimentation rates (Chapter 2). However, a number of factors may limit our ability to detect a relationship between sediment runoff and reef degradation on a large scale. These include natural patterns of biogeography, the presence of factors that covary with sediment input (e.g., reduced salinity, pollutants, nutrients) and which are difficult to control or account for in geographical comparisons (Fabricius et al. 2005), the fact that changes in coral species composition do not always result in changes in overall coral cover (which is the most widely reported metric of coral reef health), and potential inaccuracies in common methods of measuring sedimentation rate, in particular sediment traps (Chapter 2; Bloesch and Burns 1980; Storlazzi et al. 2011).

While total sedimentation rate is the most common measure of sedimentation reported in relation to coral cover, evidence is accumulating to suggest that sediment characteristics (e.g. size and composition) may also be important. In laboratory experiments, fine-grained sediment induced higher physiological stress in the Indo-Pacific coral *Montipora peltiformis* than other types of sediment at the same concentration (Weber et al. 2006), and sediment composition affected the survival of *Acropora willisae* recruits (Fabricius et al. 2003). In the field, the cover of *Montrastrea annularis* and *M. cavernosa* on Puerto Rican reefs decreased with increasing fined-grained fraction of sediment (Acevedo et al. 1989), while growth rates and cover of *M. annularis* decreased with increased loads of terrigenous sediment (Torres and Morelock 2002). Note that fine-grained sediment fraction has been suggested to represent sediment of terrestrial origin (Nemeth and Nowlis 2001); however, to the best of our knowledge, this relationship has never been empirically tested.

The present study explores whether a relationship exists at a regional scale between coral reef benthic composition and reef sediment characteristics across eastern Caribbean islands. Sedimentation is an important management concern in the Caribbean region, where rapid development has been associated with increased erosion (MacDonald et al. 1997) and potential impacts on downstream coral reefs (Cortés 1993; Spalding 2004; Rogers et al. 2008). The volcanic islands of the eastern Caribbean, in particular, with their rugged topography and small size which constrains development to areas near the coast, may be prone to increased sediment yields and associated problems to coastal ecosystems (Rojas et al. 1988; Cox et al. 2006; Ramos-Scharrón and MacDonald 2007; Larsen and Webb 2009). The sediment characteristics we specifically consider are the composition and grain size of sediments collected immediately adjacent to the reefs. On fringing reefs near volcanic lands, the non-calcareous fraction of reef sediment can be assumed to have originated from land (Brooks et al. 2007). The magnitude of this terrigenous fraction in surface sediment has been shown to reflect the importance of and distance from a terrigenous sediment source (Subba Rao 1958; Maxwell and Swinchat 1970; Perry and Taylor 2004; Badran and Al Zibdah 2005; Ryan et al. 2008; Alonso-Hernandez et al. 2011). The analysis of surface sediment composition could therefore be a rapid and inexpensive index of terrestrial influence on reefs.

Methods

Study area and sediment sample collection

Coral reef surveys and initial sediment sampling were carried out between January and March 2009 at 22 sites around 11 islands in the eastern Caribbean (Figure 3.1; Table 3.1). Additional, more detailed sediment sampling was conducted at two of the islands (Saba and Saint Lucia) in December 2010 and June 2011, respectively (Figure 3.2). All study islands lie at the edge of the Caribbean tectonic plate and were formed by the west-northwest subduction of the Atlantic lithosphere under the Caribbean plate (Defant et al. 2001). All islands in this study are volcanic in origin and many have a very rugged topography, with a maximum elevation of up to 958 m (Saint Lucia). Fringing reefs are the typical coral reef development around all islands sampled.

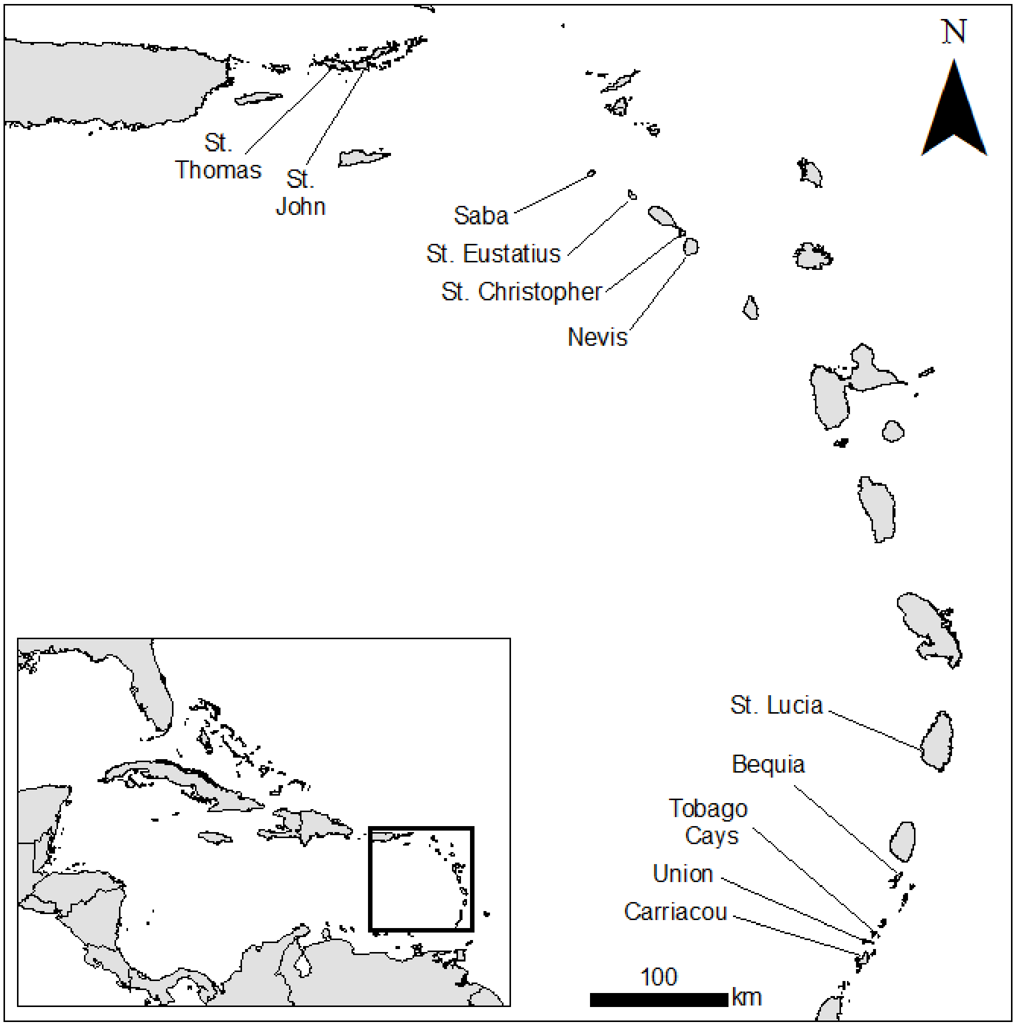

Figure 3.1. Eastern Caribbean islands where benthic surveys of coral reefs and sediment sampling were performed

Table 3.1. Location of reef surveys and sediment sampling sites in the eastern Caribbean. Site codes are used in Figure 3.6.

Island	Site name (code)	Latitude	Longitude
St. Thomas	Flat Cay (STT1)	18°19.093' N	64°59.462' W
St. Thomas	Black Point (STT2)	18°20.651' N	64°59.126' W
St. Thomas	Botany Bay (STT3)	18°21.482' N	65°02.025' W
St. John	Haulover (STJ1)	18 ° 20.916’N	64 ° 40.711’W
Saba	Greer Gut (SAB1)	17°36.703' N	63°14.501' W
Saba	Tent Reef (SAB2)	17°37.006' N	63°15.395' W
Saba	Porites Point (SAB3)	17°37.829' N	63°15.523' W
St. Eustatius	Twin Sisters (STA1)	17°31.007' N	63°00.190' W
St. Eustatius	Double Wreck (STA2)	17°28.792' N	62°59.641' W
St. Eustatius	Mushroom (STA3)	17°27.759' N	62°58.657' W
St. Eustatius	Barracuda (STA4)	17°28.088' N	62°59.495' W
Nevis	Basin (NEV1)	17°10.898' N	62°40.870' W
St. Christopher	Green Point (SKT1)	17°13.618' N	62°39.822' W
St. Lucia	Grande Caille (SLU1)	13°52.698' N	61°04.522' W
St. Lucia	Rachette Point (SLU2)	13°52.397' N	61°04.012' W
St. Lucia	Superman's Flight (SLU3)	13°50.179' N	61°04.066' W
Bequia	NW Point (BE1)	13°00.999' N	61°14.957' W
Bequia	Devil's Table (BE2)	13°00.705' N	61°14.975' W
Tobago Cays	Petit Bateau (TC1)	12°37.886' N	61°21.599' W
Union	Thompson Reef (UNI1)	12°35.544' N	61°24.671' W
Carriacou	Jack-a-Dan (CAR1)	12°29.754' N	61°28.046' W
Carriacou	Sandy Island (CAR2)	12°29.240' N	61°28.934' W

In 2009, a single sample of sediment (~ 250 ml) was collected from the surface layer (to a substrate depth of 5 cm) in a soft-bottom area immediately adjacent (maximum 5 m away) to the reef surveyed at each site. Water depth was ~10 m at all sites. Such fore-reef environments tend to have better preservation of sediment compared to back reefs or channels because of lower rates of transport and biogenic re-working (Perry 1996). In

2010 and 2011, to better understand the relationship between surface sediment composition and terrigenous sediment input, I collected sediment samples at regular intervals along the coast in Saba and Saint Lucia. The sampling locations at these two islands were chosen because of their proximity to known sources of terrigenous sediment input. In Saba, four replicate sediment samples were collected at a depth of ~10 m, at each of 10 stations located at 100 m intervals along the coast, both upstream and downstream of a sand quarry (Figure 3.2). In Saint Lucia, three replicate samples were collected at a depth of 15 m at each of four sites located within 1 km of the Soufriere River and at each of three sites within 1 km of the Anse Galet River (Figure 3.2). These sites were located at irregular intervals (200-500 m apart) that correspond to a subset of sites surveyed for another study (Chapter 5). No storm or unusually high rainfall had occurred at any sampling site for at least one month prior to sampling.

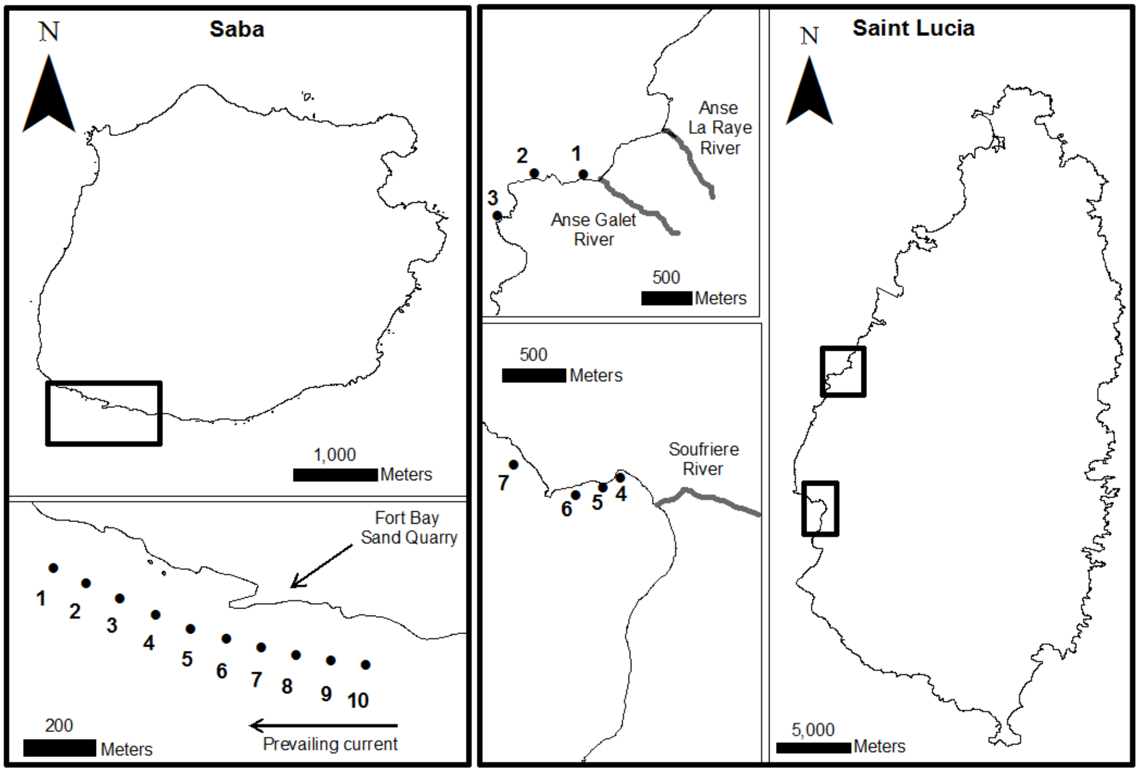

Figure 3.2. Approximate location of sampling sites for surface sediment in Saba and Saint Lucia. In Saba, the dominant current goes from east to west and there is significant sediment input from a quarry located in Fort Bay. In Saint Lucia, samples were taken at various distances from the Anse Galet and Soufriere Rivers.

Benthic surveys

Benthic surveys were conducted in 2009 at 10 m depth on one to four fringing reef sites on the leeward side of each island. At each site, three 30 m transects were deployed haphazardly, parallel to shore, in the fore-reef zone; transects were at least 10 m apart. A digital photograph of the benthos was taken every meter on each transect (i.e., 30 photos per transect) from a distance of 0.75 m above the reef. The entire resulting photograph (0.41 m x 0.61 m; 0.25 m^2) was used in subsequent analyses. Percent cover of benthic organisms was quantified using the software CPCe version 3.6 (Kohler and Gill 2006). Twenty random points were overlaid onto each photograph and the organism directly under the point was identified. The benthic types recorded were: hard coral (identified to species), macroalgae, turf algae, sponges, gorgonians, crustose coralline algae, filamentous cyanobacteria, sediment, pavement and rubble. The hard corals *Montrastraea annularis*, *M. faveolata* and *M. franksii* were considered as one taxon (*M. annularis* complex) because of difficulties in identifying the different species in small colonies from photographs. Percent cover was calculated for each replicate transect as the number of random points identified as a given benthic type (or species, in the case of corals) divided by the total number of points scored.

Sediment analysis

Each sediment sample was rinsed twice with distilled water to remove salts and decanted, then dried to constant weight at 70^{o}C. Each dry sample was separated into two subsamples by coning (Lewis and McConchie 1994), one for size analysis and the other for composition analysis. For size analysis, each dry sediment subsample was weighed and then sieved to obtain the fraction smaller than 63 μm (Smith et al. 2008). For composition analysis, each subsample was weighed, treated with a 10 % hydrochloric acid solution to dissolve all the carbonates, rinsed twice, redried, and reweighed (Perry 2000). The remaining sediments can be assumed to be terrigenous (Torres and Morelock 2002; Brooks et al. 2007). The proportion of terrigenous sediment was calculated by dividing the weight of the terrigenous fraction by the weight of the entire subsample. The proportion of fine-grained sediment was calculated by dividing the weight of the fraction smaller than 63 μm by that of the entire subsample before it was sieved. Organic content was assessed by treatment with sodium hypochlorite (Torres and Morelock 2002) and in all samples was less than 1% by weight.

Statistical analysis

I first tested whether the assumed relationship between the proportion of fine-grained (< 63 µm) sediment and the proportion of terrigenous material in samples was present, using a parametric correlation test. I then established the relationship between sediment composition and runoff. In Saint Lucia, the stations were located at increasing distance from the nearest sediment input (Anse Galet and Soufriere rivers). In Saba, the largest sediment input (quarry in Fort Bay) was located in the middle of the east-west line of sampling stations, with the predominant current moving west. Variation in the proportion of terrigenous sediment among stations in each area (Saba, Anse Galet and Soufriere) was assessed using Jonckheere-Terpstra tests of ordered alternatives because heteroscedasticity prevented the use of parametric statistics. For Anse Galet and Soufriere, I tested the hypothesis that the proportion of terrigenous sediment decreases with increasing distance from input. For Saba, because of the strong prevailing current, the proportion of terrigenous sediment was expected to increase from upstream (east) to downstream (west) of the source of input. Data were analyzed using PASW Statistics 18.

To examine the relationships between the cover of major benthic groups at each site (dependent variables) and sediment characteristics (source and size), I used mixed-effects models and a correlation structure. This method is well suited to the nested sampling design (i.e., transects within sites within islands) of the study, and allowed partitioning of the variation in reef composition attributable to islands (random effect) as well as the proportion of terrigenous sediment and the proportion of fine-grained sediment (fixed effects). Nested mixed-effects models can significantly improve inference about ecological processes across levels of organization over simple regression (McMahon and Diez 2007). Island identity was the only random effect that could be included in the mixed-effects models because data on fine-grained and terrigenous content of sediment were only available at the site level. Therefore a compound symmetry correlation structure between samples was also tested by comparing models with one of two correlation terms (i.e., either site within island or island only). Compound symmetry correlation can be used instead of random effects to account for a lack of independent samples caused by correlations among variables across different scales (Zuur et al. 2009), and tests for correlation in the residuals. The analyses were carried out using models with normal errors and constant variance following arcsine transformation of the dependent variable, which is the best method for analysing percentage cover data (Crawley 2007).

For each dependent variable (percent cover of coral [all species combined], macroalgae, sponges, gorgonians, turf algae, coralline algae and filamentous cyanobacteria), the protocol outlined in Zuur et al. (2009) for model selection was followed. First, the optimum random-effects structure was selected by comparing generalized least square (GLS) models that included no random structure to mixed-effect models with random intercept, using the most complex fixed effects (2-way interaction between the proportion of terrigenous sediment and proportion of fine-grained sediment). Models were compared using Akaike's Information Criterion (AIC). AIC values represent the trade-off between model fit and model complexity, where the lowest value represents the best trade-off. The model that had the lowest AIC value was then used to select the most appropriate correlation structure. Random structure was re-tested using the optimum correlation structure. Random and correlation structures were chosen based on minimum AIC scores using the restricted maximum likelihood (REML) estimation method. Finally, the optimum model (with respect to random and correlation structure) was used to select the fixed structure (terrigenous content, fine-grained content), where terms that were not significant were successively removed until all variables remaining significantly improved model fit. Fixed structure selection was carried out using maximum likelihood (ML). Final models were computed using REML. Homogeneity was assessed by graphical methods (Zuur et al. 2009). Because I observed no heterogeneity in the residuals, I did not test for model improvements by including variance parameters. All analyses were conducted in R 2.13.1 (R Development Core Team 2009).

Although the use of a single sediment sample (surface sediment or cores) is common in sedimentary studies because of a typically low spatial variability in sediment deposition at a small scale (Perry and Taylor 2004; Badran and Al Zibdah 2005; Alonso-Hernandez et al. 2011), I investigated the effect of the lack of sediment replication at each site on my analyses. An estimation of within-site variability in surface sediment was available for one site sampled in this study (Rachette Point—Saint Lucia), as well as 20 sites near those in this study in Bequia and Saba. At each site, four to 12 surface sediment samples were randomly collected from a ~75 m^2 area. The average coefficient of variation for sediment characteristics at those 21 sites was used to estimate standard deviations for the same variables at other sites. To evaluate the robustness of my results given this variability, I conducted an error (or uncertainty) propagation analysis (Lo 2005; Benke et al. 2008). For each significant dependent variable identified in the analyses described above, the final model was run again 1000 times using a value randomly assigned from a Gaussian distribution based on the mean and standard deviation of sediment characteristics at each site. I then calculated the mean P-value and 95% confidence interval from the 1000 iterations of the models.

Finally, non-metric multi-dimensional scaling was used to investigate differences in coral species assemblages among sites in relation to sediment characteristics using the software PRIMER version 6.1.9 (PRIMER 2006). Sites were separated in “low” and “high” categories based on natural breaks in the distributions of sediment composition and size, which for each sediment characteristic produced two groups of roughly equal sizes. In the case of sediment composition, “low” sites had between 0-14% terrigenous fraction and “high” sites between 29-95%. For sediment size, “low” sites had 0-0.8% fine (< 63 μm) fraction, and “high” sites 2-18%. To compare overall coral assemblages between sites, an analysis of similarity (ANOSIM) was performed based on the percent of cover of individual coral species using Bray-Curtis similarity coefficients (Clarke and Warwick 1994). Data were square-root transformed prior to calculating pair-wise similarities to increase the weighting of rare taxa and reduce the weighting of more abundant ones. ANOSIM generates an R statistic, which varies between 0 (sample similarities are comparable within and between groups) and 1 (all samples within group are more similar to each other than to any sample across groups) and which is tested for difference from zero with a permutation test (in this study, 999 permutations). Differences in coral community composition between sites were visualized using multidimensional scaling (MDS) plots. To identify which coral species contributed most to the dissimilarity between groups, the similarity percentage analysis (SIMPER) was used. Mixed-effect models were then fitted for each species that contributed at least 5% of the dissimilarity between groups. The model-fitting procedure used was as described above except that the fixed effects were limited to the proportion of terrigenous sediment, which was the only variable identified in the ANOSIM analyses as having an impact on coral species composition (see Results). Model selection therefore was limited to finding the optimum random and correlation structures.

Results

Relationship between terrigenous and fine-grained content

There was no significant correlation between the proportion of terrigenous sediment and the proportion of fine-grained sediment (< 63 μm) in a given sample ($r = 0.11$, n = 23, P = 0.62; Figure 3.3).

Relationship between surface sediment composition and terrestrial input

In Saba, the proportion of terrigenous sediment varied between 72% and 96% (Figure 3.4). Terrigenous content was significantly different among sites and generally increased from east to west (i.e., in a downstream direction) with highest levels at sites downstream of the quarry in Fort Bay (Jonckheere-Terpstra test, $T = 58$, P < 0.001). In Saint Lucia, terrigenous sediment accounted for between 15.9 and 86.9% of total sediment in surface samples (Figure 3.4). At both sites, terrigenous content varied significantly among stations and generally decreased with increasing distance from the mouth of the river (Anse Galet: $T = 27$, P = 0.003; Soufriere: $T = 44$, P = 0.016).

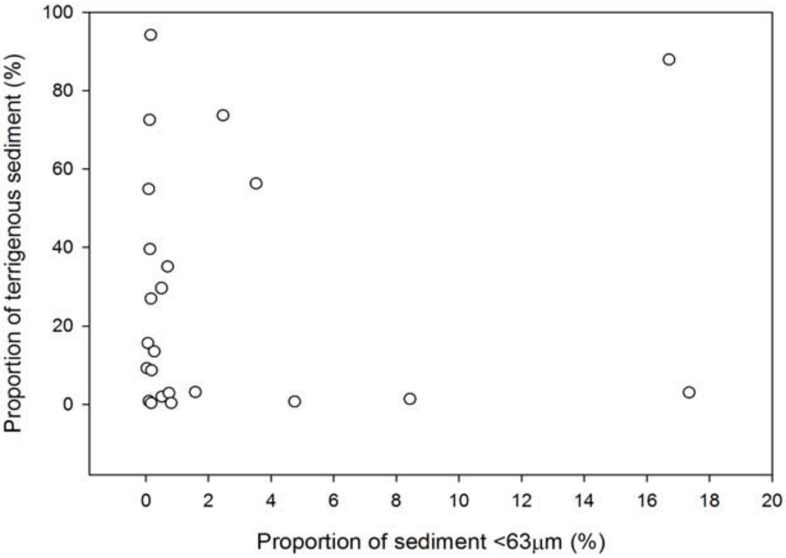

Figure 3.3. Relationship between terrigenous fraction and fine-grained (<63 µm) fraction in surface sediments collected near fringing coral reefs around 11 eastern Caribbean islands

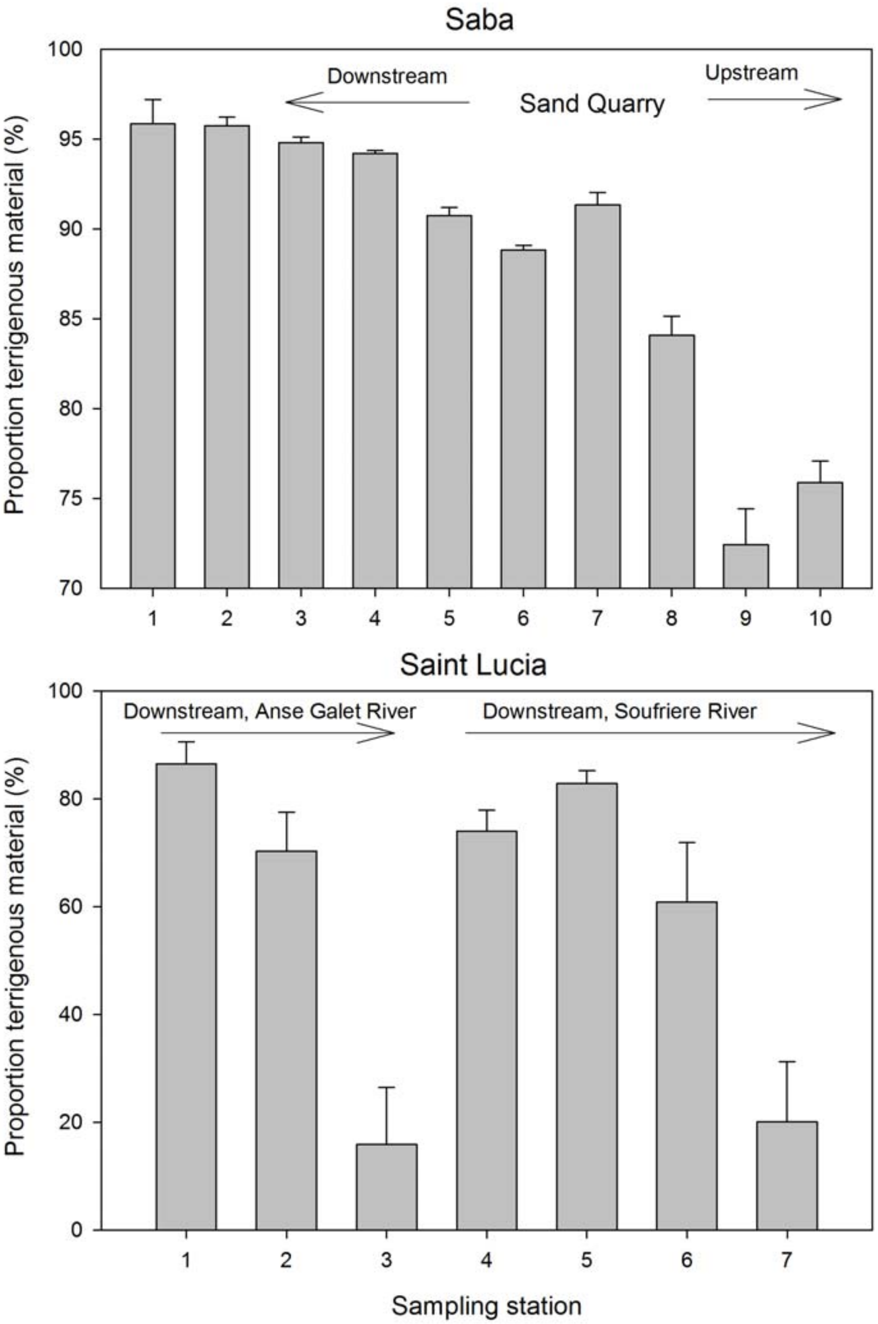

Figure 3.4. Proportion of terrigenous (non-calcareous) material in surface sediment at multiple sampling stations in Saba and Saint Lucia. The location of stations is shown in Figure 3.2. Each bar is the mean of 3 (Saint Lucia) or 4 (Saba) samples, and error bar represents standard deviation. Note the different scales on the Y-axis.

Sediment characteristics and benthic cover of major taxonomic groups

There were significant relationships between sediment characteristics and the percent cover of four of the seven biotic benthic groups examined. In all four cases, the best model was the generalized least square model with a site/island correlation structure and the proportion of terrigenous sediment as the only fixed effect.

There was a significant inverse relationship between the proportion of terrigenous sediment and percent cover of coral, macroalgae and turf algae, and a significant positive relationship with cover of sponges (Figure 3.5; Table 3.2). The proportion of fine-grained sediment did not significantly improve the fit of any of the models. No relationship was found between sediment source or size and the percent cover of gorgonians, filamentous cyanobacteria or crustose coralline algae.

The error propagation analysis suggests that the results of the final generalized least square models were generally robust. The sediment samples collected in Bequia, Saba and Saint Lucia showed an average coefficient of variation of 6.3 % (± 1.8% standard deviation) for the proportion of terrigenous sediment. Assuming that this variability is characteristic of other sites, the calculated 95% confidence intervals of P-values were well below 0.05 for the cover of macroalgae, turf algae, sponge and *Montastrea annularis* complex, while for coral cover the confidence interval ranged from 0.02 to 0.11 (Table 3.2). This indicates that the relationship between the proportion of terrigenous sediment and the cover of coral, which had a p-value of 0.046 based on one sediment sample, could become non-significant with replicated sediment samples.

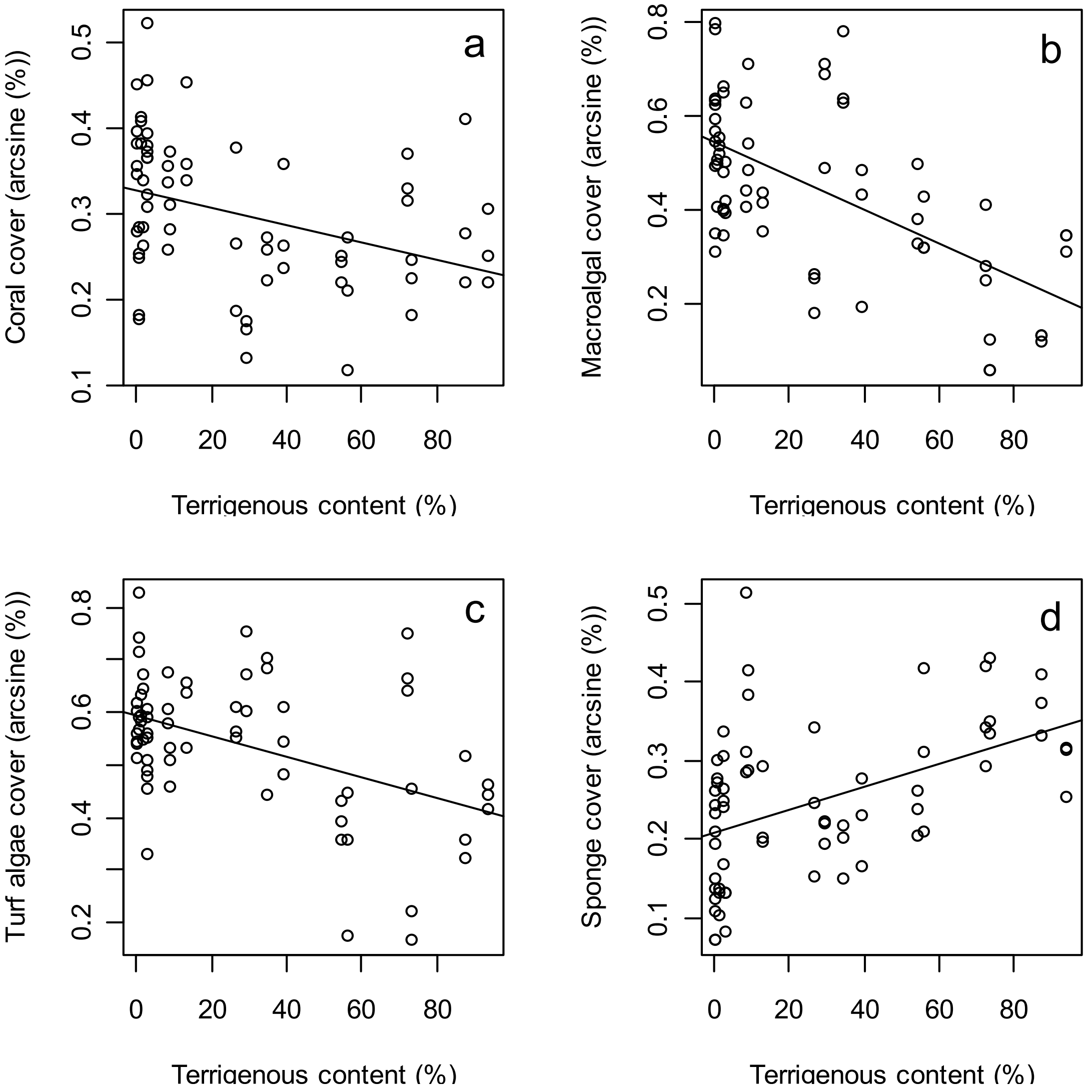

Figure 3.5. Percent cover (arcsine transformed) of (a) coral, (b) macroalgae, (c) turf algae and (d) sponges in relation to the proportion of terrigenous sediment on coral reefs around 11 eastern Caribbean islands. The solid lines represent the best fit of generalized least-square models with site/island correlation structure (see Methods)

Table 3.2. Parameter estimates, standard errors (SE), and significance statistics of optimum mixed-effects models explaining variation in percent cover of coral, macroalgae, sponges, turf algae and the coral Montrastrea annularis complex on fringing reefs across 11 eastern Caribbean islands. Dependent variables were arcsine transformed. 95% CI of P represents the confidence interval around the P-value of the effect of terrigenous fraction as estimated by an error propagation analysis (see Methods)

Dependent variable	Parameter	Estimate	SE	T	P	95% CI of P
Coral	Intercept	0.327	0.021	15.94	<0.0001	
	% terrigenous	-0.001	0.001	-2.03	0.046	0.020-0.108
Macroalgae	Intercept	0.542	0.039	13.94	<0.0001	
	% terrigenous	-0.004	0.001	-3.83	0.0003	<0.0001-0.001
Turf algae	Intercept	0.594	0.030	19.56	<0.0001	
	% terrigenous	-0.002	0.001	-2.71	0.009	0.003-0.029
Sponges	Intercept	0.208	0.022	9.53	<0.0001	
	% terrigenous	0.002	0.001	2.81	0.007	0.003-0.019
M. annularis complex	Intercept	0.178	0.026	6.77	<0.0001	
	% terrigenous	-0.002	0.0005	-3.15	0.0025	0.0011-0.0065

Sediment characteristics and coral species composition

The non-metric multi-dimensional scaling plot shows two distinct clusters of sites, based on the proportion of terrigenous sediment (Figure 3.6). The stress value (0.18) of the MDS plot was relatively high, suggesting that it does not give a very accurate visual representation of inter-site differences. Nonetheless, differences in coral species composition among sites were significant (ANOSIM, P = 0.005)

The SIMPER analysis identified 15 different coral species which, together, contributed 90% of the dissimilarity between low and high terrigenous groups (Table 3.3). *Montastrea annularis* complex was the taxon that contributed the most to differences between groups, followed by *Porites porites*; both were more abundant at sites with sediment of low terrigenous content (Table 3.3).

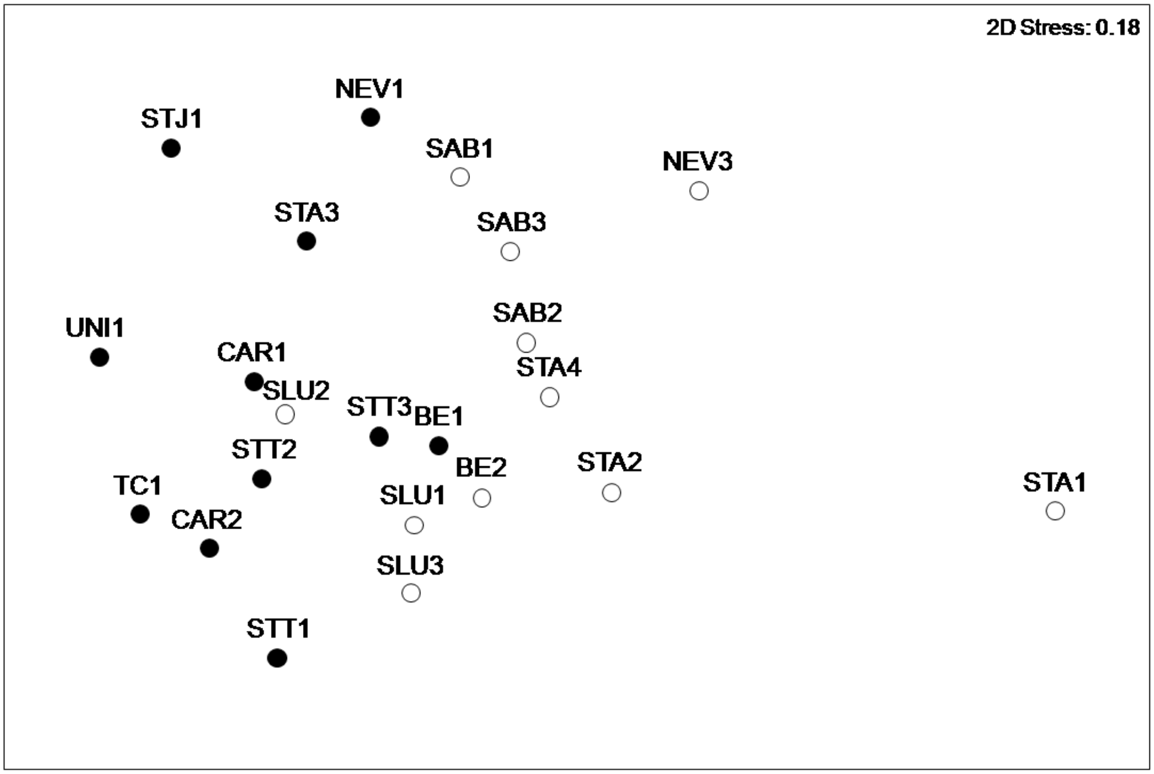

Figure 3.6. Non-metric multi-dimensional scaling plot of eastern Caribbean fringing reef sites based on the similarity (Bray-Curtis on square-root transformed percent cover) of coral species composition. Solid circles represent sites with sediments containing a low (0-14%) terrigenous fraction, open circles sites with a high (29-95%) terrigenous fraction. Site codes are given in Table 3.1

Mixed-effects models were fitted to explain inter-site variation in percent cover of the 10 coral taxa that each contributed at least 5% to the dissimilarity between groups (Table 3.3). Of those, the only significant relationship involved *Montastrea annularis* complex, whose cover decreases at sites with increasing terrigenous fraction. The generalized least-square model with island/site correlation provided the best fit (Figure 3.7; Table 3.3).

There were no significant differences in species composition between sites with high and low proportion of fine-grained sediment (ANOSIM, P = 0.27).

Table 3.3. Summary of results from a Similarity Percentage (SIMPER) analysis of coral cover at 22 eastern Caribbean sites, grouped according to terrigenous fraction in surface sediment (low: 0-14%; high: 29-95%). Mean percent cover of coral taxa contributing cumulatively to 90% of the dissimilarities in coral community composition between the two groups are shown. Standard errors are given in parentheses

Species	% cover at low terrigenous sites	% cover at high terrigenous sites	Individual contribution (%)	Cumulative contribution (%)
Montastraea annularis complex	3.77 (1.06)	1.21 (0.32)	13.82	13.82
Porites porites	1.75 (0.76)	0.23 (0.09)	11.54	25.36
Montastraea cavernosa	0.77 (0.26)	1.08 (0.24)	7.33	32.69
Porites astreoides	1.91 (0.39)	1.50 (0.39)	7.1	39.79
Siderastrea siderea	0.98 (0.26)	1.16 (0.20)	6.18	45.97
Millepora alcicornis	0.22 (0.05)	0.60 (0.28)	6.15	52.12
Colpophyllia natans	0.48 (0.13)	0.19 (0.08)	6.03	58.15
Meandrina meandrites	0.14 (0.07)	0.38 (0.14)	5.87	64.02
Diploria strigosa	0.31 (0.15)	0.32 (0.08)	5.53	69.56
Madracis mirabilis	0.31 (0.13)	0.10 (0.06)	5.27	74.82
Agaricia agaricites	0.23 (0.09)	0.03 (0.01)	4.36	79.18
Diploria labyrinthiformis	0.09 (0.05)	0.14 (0.07)	3.61	82.79
Dichocoenia stokesii	0.01 (0.01)	0.10 (0.05)	2.92	85.71
Madracis dedactis	0.09 (0.04)	0.03 (0.02)	2.77	88.48
Siderastrea radians	0.04 (0.02)	1.16 (0.20)	2.72	91.2

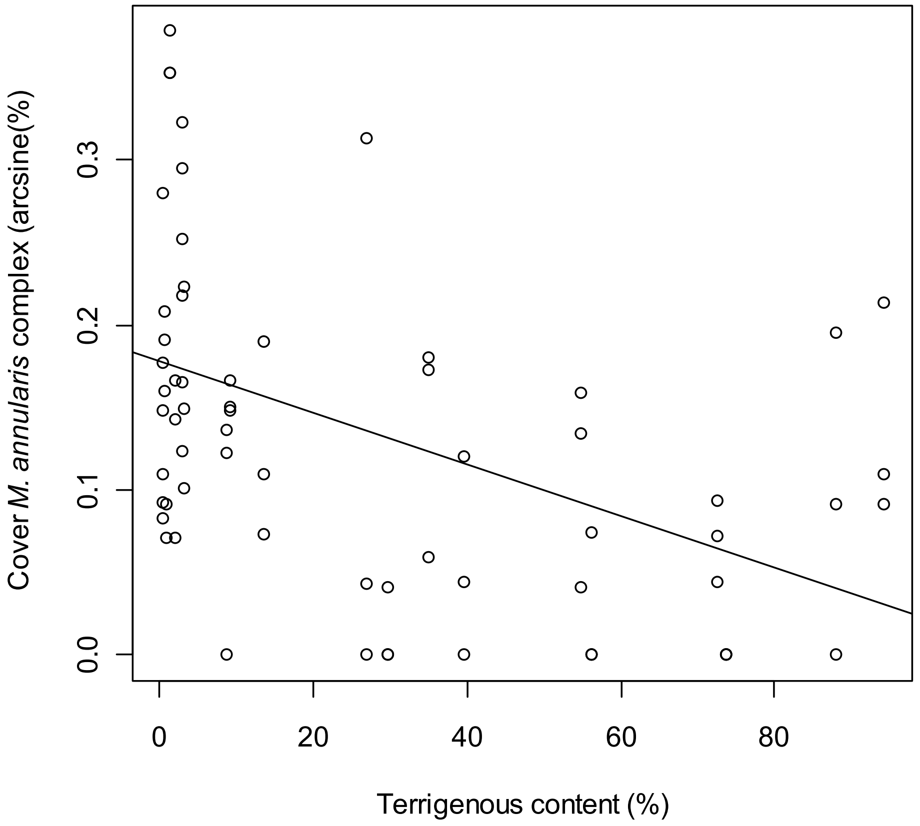

Figure 3.7. Percent cover (arcsine transformed) of* Montastrea annularis *complex in relation to the proportion of terrigenous sediment on fringing reefs around 11 eastern Caribbean islands. The solid line represents the best fit of a generalized least-square model with site/island correlation structure (see Methods)

Discussion

The benthic composition of fringing coral reefs across the 1,200-km-long eastern Caribbean island chain varied with the proportion of terrigenous sediment found near these reefs. The cover of coral, macroalgae and turf algae was lower on reefs where surface sediment had a high terrigenous fraction, while sponge cover was higher. Moreover, there were significant differences in coral species assemblages between sites of high and low proportion of terrigenous sediment. By contrast, benthic composition did not vary with the proportion of fine-grained sediment on the reef. This study is the first to uncover a large-scale association between sediment characteristics and coral reef composition.

I used an unconventional method to assess terrestrial sediment influence in this study: the collection of surface sediment located immediately adjacent to reefs. A link between levels of terrigenous material in surface sediment and runoff from land has been shown in a variety of settings and at various scales in coastal waters around the world (Subba Rao 1958; Maxwell and Swinchat 1970; Orpin et al. 2004; Perry and Taylor 2004; Badran and Al Zibdah 2005). I confirm this link for reef-associated sediments in the eastern Caribbean. Surface sediment samples from multiple stations in Saba showed a marked increase in terrigenous fraction near and downstream of a quarry. It should also be noted that the Greer Gut site, where surface sediment was sampled during a reef survey in 2009 and which is ~740 m east (upstream) of the nearest sampling station, showed lower levels of terrigenous material than all other stations in Saba, which is consistent with this east-west trend. Similarly, surface sediment near two rivers in Saint Lucia generally showed higher terrigenous content closer to the mouth of the rivers. Nevertheless, sediment composition reflects both sediment transported from land and that produced on or near the reef. Because sediment characteristics are influenced by the type of reef growth in an area (Netto et al. 2003), a higher proportion of terrigenous sediment may indicate not only increased runoff from land, but also a less extensive reef development (i.e., less calcium carbonate produced *in situ* to dilute the terrigenous fraction). Geographical variation in reef extent could therefore confound any cross-island comparisons of sediment composition. However, across the 11 islands sampled in the present study, there was a relationship between topography (measured as the ratio of maximum elevation to surface area – a proxy for slope) and mean terrigenous fraction (P=0.012), with more terrigenous-rich sediment around more steeply-sloped islands. Unless steep islands consistently have less extensive reefs, this relationship supports the idea that the differences in sediment composition observed here are largely due to differences in terrestrial input.

Reefs with a high proportion of terrigenous sediment, reflecting a large terrestrial influence, had lower coral cover and different assemblages of coral species. Low coral cover was expected given the negative responses of corals to sediment in small-scale laboratory and field studies (Dodge et al. 1974; Rogers 1983; Rogers 1990; Nemeth and Nowlis 2001). Interestingly, differences in coral species composition between sites with sediment of high and low terrigenous fractions were due to small changes in many different species (i.e., 15 species contributing to 90% of dissimilarity) rather than large changes in few species. Nevertheless, *Montastraea annularis* complex was the most important taxon in determining differences in coral species assemblages between sites with sediment of high and low terrigenous content, and the only taxon to vary significantly in cover with varying proportion of terrigenous sediment. The results are generally consistent with previous studies suggesting that *Montrastrea annularis* complex is sensitive to sedimentation (Hubbard and Pocock 1972; Rogers 1983; Acevedo et al. 1989; Torres and Morelock 2002). Other species, such as *Madracis mirabilis*, *Agaricia agaricites* and *Colpophyllia natans*, are also known to be negatively affected by sedimentation (Bak 1978; Nugues and Roberts 2003), and their cover was lower on reefs with more terrigenous sediment in this study. In contrast, several coral species (*Montastrea cavernosa*, *Siderastrea siderea*, *Meandrina meandrites*, *Diploria* *strigosa*, *D. labyrinthiformis*, *Dichocoenia stokesii* and *S. radians*) and the hydrozoan *Millepora alcicornis* were more abundant at sites with higher terrigenous sediment. *S. siderea* and *D. strigosa* have been suggested to be resistant to sedimentation (Mallela et al. 2004), which is consistent with my results, but *M. meandrites* has previously been categorized as sensitive to sedimentation (Hubbard and Pocock 1972). However, the latter conclusion stems from direct applications of sediment to the coral surface and not from field observations of distribution in relation to sediment composition. Shifts in coral species assemblages under varying sediment regimes have also been reported in Kenya (McClanahan and Obura 1997), which highlights the importance of monitoring the cover of individual coral taxa, in addition to overall abundance.

The extent of macroalgae, turf algae and sponge cover was also associated with the proportion of terrigenous material present around eastern Caribbean reefs. Macroalgae have shown variable responses to sedimentation. For example, growth, recruitment and survival of the macroalga *Sargassum microphyllum* decreased with increased sediment load (Umar et al. 1998), but macroalgae were more abundant on reefs with higher sediment trap accumulation rates in Saint Lucia (Nugues and Roberts 2003). Similarly, cover of turf algae was unaffected by sedimentation on Kenyan reefs (McClanahan & Obura 1997), while it was greater at higher trap accumulation rates in Saint Lucia (Nugues and Roberts 2003). In the present study, the cover of both groups of algae was lower at increasing proportions of terrigenous sediment. These apparently conflicting results may be due to differences in scale (i.e., intra- vs inter-island), as well as differences in the measure of sediment (overall or trap accumulation rate vs proportion of terrigenous sediment). The response of algae to sediment, like that of coral, is likely to vary by species, which may also explain the variable results from past studies.

Nevertheless, the negative relationship between terrigenous sediment and overall cover of macroalgae and turf algae shown here across multiple islands suggests that algae may not necessarily fill the space left by disappearing corals. Finally, reefs with high proportion of terrigenous sediment had higher cover of sponges. A similar pattern of higher sponge cover at sites with higher sedimentation rates has been found in Indonesia (Bell and Smith 2004) and in the Columbian Caribbean (Zea 1994). Decreases in the cover of sediment-intolerant benthic organisms may reduce competition for space, allowing sponges to increase in cover. Sedimentation may also change the community composition of sponges (Bell & Smith 2004) towards fast-growing encrusting or boring species (Carballo 2006), which may have negative repercussions on corals through competitive interactions (e.g. Aerst & VanSoest 1997). Indeed, increases in clionid sponges have occurred concurrently with declines in coral cover in the Florida Keys (Ward-Paige et al. 2005). Interestingly, all three functional groups that decreased with increasing proportion of terrigenous sediment here are photosynthetic, suggesting that increased turbidity associated with higher runoff could be an important mechanism causing these patterns.

The proportion of terrigenous sediment did not covary with the proportion of fine-grained sediment (< 63 microns) across the reef sites surveyed. Sediment with low terrigenous content had a highly variable fine-grained fraction (0 to ~18%), while sediment samples with a negligible fine-grained fraction also varied greatly in terrigenous content (0 to nearly 100%). This result indicates that, at least for the eastern Caribbean, the amount of fine-grained (< 63 microns) sediment is a poor index of sediment of terrestrial origin, and its use as such (e.g., Nemeth and Nowlis 2001) could lead to inaccurate estimates of terrigenous sediment input. In addition, no relationship was found between overall benthic composition or coral species composition and the proportion of fine-grained sediment. Fine-grained sediment has been shown to induce more stress than larger-grained particles in at least one species of coral (Weber et al. 2006) and, for this reason, it has sometimes been specifically monitored in addition to overall sedimentation loads (Smith et al. 2008). However, stress caused by sediment of different grain sizes varies by species in Caribbean corals, with some being sensitive to small grain sizes and others to larger grain sizes (Hubbard and Pocock 1972). The lack of any observed effect of sediment grain size in the present study could be due to the relatively low proportion of fine-grained sediment in my samples (maximum: 18%), which may be below the threshold needed to induce a detrimental effect.

Sedimentation composition appears to play a geographically consistent role in modifying coral reef communities in the eastern Caribbean, and perhaps more broadly across the Caribbean region. The relationships between sediment characteristics and reef composition uncovered in this study are admittedly correlational, and potential covariates of sedimentation were not controlled or measured. However, the association between the terrigenous fraction of sediment and several aspects of benthic composition (including coral cover) is a first indication that simple analyses of surface sediment may be a suitable approximation of terrigenous sediment stress to a given reef. This finding has important implications for coral reef monitoring programs which may operate on small budgets and with a limited capacity. Moreover, the facts that the relationship between terrigenous content of surface sediment and coral cover was only marginally significant ($P=0.046$; with confidence interval overlapping non-significant values in the error propagation analysis), and that many coral species increased in cover with increases in the terrigenous content of surface sediment, suggest that it is important to consider changes in coral communities as well as overall coral cover when monitoring ecological changes on coral reefs along a gradient of sedimentation input.

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Chapter 4.

Temporal trends in terrigenous sediment input near eastern Caribbean reefs

Abstract

Increased sedimentation due to coastal development is considered an important threat to coral reefs. However, the field techniques most commonly used by reef ecologists to measure sediment input have been acknowledged to be largely inadequate. Changes in sediment supply and storage have been identified in many coastal settings using sediment cores, yet the method has seldom been used near coral reefs. Here, I apply this technique to investigate changes in sediment input over time near 15 reefs across five eastern Caribbean islands. Cores collected near clear sources of sediment showed a significant increase in input of non-calcareous material (proxy for terrigenous input) over time, while those in areas of low input or further from a source did not. ^{210}Pb dating on cores in Saint Lucia showed high mass accumulation rates for this environment of up to 1.22 $g*cm^{-2}*year^{-1}$. A slight increase in mass accumulation rates over the past 4 decades was mainly driven by an increase in accumulation of terrigenous sediment. These results indicate that there has been an increase in the accumulation of terrigenous sediment on the coral reefs of several Caribbean islands, likely as a result of enhanced erosion in upstream watersheds.

Introduction

Anthropogenic activities that disrupt natural vegetation can greatly increase erosion rates in watersheds and sediment yields to downstream coastal ecosystems (Neil et al. 2002, Syvitski et al. 2005, Wilkinson and McElroy 2007). Volcanic islands in the tropics are at particularly high risk of accelerated erosion due to a combination of factors. Many islands experience high precipitation rates and have small but high-gradient watersheds (Milliman and Syvitski 1992, Dearing and Jones 2003), and several have undergone rapid development in the last several decades, resulting in documented increases in sediment yield (Rawlins et al. 1998; Ramos-Scharrón and MacDonald 2005; Ryan et al. 2008; Mallela et al. 2010). Such islands are often ringed by fringing coral reefs, and increased sedimentation is recognized as an important stressor to coral communities (Rogers 1990, Torres 2001, Fabricius et al. 2005, Hawkins et al. 2006). Globally, coral cover on reefs has declined markedly in the past 30 years (Gardner et al. 2003, Bruno and Selig 2007). Understanding the factors driving coral reef degradation is important not only for intrinsic conservation reasons, but also because coral reef ecosystems provide an important source of food to millions of people (Spalding 2004, Burke et al. 2011) and are the basis of expanding tourism industries, which are the most important economic activity on many tropical islands (Carr and Heyman 2009).

Despite the recognized impact of sedimentation on corals, there remains a surprisingly limited understanding of recent (i.e. decadal) changes in sediment accumulation rates in any region of the world. Coral reef ecologists have typically measured sedimentation rate using traps (Hodgson 1989, Edinger et al. 1998, Nemeth and Nowlis 2001, Torres 2001, Torres et al. 2001, Nugues and Roberts 2003, Mallela et al. 2004, Wielgus et al.

2004, Wilson 2005, Dikou and van Woesik 2006, Dutra et al. 2006, Done et al. 2007, Fisher 2007, Fisher et al. 2008, Smith et al. 2008). Sediment traps have many recognized flaws (Gardner 1980, Storlazzi et al. 2011) and they provide data only for the time period during which they are monitored. Sediment traps therefore are of limited use to establish long-term changes in sedimentation regime. In contrast, sediment cores are eminently suitable for this purpose. Cores are commonly employed to investigate sedimentary processes over time in various environments, through stratigraphic and radioisotope dating analysis (Patchineelam and Smoak 1999, Crusius et al. 2004, Sanders et al. 2006).

Accumulation rates in coastal sediment cores can be measured using short-lived radioisotopes (SLR) such as ^{137}Cs and ^{210}Pb as date markers (Cochran et al. 1998, Holmes 1998, Draut et al. 2009). Cesium-137 was added to the environment by nuclear-weapon testing that began around 1952 and peaked in 1963. In a core with well-preserved stratigraphy, the ^{137}Cs profile is expected to mimic production, with a peak in ^{137}Cs activity associated with sediment deposited in 1963 (Livingston and Bowen 1979, Smith and Ellis 1982, Holmes 1998). Lead-210 is a naturally-occurring daughter product in the ^{238}U decay series, and from the atmosphere gets adsorbed to and incorporated into depositing sediment (Holmes 1998). It has a half-life of 22.3 years. Excess ^{210}Pb (i.e., in excess of equilibrium activity supported by parent isotopes) characterizes sediment deposited within the past ~100 years (Holmes 2001) and can be used to model rates of sediment accumulation and mixing (e.g., Nittrouer et al., 1979; Crusius et al., 2004). ^{210}Pb and ^{137}Cs have recently been used to assess variations in sedimentation near coral reef ecosystems in US territories in Hawaii (Draut et al. 2009) and in the Caribbean (Brooks et al. 2007, Ryan et al. 2008), but their application in this environment is still limited (Ryan et al. 2008; however see Hubbard et al. (1990) and Palmer et al. (2010) for examples of the use of radiocarbon to date reef sediment on a time scale of millennia).

In addition to providing information on sedimentation rates, sediment cores allow the examination of changes in sediment composition over time (Wilson and Lokier 2002, Palmer et al. 2010). Sediments near many coral reef ecosystems are composed of marine-derived calcareous deposits and terrestrial-derived non-calcareous material, with small amounts of organic material (Brooks et al. 2007, Palmer et al. 2010). The proportion of non-calcareous material is often used as a proxy for terrigenous sediment input (Torres 2001, Ryan et al. 2008, Alonso-Hernandez et al. 2011). Provided stable input of calcareous material, analysis of sediment composition along the length of a core is an inexpensive way to monitor changes in terrigenous sediment accumulation over time.

In this study, I use sediment cores collected near fringing reefs throughout the eastern Caribbean to investigate changes in sedimentation over time. The small and steep volcanic islands in this region are at high risk of increased erosion owing to coastal and watershed development. I first ask if the proportion of terrigenous material that reaches fringing reefs has changed over time, and if any pattern of change can be related to land development on the nearby island. Second, I use SLR dating in two cores to assess changes in sediment accumulation rate over time at two reef sites in Saint Lucia. Quantifying changes in sedimentation patterns that have occurred directly on coral reefs is critical to better understand the effects of watershed development on corals in this region.

Methods

Sediment core sampling

Sediment cores were taken at 15 sites on five islands between October 2009 and March 2010 (Figures 4.1 and 4.2). Coring sites were chosen based on ease of access and proximity (< 50 m) to a fringing coral reef. Sites were at least 200 m apart. At each site, cores were obtained with a diver-operated slide-hammer corer (Aquatic Research Instruments) at 8-15 m water depth. The polycarbonate core barrel had an internal diameter of 69 mm. Recovered core lengths varied between 18 and 42 cm, depending on substratum hardness. Once collected, cores were kept upright and extruded in 1cm increments into Whirl-Pak® plastic bags immediately following their collection.

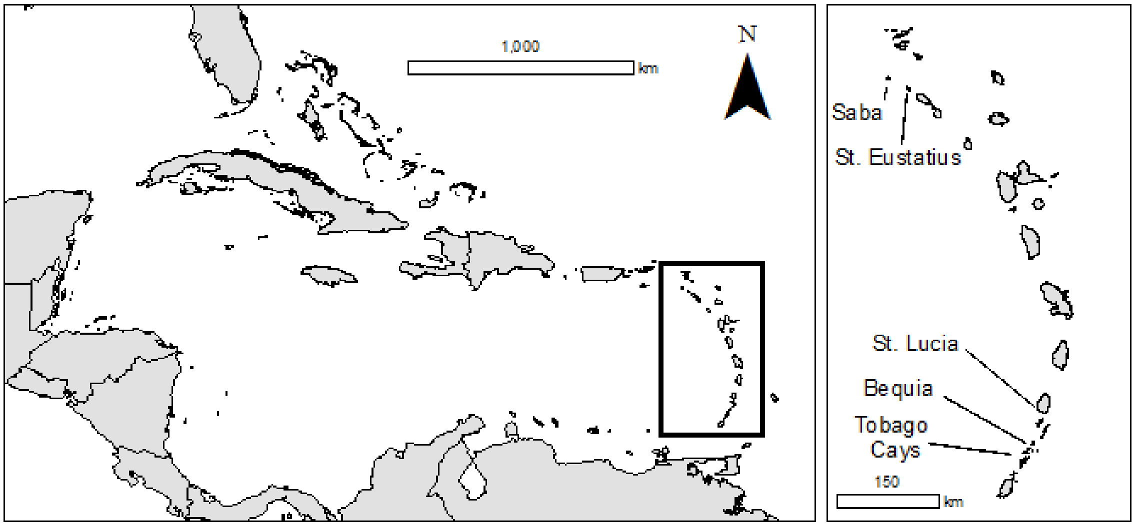

Figure 4.1. Map of Greater Caribbean region (left panel) and Eastern Caribbean islands (right panel; enlarged from left) where sediment cores were collected

Due to time constraints, only one core was sampled at a given site. As is commonly done in similar studies (Brooks et al. 2007, Ryan et al. 2008), I chose to allocate available resources to sample multiple sites rather than replicate cores at one site.

Previous analyses indicate little small-scale (< 10 m), spatial variation in the terrigenous content of surface sediment (coefficient of variation ~ 5%; Chapter 3).

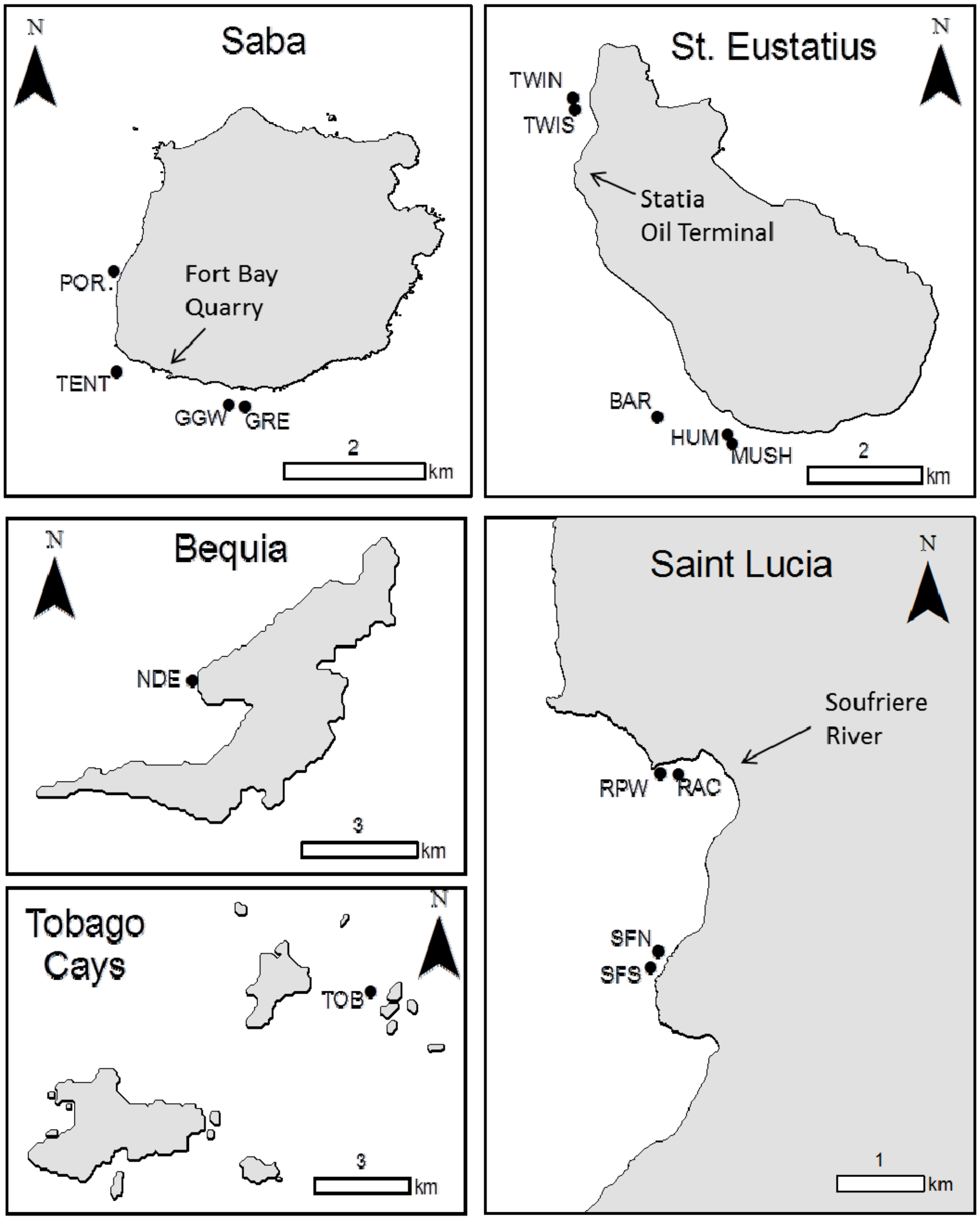

Figure 4.2. ***Location of sediment core sampling sites on the Caribbean islands of Saba, St. Eustatius, Saint Lucia, Bequia and the Tobago Cays. To keep the scales similar across maps, the map for Saint Lucia is focused around the town of Soufriere, on the southwest coast.***

Terrigenous content

Terrigenous content analyses were performed on alternate extruded layers (i.e., every other cm) of the core; approximately half of the amount collected in each layer was used for these analyses. Each subsample was rinsed twice with distilled water to remove salts and decanted, then dried to constant weight at 70 ^{o}C. Samples were weighed and then treated with a 10 % hydrochloric acid solution to dissolve all the carbonates. Samples were dried again and reweighed. The remaining sediments can be assumed to be terrigenous (Torres and Morelock 2002, Brooks et al. 2007). The proportion of terrigenous sediment was calculated by dividing the weight of the terrigenous fraction by the weight of the subsample prior to treatment with hydrochloric acid. Organic content was assessed by treatment with sodium hypochlorite (Torres and Morelock 2002) and in all samples was less than 1% by weight.

Short-lived radioisotope dating

SLR analyses were conducted on two cores: Rachette Point West (RPW) and Superman's Flight South (SFS), sites to the north and south, respectively, of the Soufriere River (Figure 4.2). This river receives input from a 15 km^2 watershed and is the largest river in the vicinity of the Soufriere Marine Management Area, a network of small marine protected areas on the south west coast of Saint Lucia. The high cost of SLR analyses prevented us from dating more cores. Note that many studies have successfully characterized sedimentation history at a site based on radioisotope analyses from a single core (Cochran et al. 1998, Vaalgamaa and Korhola 2004, Lima et al. 2005, Yasuhara and Yamazaki 2005, Ruiz-Fernandez et al. 2009).

Samples were analyzed for activities of ^{210}Pb every 1-2 cm over the upper 12 cm of each core, and at 3-4 cm intervals in the deeper sections. The ^{210}Pb profile was used to calculate age and mass accumulation rate using the Constant Rate of Supply (CRS) model (Binford 1990). The terrigenous mass accumulation rate was obtained by multiplying total mass accumulation rate by terrigenous fraction in each sample. Activities of ^{137}Cs were measured in four or five samples from the sediment cores: at 1, 5, 11 and 19 cm for core SFS and 1, 10, 20, 25 and 36 cm for core RPW. SLR analyses were conducted by Flett Research Ltd, in Winnipeg, Canada.

Statistical Analyses

Change in terrigenous content over time in each core was analyzed using linear regression. The interpretation of those results is challenging because multiple tests increase the probability of finding significant results. The increased likelihood of type I error in the interpretation of multiple P-values has traditionally been corrected with the Bonferroni method, which inevitably increases the likelihood of committing type II errors (Perneger 1998). I used an alternative method, the false discovery rate (FDR), which controls the rate at which null hypotheses are falsely rejected rather than safeguarding against any false rejections, thereby offering a good balance between the risk of type I and type II errors. With my alpha value of 0.05, this means that 5% of my post-FDR significant results can be expected to be the result of chance alone. FDR has been advocated as the optimal solution for multiple comparisons in ecology (Garcia 2004, Verhoeven et al. 2005, Waite and Campbell 2006). For each of the15 significance tests I calculated the FDR-adjusted significance threshold (α_{FDR}) using the adapted linear step-up procedure (Benjamini et al. 2006) and report the q-value (FDR-adjusted P-value (Pike 2011). Linear regressions were carried out with PASW Statistics 18 software.

Results

Terrigenous content

The mean proportion of non-calcareous sediment in the cores ranged from less than 2 % in the Tobago Cays to 93 % at Tent Point in Saba (Figure 4.3). There was no evidence of bioturbation in the cores collected. Most cores exhibited an up-core increase in the proportion of non-calcareous sediment, indicating a relative increase in terrigenous sediment over time. This trend was significant in a linear regression in 6 of the 15 cores (Table 4.1; Figure 4.4). The slope of the relationship between terrigenous content and depth was most pronounced at Twin Sisters North (Saint Eustatius) followed by Superman's Flight North (Saint Lucia) (Table 4.1). Interestingly, two cores collected near one another in Saint Lucia showed different profiles. The deeper one (RAC, 15 m, Figure 4.4) showed a steady increase in non-calcareous content over time, while the shallower one (RPW, 8 m) showed no significant change (Table 4.1).

Short-lived radioisotope dating

SLR analyses were carried out on cores RPW and SFS. Neither core showed detectable levels of ^{137}Cs, which indicates that they are either too modern to have been exposed to the ^{137}Cs peak in 1963, or that the ^{137}Cs was not incorporated in these sediments. Mass accumulation rates (MAR) therefore had to be estimated with ^{210}Pb alone.

The RPW core showed an ideal ^{210}Pb profile for age estimation (Figure 4.5). The CRS model estimated variable accumulation rates with an average of 0.91 $g*cm^{-2}*year^{-1}$and a maximum of 1.22 $g*cm^{-2}*year^{-1}$ (Figure 4.6). The age at the bottom of the core (36 cm deep) was estimated at 41.4 years. The terrigenous mass accumulation rate varied from

0.64 g/cm^2/year to 1.04 g*cm^{-2}*year^{-1}, with a mean of 0.78 g*cm^{-2}*year^{-1} (Figure 4.6). Accumulation rates, both total and for the terrigenous fraction, generally increased over time, though these increases were not significant (linear regressions: total MAR, P = 0.195; terrigenous MAR, P = 0.236).

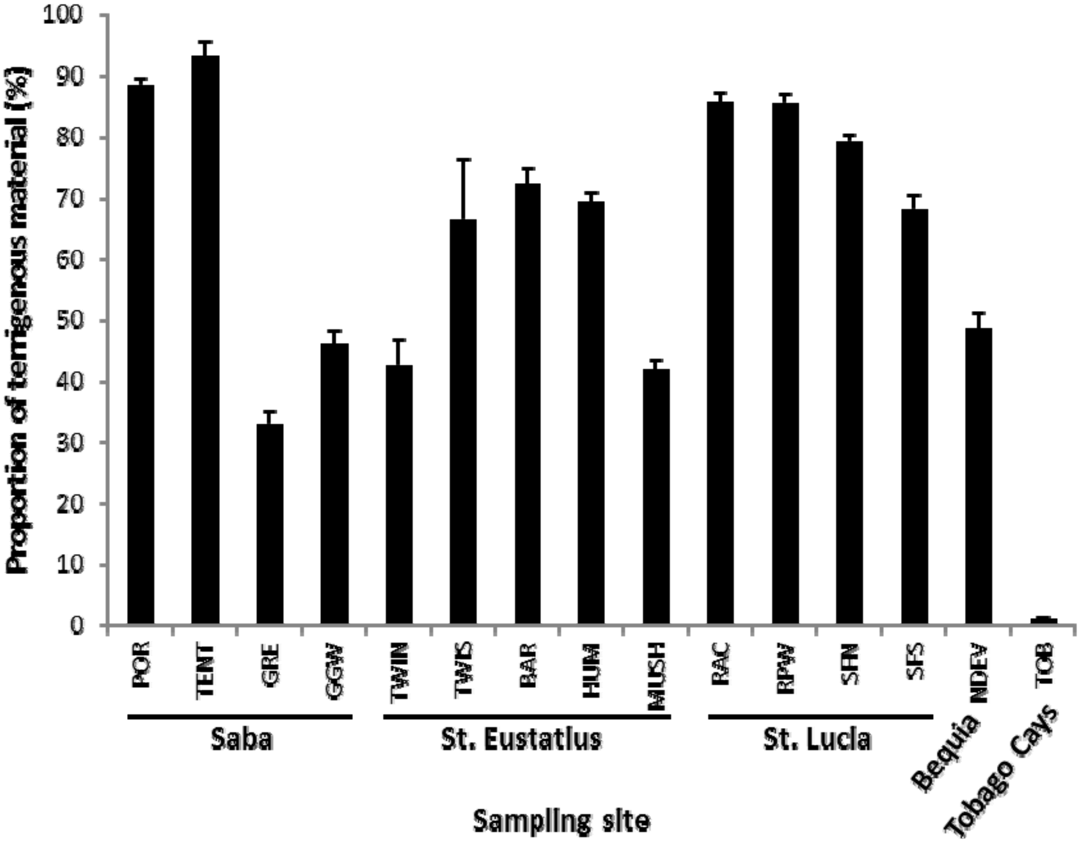

Figure 4.3. Overall mean (± 1 SD) proportions of non-calcareous sediment in cores taken near coral reefs at 15 sites near five eastern Caribbean islands. Sites are arranged by island, and islands are ordered from north to south. Sample sizes varied from 8 to 21, depending on core length.

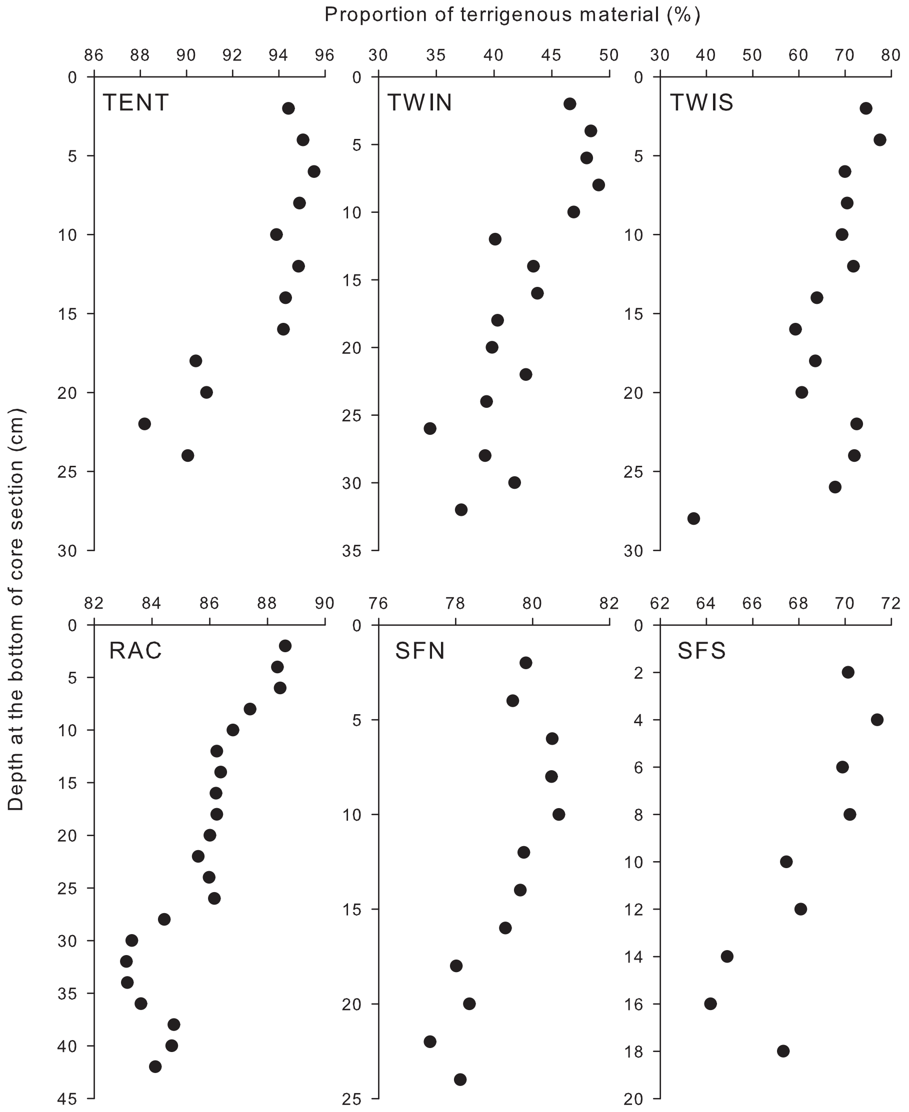

Figure 4.4. Proportion of terrigenous sediment in relation to depth of core, for all cores that show a significant increase over time (see Table 4.1). Site names are given in Table 4.1. Axes vary among cores.

Table 4.1. Equations and summary statistics for the linear regressions relating the proportion of terrigenous material (y, in %) to depth in core (x, in cm) for each core analyzed, where "q" represents the FDR-adjusted P-value. Significant regressions (q <0.05) are denoted with a *. Water depth (in m) at each sampling site is also given.

Island	Site	Water depth	Code	Regression equation	R^2	q	N
Saba	Porites Point	15	POR	y = -0.0246x + 88.824	0.02	0.52	10
Saba	Tent Point	16	TENT	y = -0.2873x + 96.785	0.71	0.004*	12
Saba	Greer Gut (2009)	20	GRE	y = -0.1182x + 34.844	0.221	0.11	15
Saba	Greer Gut (2010)	20	GGW	y = -0.1273x + 47.902	0.22	0.12	13
Statia	Twin Sisters (2009)	17	TWIN	y = -0.694x + 76.89	0.342	0.049*	16
Statia	Twin Sister (2010)	17	TWIS	y = -0.3743x + 48.933	0.682	<0.001*	14
Statia	Barracuda	18	BAR	y = -0.0438x + 73.243	0.04	0.34	21
Statia	Humps	13	HUM	y = -0.0702x + 70.563	0.17	0.12	16
Statia	Mushroom	15	MUSH	y = -0.1578x + 43.275	0.22	0.23	8
Saint Lucia	Rachette Point	15	RAC	y = -0.123x + 88.402	0.80	<0.001*	21
Saint Lucia	Rachette Point West	8	RPW	y = 0.0075x + 85.499	0.003	0.58	18
Saint Lucia	Superman's Flight (2009)	10	SFN	y = -0.1219x + 80.882	0.64	<0.001*	12
Saint Lucia	Superman's Flight (2010)	15	SFS	y = -0.375x + 71.923	0.69	0.01*	10
Bequia	Devil's Table North	10	NDEV	y = -0.0775x + 49.551	0.04	0.46	11
Tobago Cays	Petit Bateau	15	TOB	y = -0.0098x + 1.2366	0.15	0.12	20

In the SFS core, the ^{210}Pb profile was nearly vertical over the 19 cm length of the core (Figure 4.5). This could indicate significant mixing throughout the depth of sediment samples, either from water motion or bioturbation (though no evidence of bioturbation was seen during core sampling and extrusion). Alternatively, it could indicate that the sediments over the entire 17 cm of the core have accumulated over less than the 22.3-year half-life of ^{210}Pb. This second hypothesis would suggest a mean linear extension rate and total mass accumulation rate of at least 0.76 cm/year and 0.91 $g*cm^{-2}*year^{-1}$, respectively. Because this core contained on average 68 % terrigenous material, the terrigenous mass accumulation rate can be calculated as 0.62 $g*cm^{-2}*year^{-1}$.

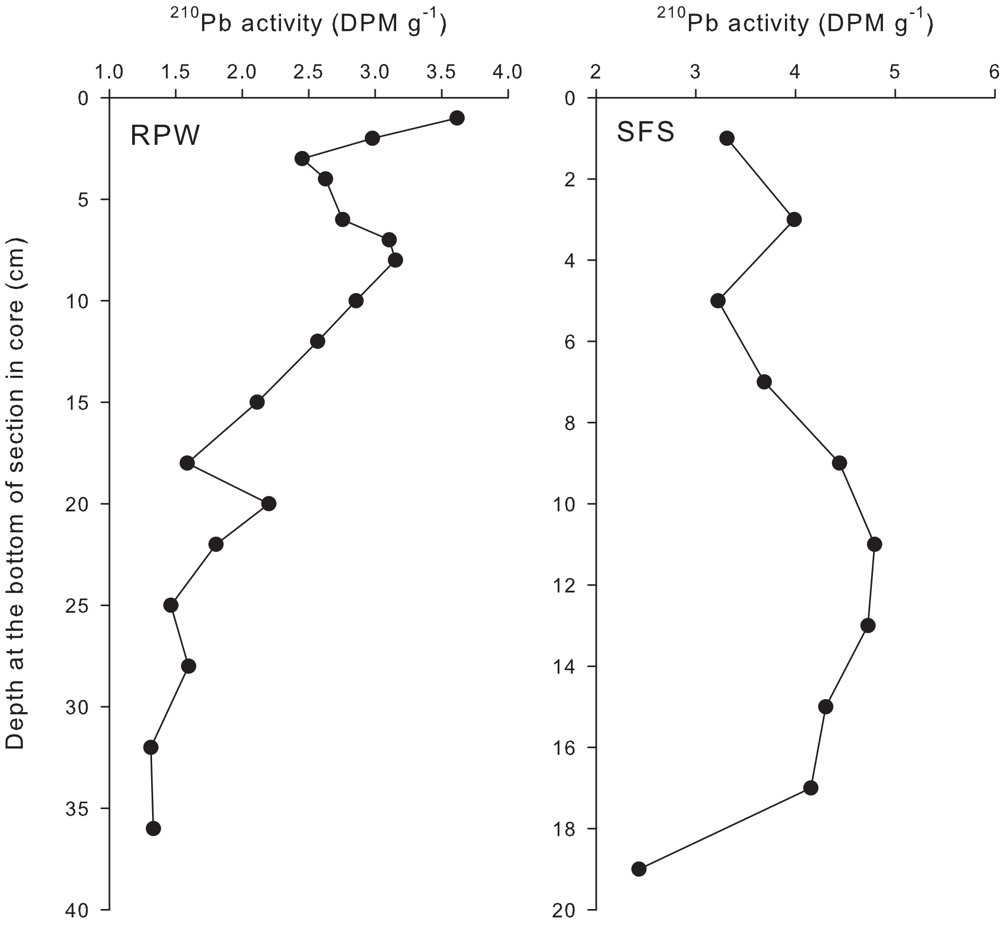

Figure 4.5. Activity of ^{210}Pb in sediment cores taken at Rachette Point West (RPW) and Superman's Flight South (SFS), in Saint Lucia

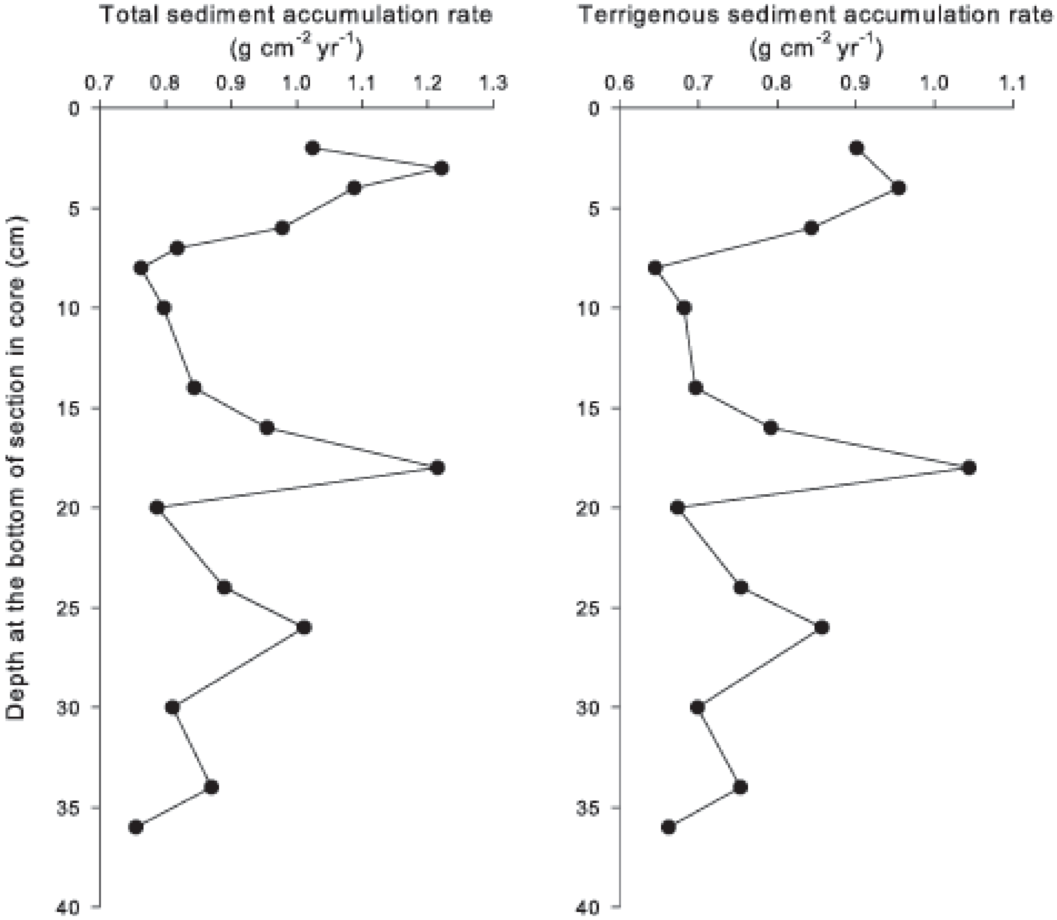

Figure 4.6. Mass accumulation rate for all sediment and for terrigenous sediment only, in relation to depth in core, for a core (RPW) taken near a coral reef just north of the Soufriere River, Saint Lucia

Discussion

Sedimentation rates near coral reefs in the eastern Caribbean region appear to have increased in the past decades, concomitantly with a change in sediment composition. I found temporal trends for increasing non-calcareous content of sediment – a proxy for terrigenous input – at six of the 15 reef sites studied. Radioisotope dating of one sediment core in Saint Lucia confirms that current sedimentation rates are high and above those recorded elsewhere in the Caribbean.

In coral reef settings, sediment composition has been shown repeatedly to be influenced by the amount of sediment input from land, which mixes with calcareous sediment of marine origin (Maxwell and Swinchat 1970, Orpin et al. 2004, Badran and Al Zibdah 2005). The absolute amount of marine calcareous sediment produced depends on the type and extent of reef development (Netto et al. 2003), thus a higher proportion of terrigenous sediment may indicate not only increased runoff from land, but also less extensive reef development (i.e., less calcium carbonate produced *in situ* to dilute the terrigenous fraction). Bearing this in mind, I found marked geographical variation in mean proportion of terrigenous material in sediment cores collected near coral reefs at 15 sites on five eastern Caribbean islands, spanning a distance of ~800 km. At one extreme, the core from the Tobago Cays (small and low-lying, uninhabited islands) showed less than 2 % terrigenous content over its entire length. At the other extreme, the core collected at Tent Point in Saba (a steep-sided island with coastal development) contained over 93 % of non-calcareous material. Fringing reefs were well developed, with similar levels of coral cover, around both islands (CB, unpublished data), suggesting that terrestrial factors are likely to be responsible for these extreme differences. In general, the levels of terrigenous material observed in this study were high for the region. For example, surface sediment in bays in Cuba and St. John (US Virgin Islands), and on fore-reefs in Puerto Rico, contained less than 25%, 20% and 10% terrigenous material, respectively (Brooks et al. 2007, Ryan et al. 2008, Alonso-Hernandez et al. 2011). By comparison, terrigenous content was higher than 25% at 14 of my 15 sites, and exceeded 50% at nine sites. This suggests higher delivery of terrigenous material on eastern Caribbean reefs compared to the US Caribbean islands and Cuba. This could be due to differences in precipitation, better erosion control or a more extensive development of mangroves, salt ponds and other sediment-trapping areas on the larger islands.

A change in terrigenous content of sediment over time at a site is strong evidence of a change in the amount of terrigenous input (Alonso-Hernandez et al. 2011). Nearly half of the cores collected in this study showed a significant increase in the proportion of terrigenous material over time, and all of those cores were taken from sites near a clear source of sediment. Tent Point (Saba; site TENT) is downstream of the Fort Bay quarry; Twin Sisters (Statia; sites TWIN, TWIS) is close to an oil terminal; and Superman’s Flight and Rachette Point (sites RAC, SFN, SFS) are both close to the Soufriere River, which drains a developed watershed (Figure 4.2). The cores collected in areas with little or no development (e.g., GRE, GGW, NDE and TOB), or further from a sediment source (e.g., POR, BAR, MUS, HUM, RPW), did not exhibit significant increases in terrigenous content over time. The association between shifting sediment composition and land disturbance appears to be a general phenomenon. For example, a similar increase in terrigenous content was observed in cores collected nearshore and on a back reef near the developing town of La Parguera, Puerto Rico, but not on the fore reef located a few kilometers away (Ryan et al. 2008). Increases in the proportion of terrigenous material has also been recorded in cores from Coral Bay, St. John, where a rapid increase in population was accompanied by large infrastructure and road developments (Brooks et al. 2007).

The analysis of cores taken at sites in relatively close proximity to each other suggests that sediment deposition on neighbouring reefs can vary substantially. There were differences in the overall terrigenous content (e.g. GGW vs. GRE, TWIN vs. TWIS) as well as in the change in terrigenous content over time (e.g., TWIN vs. TWIS, RAC vs. RPW) for some cores sampled within a few hundred meters of each other. Small-scale patterns in terrigenous sediment deposition to a reef may be controlled in part by bathymetry, storm events, current patterns and water energy (Hubbard 1992, Brooks et al. 2007). Thus, the discrepancy between cores at Rachette Point may be due not only to distance from the sediment source, but also to differences in depth of sampling (8 m for RPW, 15 m for RAC) and concomitant differences in water energy, which was likely higher for the shallower core at RPW, which was also nearer the headland. Deeper (and lower-energy) reefs tend to experience less resuspension and flushing, and therefore higher sedimentation rates, compared to shallower depth (Wolanski et al. 2005).

Based on ^{210}Pb dating, mass accumulation rates at our sites in Saint Lucia are high for a fore reef environment. Mean total mass accumulation rates (MAR) calculated with the CRS model for core RPW, which had an ideal ^{210}Pb profile, was 0.91 $g*cm^{-2}*year^{-1}$. This is considerably higher than the 0.15 $g*cm^{-2}*year^{-1}$reported in Coral Bay, St John (Brooks et al. 2007) based on ^{210}Pb profiles, and higher than the rates measured in three reef environments in Puerto Rico using the same method (nearshore: 0.42 $g*cm^{-2}*year^{-1}$; back reef: 0.39 $g*cm^{-2}*year^{-1}$; fore reef: 0.24 $g*cm^{-2}*year^{-1}$; (Ryan et al. 2008)). Mass accumulation rates in core RPW were highly variable from year to year and increased slightly, though non-significantly, over time. Yearly variability in MAR reflects large rainfall events as well as wave action from storms (Draut et al. 2009). Because this core was obtained at a fairly shallow (8m) depth, deposition is likely to have been more heavily influenced by wave action than for deeper cores. The terrigenous content of core RPW was also highly variable over time (R^2= 0.003, q = 0.58). It is likely that a better depositional record would be found in deeper cores, such as RAC which was collected nearby but at a depth of 15 m. Unfortunately, the results for core SFS need to be interpreted with care as ^{210}Pb levels remained similar throughout this core. If the nearly vertical profile is due to a high supply of sandy material rather than bioturbation, then the MAR in this core would be the same as for RPW. Estimated accumulation of terrigenous material is lower than that of RPW, which is consistent with a greater distance from the river mouth.

To my knowledge, this study is the first to derive sediment composition information and accumulation rates for recent decades from sediment cores taken in very close proximity to coral reefs. The history captured in these cores is therefore likely to reflect accurately the sedimentation stress experienced by corals. From a methodological perspective, my results indicate that well-preserved stratigraphy can be obtained from such cores and that short-lived radioisotopes can be used effectively as a dating tool in a coral reef environment. The success of this approach is likely to be enhanced by collecting cores on the deeper parts of the reef (~15 m), where wave action is lower and sediment grain size is smaller. From a conservation management perspective, my results show that the proportion of terrigenous material incorporated in near-reef sediment over time has increased significantly at sites near readily-identified sediment sources, but not at sites further away from terrigenous sediment input. This result points to local development as the source of increased terrigenous sediment, rather than long-distance transport from major inputs such as the Amazon or Orinoco rivers. The accumulation rates I estimated in Saint Lucia were considerably higher than any previously recorded near Caribbean islands. Both lines of evidence point towards a high level of sedimentation stress on eastern Caribbean reefs, but also towards clear solutions to the problem. Compared to many other threats to healthy coral reefs (e.g., disease, bleaching) which are exceedingly difficult to control, increased sedimentation is a local stressor, often with a clear source. New developments on small islands such as those in the eastern Caribbean inevitably occur near the coast. This is especially important in steep watersheds and areas with limited wetland development, where there is little natural redeposition of eroded soil. A greater emphasis on preventative measures to control run-off would benefit eastern Caribbean coral reefs.

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Chapter 5.

Effect of protection and sediment stress on coral reefs in Saint Lucia

Abstract

The extent to which Marine Protected Areas benefit corals is contentious. On one hand, MPAs could enhance coral growth and survival through increases in herbivory within their borders; on the other, they are unlikely to prevent disturbances, such as terrestrial runoff, that originate outside their boundaries. I examined the effect of spatial protection and terrestrial sediment on the benthic composition of coral reefs in Saint Lucia. In 2011, I resurveyed 21 reefs that had been surveyed in 2001 and analyzed current benthic assemblages as well as changes in benthic cover in the past decade in relation to protection status (in or out of marine protected areas) and terrestrial sediment influence (measured as the proportion of terrigenous material in reef-associated sediment). I included depth (5 and 15 m) as an additional factor. Benthic cover of all biotic components has changed significantly in the past decade, including a decline in coral and increase in macroalgae. Protection status was not a significant predictor of either current benthic cover or changes in the past decade, for any of the benthic components, whereas terrigenous content of sediment and depth were both significantly related to several components. Sites with a higher proportion of terrigenous sediment were associated with lower current coral cover, higher macroalgal cover and greater coral declines. My results suggest that terrestrial sediment is an important factor in the

degradation of coral reefs in Saint Lucia and that conservation efforts on this island need to incorporate measures to reduce runoff from land.

Introduction

In the past few decades, multiple threats have contributed to large declines in coral cover worldwide (Bruno and Selig 2007). This phenomenon has been especially dramatic in the Caribbean (Gardner et al. 2003), where the decline in coral has been associated on many reefs with an increase in macroalgae (Hughes 1994). Driving factors for this shift include direct impacts on coral from hurricanes, disease, bleaching and runoff, as well as the indirect impacts of the release of top-down control of macroalgae from overfishing of fish herbivores and mass mortality of the grazing black-spined sea urchin *Diadema antillarum* (Aronson and Precht 2006, Sotka and Hay 2009). A high cover of macroalgae reduces the space available for coral recruitment and the relative herbivory pressure per unit area, which may result in a positive feedback loop that helps maintain macroalgal dominance. The stability of the macroalgae-dominated state has been debated (Mumby 2009b), yet it is clear that a higher biomass of herbivores, which exert a stronger control on macroalgae, is beneficial to corals (Williams and Polunin 2001, Hawkins and Roberts 2004, Mumby 2009a). In this context, marine protected areas (MPAs), within which all extractive activities are banned, should have positive effects on coral through increases in herbivorous fish populations (Côté et al. 2001, Roberts et al. 2001, Kaunda-Arara and Rose 2004, Francini-Filho and de Moura 2008, Guarderas et al. 2011).

Nevertheless, whether protected or not, corals remain vulnerable to factors originating outside reserves such as runoff, storms, disease and increased water temperatures

(Jameson et al. 2002). While the latter three threats are virtually impossible to manage directly, runoff may be more easily controlled. The benefits to reef health of reducing runoff may be considerable given that sediment has been shown to decrease light available for photosynthesis, inhibit recruitment, reduce growth and cause stress and mortality to a wide variety of corals (Dodge et al. 1974, Rogers 1983, Hodgson 1990, Babcock and Davies 1991, Piniak and Brown 2008). Controlling runoff, particularly upland of marine protected areas, may be a sound management strategy to enhance coral cover, or at least reduce significantly its rate of loss.

In this study, I examine the effects of marine protection and terrestrial sediment on the benthic composition of coral reefs. I focused on the coral reefs of Saint Lucia, a small volcanic island in the eastern Caribbean, which is at high risk of accelerated erosion owing to its small, steep watersheds with high precipitation rates (Milliman and Syvitski 1992, Dearing and Jones 2003). A series of small no-take MPAs, known as the Soufriere Marine Management Area (SMMA), was created in 1995 on the west coast of the island. These MPAs have a high level of compliance (Roberts et al. 2001), and within six years of establishment, total biomass of fishes had quadrupled inside the reserves and tripled outside the reserves, with the greatest increase observed for herbivores (Hawkins et al. 2006). However, the initial benefits of the SMMA did not extend to coral, which decreased in cover by 35-46% over this period, owing to disease (in 1997), bleaching (in 1998), hurricane damage (in 1999) and chronic sedimentation stress from the Soufriere River (Nugues 2002, Schelten 2002, Nugues and Roberts 2003). Another no-take MPA – the Canaries-Anse-La-Raye Marine Management Area (CAMMA), was created in 2001, 10 km north of the SMMA. The long-term effect (> 6 years) of the SMMA and the CAMMA on coral has not yet been documented.

I specifically asked whether (1) current benthic composition on St Lucian reefs and (2) the changes, both absolute and relative, observed in the cover of major benthic groups over the last 10 years vary in relation to protection and terrestrial influence. To answer these questions, I revisited in 2011 multiple sites located in and out of MPAs, which were surveyed a decade ago (Schelten 2002). To evaluate terrestrial sediment stress, I sampled surface reef sediment and measured the proportion of terrigenous (non-calcareous) material in this sediment. Surface sediment composition has been shown to reflect input of terrestrial sediment in a variety of settings (Subba Rao 1958, Maxwell and Swinchat 1970, Orpin et al. 2004, Perry and Taylor 2004, Badran and Al Zibdah 2005), including coral reefs in the eastern Caribbean (Chapter 3).

Methods

Study area

Coral reef surveys and sediment sampling were carried out on the west coast of Saint Lucia, in the eastern Caribbean (Figure 5.1). Saint Lucia has a steep terrain and depth increases quickly with distance from shore. Fringing reefs are the typical reef formation around the island, and the only type of coral reef surveyed in this study. Twelve of the survey sites were located inside effective marine protected areas, either within the Soufriere Marine Management Area (SMMA) or the Canaries-Anse-La-Raye Marine Management Area (CAMMA).

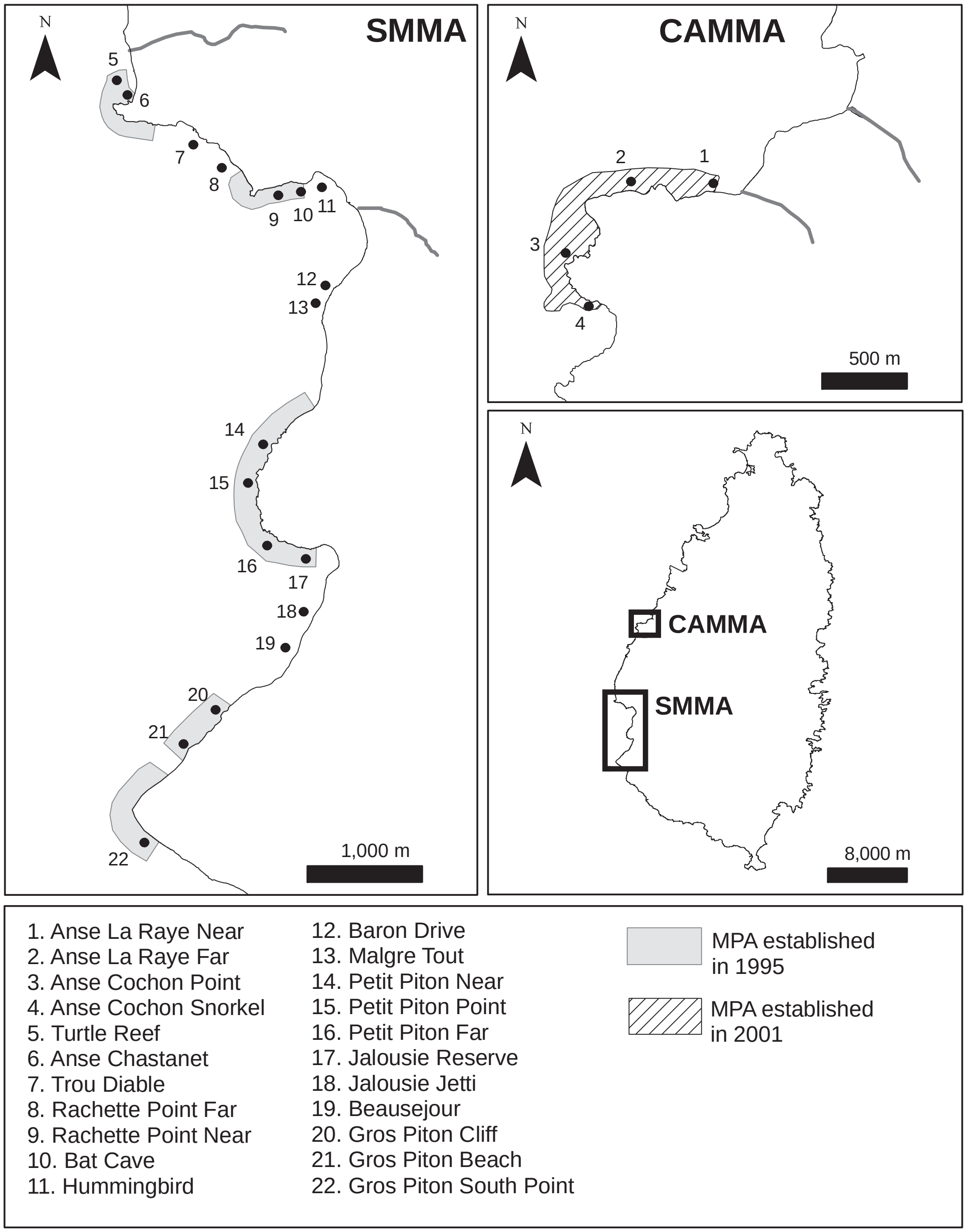

Figure 5.1. Location of sampling sites in Saint Lucia. Grey areas represent the no-take marine protected areas of the Soufriere Marine Management Area (SMMA), and the hashed ones those of the Canaries-Anse-La-Raye Marine Management Area (CAMMA). The location of the two management areas is shown on the middle-right panel. All sites were surveyed at both 5 m and 15 m, except sites # 1 and 6 (5m only), and 5 and 19 (15 m only). Site # 16 was surveyed in 2011 only; all others were surveyed in both 2001 and 2011

Early surveys of benthic cover (2001)

Benthic cover at 27 sites along a 16-km stretch of coast was estimated in 2001 using 8–16 1-m^2 quadrats, placed at computer-generated 1-5 m intervals along the reef at each of two depths, 5 and 15 m (Schelten 2002). Divers estimated visually the percent cover (%) of coral (all species combined), sponges, macroalgae (thick and/or leathery, > 1 cm in height), turf algae (diminutive filaments, < 1 cm in height), crustose coralline algae and filamentous cyanobacteria (Schelten 2002).

Current surveys of benthic composition (2011)

In May and June 2011, benthic composition was re-assessed at 21 of the sites surveyed in 2001 and at one additional site (Figure 5.1). Benthic surveys were conducted at 5 and 15 m depth at 18 of the sites, and at only one depth at four sites where reef development was minimal or absent at the other depth. At each site, scuba divers deployed three 30 m transects haphazardly on the reef, parallel to shore. Transects were at least 10 m apart. Every two meters on each transect, four contiguous photographs were taken from a distance of 0.75 m above the reef. The four photographs together (totaling 0.82 m x 1.22 m) formed a one-meter quadrat; there was a total of 15 such quadrats per transect. Percent cover of benthic organisms was quantified using the software CPCe version 3.6 (Kohler and Gill 2006). Ten random points were overlaid onto each photograph (forty points per 1 m^2 quadrat) and the organism directly under the point was identified. The benthic types recorded were the same as Schelten (2002): hard coral, macroalgae, turf algae, sponges, crustose coralline algae, filamentous cyanobacteria. Percent cover was calculated for each replicate unit as the number of random points identified as a given benthic type divided by the total number of points scored. Transects were the replicate unit for the analysis of current benthic cover, whereas quadrats were used as the replicate unit in the comparisons between 2001 and 2011 since no transects were used in the 2001 surveys.

Sediment composition

Three replicate samples of sediment (~ 100 ml) were collected from the surface layer of sediment (to a substrate depth of 5 cm) in a soft-bottom area immediately adjacent (maximum 5 m away) to each transect at each site surveyed in 2011. Such fore-reef environments tend to have better preservation of sediment compared to back reefs or channels because of lower rates of transport and biogenic re-working (Perry 1996).

In the laboratory, each sample was rinsed twice with distilled water to remove salts and decanted, then dried at room temperature. Each dry sample was separated into two subsamples by coning (Lewis and McConchie 1994), one for archiving and the other for composition analysis. Samples were weighed and then treated with a 10 % hydrochloric acid solution to dissolve carbonates. Following four rinses with deionized water, samples were dried again and reweighed. The remaining sediments can be assumed to be terrigenous (Torres and Morelock 2002; Brooks et al. 2007). The proportion of terrigenous sediment was calculated by dividing the weight of the terrigenous fraction by the weight of the subsample prior to treatment with hydrochloric acid. Organic content was determined by loss on ignition (LOI) after at least 2.5 hours at 550°C (Dean 1974), and was low (< 5 %) in all samples. Organic content was therefore not considered in subsequent analyses.

Statistical analyses

Determinants of current benthic composition

I used mixed-effects models and a correlation structure to evaluate variation in the cover of major benthic groups at the 22 sites surveyed in 2011 in relation to three (fixed) effects: sediment composition, depth (5 vs 15 m) and protection status (protected vs unprotected). I included depth as a fixed effect as it was expected to influence community composition (Sheppard 1982, Chiappone et al. 2001) and I was interested in its possible interactions with sediment composition and protection status. I also included region (Anse La Raye vs Soufriere) as a random effect. Site could not be included as a random effect in the mixed-effects models because data on terrigenous content of sediment were only available at the site rather than at the transect level. Therefore a compound symmetry correlation structure was also tested by comparing models with one of two correlation terms, i.e. either site within region or region only. Compound symmetry correlation can be used instead of random effects to account for a lack of independent samples caused by correlations among variables across different scales (Zuur et al. 2009), and tests for correlation in the residuals. The analyses were carried out using models with normal errors and constant variance following arcsine transformation of the dependent variable, which is the best method for analysing percentage cover data (Crawley 2007).

For each dependent variable (percent cover of coral, macroalgae, sponges, turf algae, coralline algae, filamentous cyanobacteria), I followed the protocol outlined in Zuur et al. (2009) for model selection. First, the optimum random-effects structure was selected by comparing generalized least square (GLS) models that included no random structure to mixed-effect models with random intercept, using the most complex fixed effects (3-way interaction between the proportion of terrigenous sediment, depth and protection status). Models were compared using Akaike's Information Criterion (AIC). AIC values represent the trade-off between model fit and model complexity, where the lowest value represents the best trade-off. The model that had the lowest AIC value was then used to select the most appropriate correlation structure. Random structure was re-tested using the optimum correlation structure. Random and correlation structures were chosen based on minimum AIC scores using the restricted maximum likelihood (REML) estimation method. Finally, the optimum model (with respect to random and correlation structure) was used to select the fixed structure (terrigenous content, depth and protection status), where terms that were not significant were successively removed until all variables remaining significantly improved model fit. Fixed structure selection was carried out using maximum likelihood (ML). Final models were computed using REML. Homogeneity was assessed by graphical methods (Zuur et al. 2009). Because I observed no heterogeneity in the residuals, we did not test for model improvements by including variance parameters. All analyses were conducted in R 2.13.1 (R Development Core Team 2009).

Determinants of long-term changes in benthic composition

I calculated the changes in cover of major benthic groups between 2001 and 2011 in relation to protection status and sediment composition. Changes in benthic cover at these sites from 1996 to 2002 have been reported previously (Schelten 2002, Hawkins et al. 2006). I chose to focus on the decade 2001-2011 to cover a period after the 1998 bleaching event and the passage of Hurricane Lenny in 1999, both of which caused extensive mortality on the reefs of Saint Lucia (Schelten 2002). Moreover, this time period covers the first decade since the establishment of the CAMMA.

I first evaluated absolute changes in benthic cover of each major group over the last decade using repeated-measures ANOVAs, with sites as the subjects and year as the within-subject factor. Because quadrats used in reef surveys were not permanent and their exact location changed with each survey, site was used as the unit of repeated measurement in these analyses, with site-level benthic cover obtained by averaging across all quadrats (irrespective of transect for 2011).

I then estimated the importance of terrigenous content of sediment, protection status and depth for the annual rate of (relative) change in benthic cover of each major benthic group using mixed-effects models as described above. For this analysis, changes in benthic cover were calculated relative to the original survey (i.e. ($100*[Cover_{end} - Cover_{start}]/Cover_{start}$)/year), similar to Gardner et al. 2003) to control for varying initial cover, and expressed as annual rates in terms of percentages. In these mixed-effects models, the only random factor was region. The site effect was not accounted for in a compound symmetry correlation since data were only available at the site level.

Relationship between protection and sediment composition

I performed a t-test to compare the proportions of terrigenous sediment in and out of MPAs. The dependent variable was arcsine-transformed prior to the analysis, which was carried out in PASW Statistics 18.

Results

Determinants of current benthic composition

Protection status was not a significant predictor of current benthic cover in any of the models (Table 5.1). However, there were significant relationships between the cover of four of the six major benthic components considered and either sediment composition or depth or both. In all cases the best model was a generalized least-square with region/site correlation terms (Table 5.1). Current coral cover was best explained by sediment composition and depth, with higher coral cover when terrigenous content was lower (Figure 5.2a) and at shallower depth (Figure 5.3a). Macroalgal cover increased with terrigenous content (Figure 5.2b) and depth (Figure 5.3b), with a significant negative interaction between those factors (Table 5.1). Cover of sponge and filamentous cyanobacteria were both best explained by depth only. Both were more abundant at 15 m than at 5 m (Figure 5.3c &d). The cover of coralline algae and turf algae did not vary with either protection, sediment composition or depth.

Table 5.1. Parameter estimates, standard errors (SE), and significance statistics of optimum mixed-effects models explaining variation in percent cover of coral, macroalgae, sponge and filamentous cyanobacteria in 2011, and annual rate of change in coral cover (2001 – 2011) on fringing reefs at 22 sites in Saint Lucia. Cover data were arcsine transformed. Annual rate of change in coral cover was calculated relative to initial cover (see Methods)

Dependent variable	Parameter	Estimate	SE	t	P
Coral	Intercept	0.396	0.030	12.92	<0.0001
	% terrigenous	-0.0016	0.0004	-3.81	0.0002
	depth	-0.032	0.016	-2.014	0.0470
Macroalgae	Intercept	0.121	0.040	3.04	0.0029
	% terrigenous	0.0015	0.0006	2.56	0.0107
	Depth	0.149	0.051	2.91	0.0042
	% terrigenous*depth	-0.002	0.0008	-2.41	0.0176
Sponge	Intercept	0.201	0.013	14.89	<0.0001
	Depth	0.061	0.012	5.17	<0.0001
Filamentous cyanobacteria	Intercept	0.122	0.026	4.74	<0.0001
	Depth	0.052	0.012	4.49	<0.0001
Change in coral cover	Intercept	-2.005	0.886	-2.26	0.0297
	% terrigenous	-0.032	0.013	-2.45	0.0191
	depth	-2.142	0.648	-3.31	0.0022

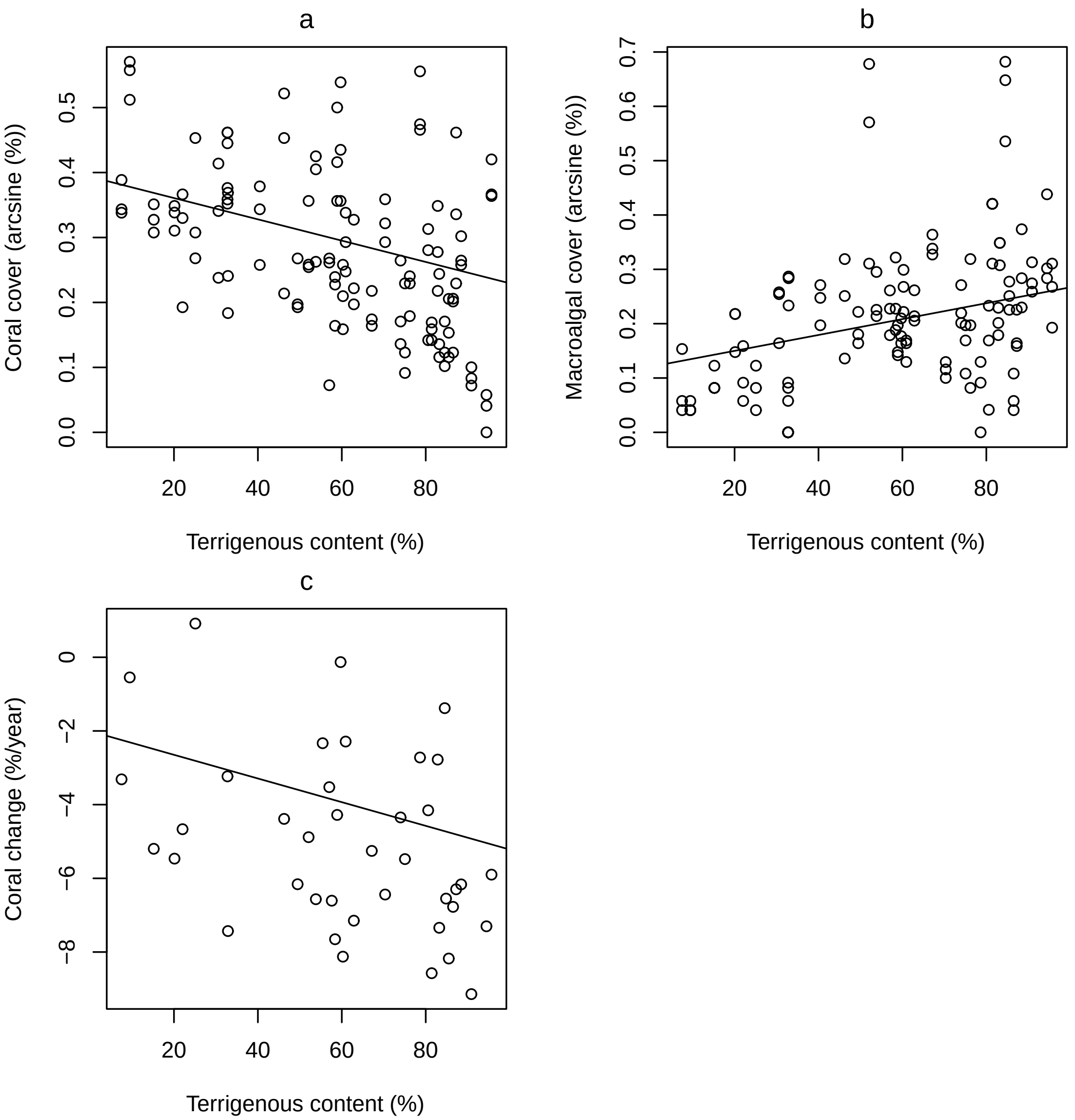

Figure 5.2. Cover of (a) coral, (b) macroalgae in 2011 (arcsine %), and (c) annual rate of relative change in cover of coral from 2001-2011 (see Methods for equation), in relation to terrigenous content of reef sediment

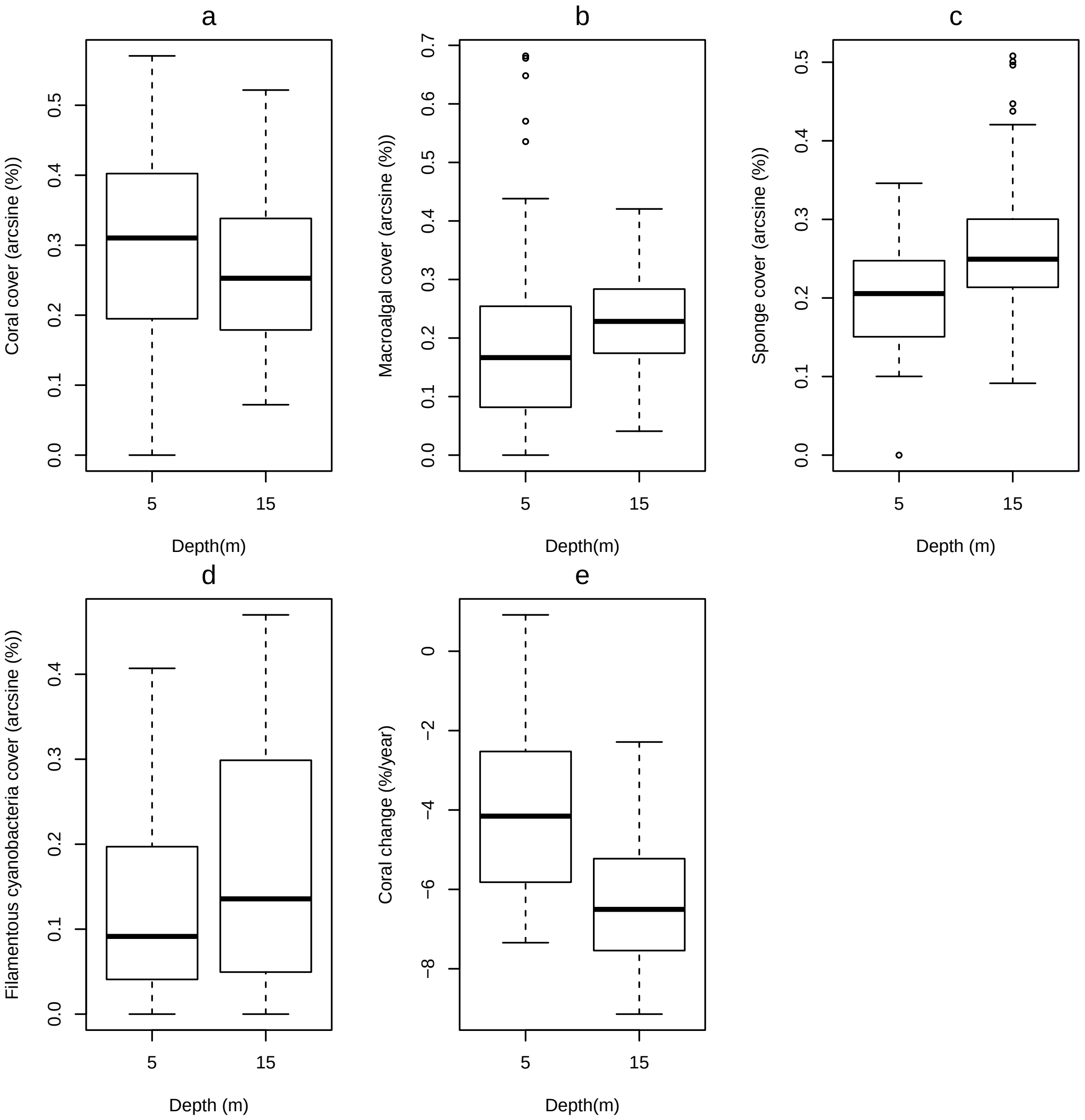

Figure 5.3. Cover of (a) coral, (b) macroalgae, (c) sponge and (d) filamentous cyanobacteria in 2011 (arcsine %), and (e) annual rate of relative change in cover of coral from 2001-2011 (see Methods for equation), at depths of 5 and 15 m

Long-term changes in benthic composition

The patterns of absolute change in cover of benthic components from 2001 to 2011 were similar at 5 m and 15 m depth, although initial cover and magnitude of change varied (Figure 5.4). There were significant differences in the cover of all major benthic groups shown in Figure 4 between 2001 and 2011, except for crustose coralline algae at

5 m and sponge and cyanobacteria at 15 m (Tables 5.2 and 5.3). Most notably, mean coral cover decreased by 7–13% (in absolute terms) and turf algae by 9–25%. Macroalgal cover increased by 5–9% over a decade.

Variation in annual rate of relative change in coral cover over the last decade was best explained by a generalized least-square model, with depth and proportion of terrigenous sediment as fixed factors (Table 5.1). Protection status was not a significant factor. The annual rate of coral loss was higher at sites that were deeper (Figure 5.3e) and at sites with a higher proportion of terrigenous sediment (Figure 5.2c). There was no effect of protection or sediment composition on the rate of change of any other benthic component analyzed.

Relationship between protection and sediment composition

The proportion of terrigenous sediment was similar within and out of MPAs (mean ± standard deviation; unprotected: 71.4 ± 23.0 %; protected: 54.3 ± 23.8 %; t = 1.248, df = 46, P = 0.22).

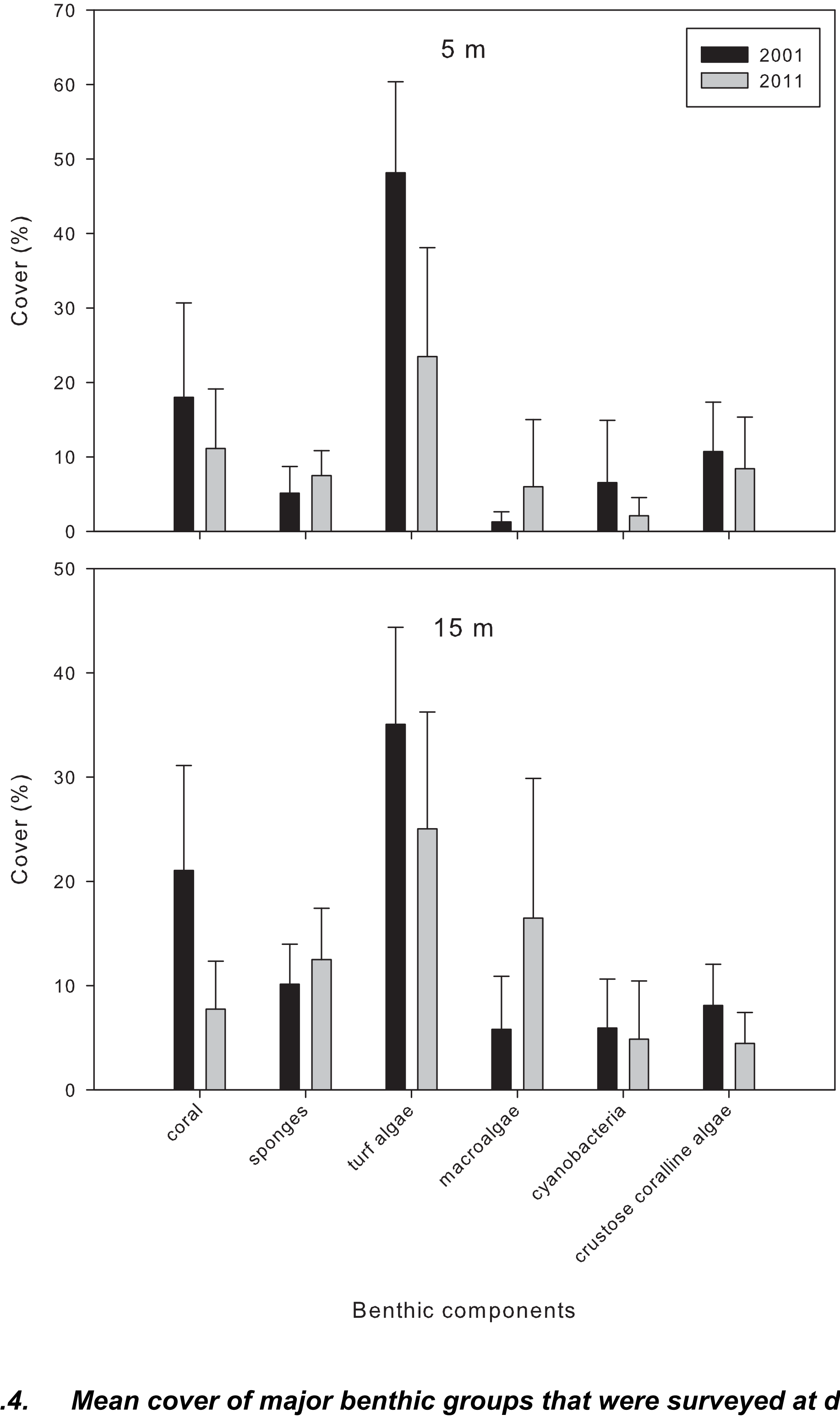

Figure 5.4. Mean cover of major benthic groups that were surveyed at depths of 5 m and 15 m in 2001 and 2011. Bars represent standard deviation. N = 19 sites

Table 5.2. Results of repeated-measures ANOVAs comparing the cover of major benthic components at 5 m depth on coral reefs of Saint Lucia between 2001 and 2011, with mean change in absolute percent cover for each group. * denotes significant changes

Benthic component	Mean change in absolute cover (%)	$F_{1,18}$	P
Coral	-6.8	14.49	0.002*
Sponge	+2.3	13.196	0.002*
Turf algae	-26.4	25.12	<0.0001*
Macroalgae	+5.0	6.49	0.02*
Cyanobacteria	-4.7	5.56	0.03*
Crustose coralline algae	-2.0	1.62	0.22

Table 5.3. Results of repeated-measures ANOVAs comparing the cover of major benthic components at 15 m depth on coral reefs of Saint Lucia between 2001 and 2011, with mean change in absolute percent cover for each group. * denotes significant changes

Benthic component	Mean change in absolute cover (%)	$F_{1,18}$	P
Coral	-12.4	67.20	<0.0001*
Sponge	+1.5	0.99	0.33
Turf algae	-9.3	11.50	0.003*
Macroalgae	+8.7	9.94	0.006*
Cyanobacteria	-1.7	2.44	0.14
Crustose coralline algae	-4.3	30.91	<0.0001*

Discussion

This study shows significant shifts in coral reef community composition in Saint Lucia in the last decade, and highlights strong links between the terrigenous content of reef-associated sediment—a proxy of terrestrial influence on reefs—and both the rate of coral decline and current coral cover. The layer of sediment collected in this study (i.e., the top ~5cm) represents approximately 5 years of accumulation at sites with high sediment load (Chapter 4) and even longer at sites with slower accumulation. It therefore reflects the nature of the sediment deposited at a site over a significant portion of the last decade. Importantly, protection status appeared to have no impact on benthic assemblages, perhaps because sediment composition was similar in and out of protected areas. The MPAs of Saint Lucia, while successful at protecting fishes, have not had a similar effect on corals.

The cover of coral and macroalgae in 2011 varied significantly with the proportion of terrigenous content in reef sediment. This relationship was negative for coral, which is consistent with the known detrimental effects of sediment on coral (Dodge et al. 1974, Rogers 1983, Rogers 1990, Fabricius et al. 2005), and with a large-scale study showing a strong spatial association between low coral cover and high terrestrial influence on reefs (Chapter 3). On the other hand, there was a positive relationship between the cover of macroalgae and terrigenous content of sediment. These results contrast with a previous study conducted throughout the eastern Caribbean, in which macroalgal abundance was negatively correlated with levels of terrigenous sediment (Chapter 3). The discrepancy may be caused by differences between the two studies in the algal dominant species. In both cases, the two most abundant taxa were *Lobophora variegata* and *Dictyota* spp. In the present study, the overall mean macroalgal cover was 5.8 ± 7 % (mean ± standard deviation), with the majority of cover provided by *L. variegata* (5.0 ± 9.5 %) and only a small proportion by *Dictyota* spp. (0.3 ± 0.6 %). By contrast, in the eastern Caribbean study, the mean macroalgal cover was substantially higher (19.3 ± 12.2 %), with the cover of *Dictyota* spp. (13.2 ±10.3 %) exceeding greatly that of *L. variegata* (2.7 ± 4.8 %). The contrasting results could be explained if *L. variegata* has a higher tolerance to high sedimentation than *Dictyota* spp. To my knowledge, the responses of these macroalgae to sediment load and composition have never been directly investigated, and more research is needed to fully understand these results.

The current cover of several benthic components (coral, macroalgae, sponges, filamentous cyanobacteria) varied significantly with depth in a manner consistent with known patterns of depth zonation on coral reefs and in many other ecosystems (Sheppard 1982, Chiappone et al. 2001, Harborne et al. 2006, Kahng and Kelley 2007, Pandolfi and Budd 2008). There was a significant interaction between depth and terrigenous sediment in explaining spatial variation in the cover of macroalgae. Macroalgal cover increased more rapidly with increasing terrigenous fraction in sediment at 5 m than at 15 m, though this was driven mostly by high cover of macroalgae at two shallow sites (Anse Chastanet and Malgretout, 25.9 % and 34 % cover, respectively). The annual rate of decline in coral cover from 2001-2011 was greater at 15 m (mean: 6.2 %*year^{-1}, standard deviation: 1.9) than at 5 m (mean: 3.6 %*year^{-1}, standard deviation: 2.8), although the reason for this difference is not clear.

There was a sharp decline in coral cover between 2001 and 2011, which mirrored a similar change recorded between 1995 and 2001 (Hawkins et al. 2006). The reduction in coral cover over that earlier period was attributed to sedimentation, disease, bleaching and a hurricane (Nugues 2002, Schelten 2002). Multiple stressors have also acted on Saint Lucian reefs in the past decade. Two hurricanes have affected Saint Lucia (Dean in 2007 and Tomas in 2010), generating significant rainfall and storm surge but limited swell (Anonymous 2010, 2011), which suggests that they likely impacted corals mainly through increased sedimentation rather than direct breakage. There was also a substantial bleaching event throughout the Caribbean in 2005 (Eakin et al. 2010) but this resulted in little coral mortality and no change in coral cover in Saint Lucia (Wilkinson and Souter 2008). In contrast, I found that the decline in coral in the past decade was significantly related to the proportion of terrigenous sediment at a site, suggesting that terrestrial sediment is a particularly important factor in driving this change at this location.

The cover of all benthic components other than coral also changed significantly between 2001 and 2011, but unlike coral, these changes were not clearly associated with sedimentation. Of particular interest is the increase in macroalgae, which occurred across all sites, regardless of depth, terrestrial influence or protection status. Although the cover of macroalgae remains low (~7–15%) in absolute terms (see also Bruno et al. 2009), this increase is of concern as both *Dictyota* spp and *L. variegata*, the most common species at my sites, have been shown to inhibit coral growth, increase mortality (Jompa and McCook 2002, Box and Mumby 2007) and reduce coral fecundity (Foster et al. 2008). Shifts in benthic dominance towards lower coral cover and increased macroalgal cover have been reported on many other Caribbean reefs (Hughes 1994, Shulman and Robertson 1996), including some in remote areas that have little human influence (McClanahan and Muthiga 1998), signaling that these changes are not only or necessarily caused by local anthropogenic factors.

In conclusion, spatial protection in Saint Lucia has not affected either current benthic assemblages or changes in the biotic composition of coral reefs over the past decade. The creation of MPAs on this island has led to rapid increases in fish biomass, and in particular of herbivorous fishes (Hawkins et al. 2006). Yet, the cover of macroalgae has continued to increase both in and out of the reserves in the past 10 years, while coral cover has declined steadily. These results suggest that factors other than herbivory are controlling variation in coral cover, and that the current management of this ecosystem in Saint Lucia is not adequate to successfully conserve corals. My study shows that the influence of terrestrial sediment is one factor that is linked to coral success in Saint Lucia. Sediment accumulation rates on reefs in Saint Lucia are high and have been increasing in the past several decades (Chapters 4, 6), and this terrestrial influence is acting both within and beyond protected boundaries. I suggest that efforts to conserve coral in Saint Lucia should focus on this localized threat.

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Chapter 6.

Increase in sediment loads over coral reefs in Saint Lucia in relation to changes in land use in upstream watersheds

Abstract

Increased sedimentation is widely cited as an important stress for Caribbean coral reefs. However, for most locations we currently lack both accurate records of changes in sediment accumulation rate over reefs as well as a quantitative link between land use practices and downstream sediment yield. This chapter aims to provide this information for two watersheds in Saint Lucia. I modified a GIS-based sediment budget model originally developed in Saint John (US Virgin islands) to calculate current and past sediment yields in the two focal watersheds, and used sediment cores collected near downstream coral reefs to examine changes in sediment composition and accumulation rate over the past several decades. My results indicate increases over the last decades in accumulation rates of terrigenous sediment, originating from the upstream watersheds, as well as calcareous sediment, likely arising from the decline of corals. Changes in sediment yields over time calculated with the model were similar to changes in terrigenous sediment accumulation rate on the reef, suggesting that this simple model has good potential for being developed further into a predictive tool for sediment yield under various land use scenarios.

Introduction

Land uses that remove natural vegetation, such as agriculture and urbanization, have the potential to greatly increase erosion and sediment delivery to downstream waters (Walling 1997, Rawlins et al. 1998, Neil et al. 2002, Syvitski et al. 2005, Wilkinson and McElroy 2007). Coastal sediment yields have increased markedly following human impacts (Dearing and Jones 2003), especially in small drainage basins and where rivers drain to the coast without dams, reservoirs or wetlands (Dearing and Jones 2003, Syvitski et al. 2005). As a consequence, increased sedimentation is becoming an important threat to many coastal ecosystems worldwide (Chansang et al. 1981, Lee et al. 2006, Fraschetti et al. 2011). This is particularly true of coral reef ecosystems, which have suffered significant declines worldwide in the past several decades (Gardner et al. 2003, Bruno and Selig 2007), in part due to increased runoff (Burke et al. 2011).

Increased sediment is widely cited as a source of stress contributing to the decline of coral reefs in the Caribbean (Hubbard 1986, Acevedo et al. 1989, Rogers 1990, Nemeth and Nowlis 2001, Torres 2001), yet there is still remarkably little quantitative information on past or present rates of sediment accumulation near reefs in this region. Sedimentation rates on coral reefs have traditionally been measured using sediment traps which do not, in this environment, accurately measure accumulation of sediment (Storlazzi et al. 2011). Accumulation rates in coastal sediment can be measured more accurately using cores and short-lived radioisotopes (SLR) such as ^{210}Pb, ^{137}Cs, ^{234}Th and ^{7}Be as date markers (Cochran et al. 1998, Patchineelam and Smoak 1999, Crusius et al. 2004, Sanders et al. 2006, Draut et al. 2009). Lead-210 is a naturally-occurring daughter product in the ^{238}U decay series, and from the atmosphere gets adsorbed to and incorporated into depositing sediment (Holmes 1998). It has a half-life of 22.3

years. Excess ^{210}Pb (i.e., in excess of equilibrium activity supported by parent isotopes) characterizes sediment deposited within the past ~100 years (Holmes 2001) and can be used to model rates of sediment accumulation and mixing (e.g., Nittrouer et al., 1979; Crusius et al., 2004). Cesium-137 was added to the environment by nuclear-weapon testing that began around 1952 and peaked in 1963. In a core with well-preserved stratigraphy, the ^{137}Cs profile is expected to mimic production, with a peak in ^{137}Cs activity associated with sediment deposited in 1963 (Livingston and Bowen 1979, Smith and Ellis 1982, Holmes 1998). Therefore, ^{137}Cs can be used directly as a dating tool, as well as provide a calibration for ^{210}Pb chronology (Noller, 2000). ^{234}Th and ^{7}Be, with their short half-lives (24.3 and 53 days, respectively), can be used to assess recent deposition or mixing (Fuller et al. 1999, Draut et al. 2009). Recently, sediment cores and short-lived radioisotopes (SLR) have been used to provide a more accurate assessment of changes in sediment accumulation rate at a few locations near coral reefs in the Caribbean (Brooks et al. 2007, Ryan et al. 2008), including Saint Lucia (Chapter 4).

Saint Lucia, like many islands in the eastern Caribbean, is at particularly high risk of accelerated erosion due to its topography (i.e., small and steep watersheds), high levels of rainfall typical of tropical climates (Dadson et al. 2003, Gellis et al. 2006), and rapid coastal development (Burke et al. 2011). Coral cover on reefs in this country has declined by ~70% in the past 15 years (Schelten 2002, Hawkins et al. 2006, Chapter 5), and increased sedimentation levels have been repeatedly identified as an important cause of coral loss (Sladek Nowlis et al. 1997, Schelten 2002, Hawkins et al. 2006). Agriculture (Cox et al. 2006) and roads (Anderson 1983, Sladek Nowlis et al. 1997) have both been identified as causes of soil loss on the island, but the relative contribution of each is unknown. Increased sedimentation rates have been reported near the island's reefs (Schelten 2002, Hawkins et al. 2006), especially following large tropical storms (Sladek Nowlis et al. 1997), yet only recently have sediment cores been used to accurately identify changes in sediment accumulation rates in the coastal zone (Chapter 4). Analysis of one core at a site near Soufriere (southwest coast) indicated ~40% increases in total mass accumulation rate over the past ~40 years (Chapter 4). It remains unclear whether this is a general trend near other coral reefs. Moreover, there are still limited data for Saint Lucia, or anywhere in the Caribbean region, linking directly land use practices to sediment delivery in the coastal zone.

The objective of this study was to investigate the link between temporal variation in sediment accumulation rate over coral reefs of Saint Lucia and changes in the upland watersheds. To do so, I used a customized GIS-based model, the predictions of which I tested empirically with radioisotope analysis of sediment cores. Many models estimate soil loss based on the universal soil loss equation (USLE) with little or no field data (e.g. Cox and Madramootoo 1998, López et al. 1998, Hoyos 2005, Schiettecatte et al. 2008). USLE-based models have been shown to perform poorly at predicting sediment yields (Boomer et al. 2008), which makes them of limited value to guide decisions about land use aimed at reducing sedimentation rates to the coast. In contrast, models that incorporate extensive field measurements of sediment erosion and delivery are much more accurate, although they are clearly more difficult to develop, especially in developing countries with limited resources. One such model was developed to estimate watershed-scale erosion and sediment yield on the island of Saint John, in the US Virgin Islands (Ramos-Scharrón and MacDonald 2007a). This GIS-based model, called STJ-EROS, was based on extensive field estimates of erosion from different types of land uses (Ramos-Scharrón and MacDonald 2007b), and provided reasonably accurate sediment yield predictions for three watersheds on Saint John. Its simple structure means that it can be adapted to estimate sediment yields on other, geologically similar islands in the region (Ramos-Scharrón and MacDonald 2007a, Ramos-Scharrón 2009).

The specific goals of this study were to 1) develop the capability, with a GIS-based model, to estimate past and current sediment delivery from two watersheds in Saint Lucia; 2) quantify variation over time in sediment accumulation rate on reefs downstream of those two watersheds and use these rates to evaluate the performance of this sediment budget model; and 3) use the model to identify specific areas in each watershed that may contribute disproportionate amounts of sediment to the coastal zone. I adapted the STJ-EROS model to the Saint Lucia landscape by deriving from the literature erosion estimates for those land uses found on Saint Lucia but not on Saint John. I sampled sediment cores taken near coral reefs downstream of two watersheds and used SLR dating to examine changes in sediment accumulation rates over the past several decades, including sediment deposited shortly after the passage of Hurricane Tomas in 2010.

Methods

Study Area

Saint Lucia is a volcanic island located in the eastern Caribbean, at approximately 14°N and 61°W. It is relatively large (616 km^2) and has steep, rugged topography with peaks over 900 m. The study areas on the island were chosen based on the location of two marine protected areas, the Soufriere Marine Management Area (SMMA) on the southwest coast, and the Canaries Anse La Raye Management Area (CAMMA) on the central west coast (Figure 6.1). The SMMA receives sediment from the Soufriere River, which drains the ~ 16 km^2 Soufriere watershed. The CAMMA receives input from three nearby rivers: Petite Riviere de l'Anse, Grande Riviere de l'Anse, and Riviere Galet in a combined watershed of ~20 km^2 (Figure 6.1). Mean annual rainfall at the Soufriere weather station is 180 cm (± 47.3, standard deviation) and at the Anse La Raye station, 175 ± 32 cm (Saint Lucia Water Resources Department, based on rainfall data from 1997 to 2009).

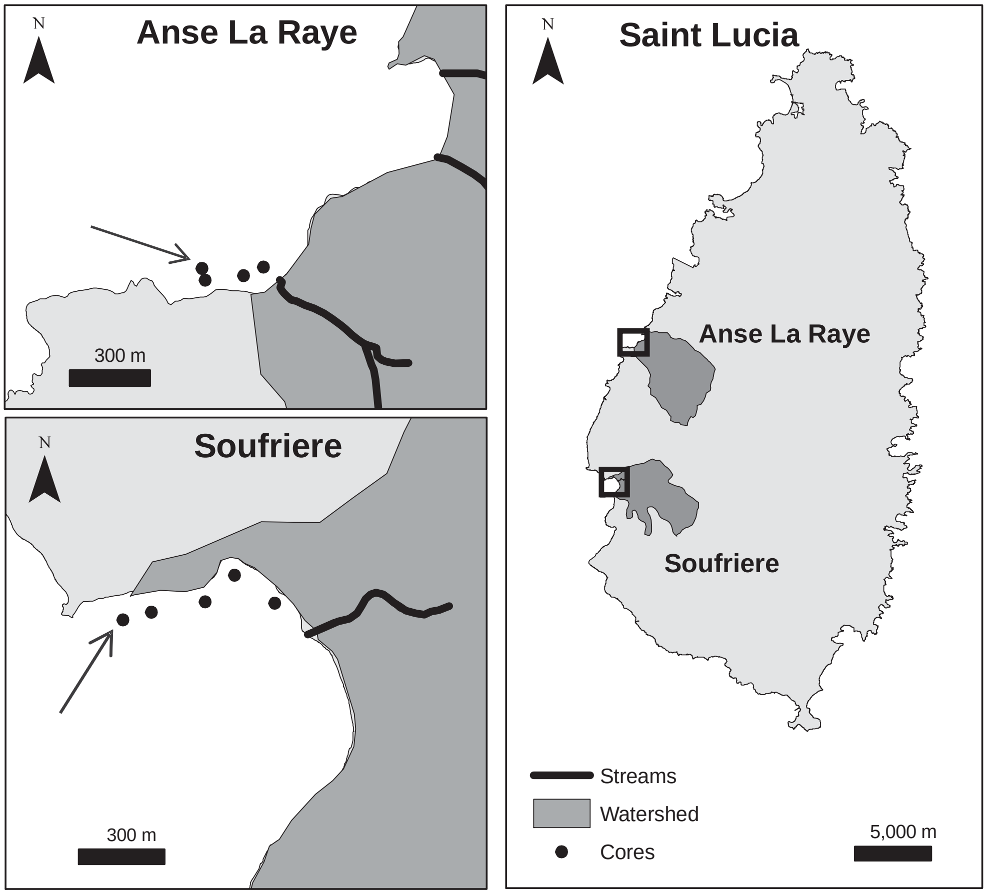

Figure 6.1. Map of Saint Lucia, showing Anse La Raye and Soufriere watersheds, major rivers (thick black lines) and core sites (black dots). The cores analyzed for short-lived radioisotopes are identified with arrows

Core collection and analysis

Sediment core sampling

Sediment cores were taken at five sites near Soufriere and four sites near Anse La Raye in 2010, at various distances from river input, and where possible at two depths (Figure 6.1). At each site, cores were obtained with a diver-operated slide-hammer corer at water depths of 7-23 m. The polycarbonate core barrel had an internal diameter of 69 mm. Divers chose the exact location of the core based on availability of sediment deposits of at least one meter deep (as determined with a thin probe that was pushed in the substratum at various locations), and drove the corer as far as possible into the sediment. Recovered core lengths varied between 25 and 79 cm, depending on substratum hardness. Once collected, cores were kept upright and extruded in 1 cm increments into Whirl-Pak® plastic bags. Samples were weighed immediately to provide the "wet weight" of the sample, in order to determine pore water content (required for bulk density). Once in the laboratory, samples were freeze-dried and then separated into two subsamples by coning (Lewis and McConchie 1994). One subsample was used for SLR analyses. The other subsample was rinsed twice with distilled water to remove salts and decanted, then dried at room temperature. This subsample was further divided in three: one for terrigenous content analysis, one for size analysis, and one for archive.

Short-lived radioisotope dating

Once dried, samples were analyzed for short-lived radioisotope (^{210}Pb, ^{137}Cs, ^{234}Th, ^{7}Be) activities by gamma emission on a Canberra Gamma Ray Photon Detector. SLR analyses were conducted on the top two centimeters and bottom one centimeter for every core sampled, to identify those with the highest amount of datable material. I then focused the rest of the SLR analyses on the one core in each watershed that was the most promising in being dated accurately with SLR (Figure 6.1). The high cost of SLR analyses prevented us from dating more cores. Note that many studies have successfully characterized sedimentation history at a site based on radioisotope analyses from a single core (Cochran et al. 1998, Vaalgamaa and Korhola 2004, Lima et al. 2005, Yasuhara and Yamazaki 2005, Brooks et al. 2007, Ruiz-Fernandez et al. 2009).

The two cores analyzed for SLR were 29 cm (Soufriere) and 39 cm (Anse La Raye) long. Cores were analyzed for activities of ^{210}Pb, ^{137}Cs, ^{7}Be and ^{234}Th every 2 cm over the upper 16 cm (Soufriere) or 12 cm (Anse La Raye) and at 4 cm intervals in the deeper sections. The ^{210}Pb profile was used to calculate age and mass accumulation rate using the Constant Rate of Supply (CRS) model (Appleby and Oldfield 1978, Binford 1990). Terrigenous and calcareous mass accumulation rates were obtained by multiplying total mass accumulation rate by terrigenous and calcareous fraction (see below) in each sample. SLR analyses were conducted at Eckerd College, Saint Petersburg, FL.

Sediment composition

Terrigenous content analyses were performed on the same layers of the core as the SLR analyses, using the acid leaching method (Milliman 1974). Samples were weighed and then treated with a 10 % hydrochloric acid solution to dissolve all the carbonates. Samples were dried again and reweighed. The remaining sediments can be assumed to be terrigenous (Torres and Morelock 2002; Brooks et al. 2007). The proportion of calcareous sediment was calculated by dividing the weight lost during the hydrochloric acid treatment by the weight of the subsample prior to treatment. The proportion of terrigenous was calculated by dividing the weight of the terrigenous fraction by the weight of the subsample prior to treatment with hydrochloric acid. Total organic matter was determined by loss on ignition (LOI) of the remaining terrigenous sample at 550° C for at least 2.5 hours (Dean 1974), and then calculated as % of the entire sample.

Size analyses

Grain size analyses were performed on the same layers as SLR and terrigenous content analyses. Samples were initially wet sieved through a 63 µm screen. The larger size (> 63 µm) fraction was further divided into sand (63 µm – 2 mm) and gravel (> 2 mm) by dry sieving. The mud size (< 63 µm) fraction was divided into silt (4 – 63 µm) and clay (< 4 µm) fractions by the pipette method (Folk 1968).

Saint Lucia sediment budget model (SLU-EROS)

Background

The SLU-EROS model was built in ArcInfo 9.3 using the Model Builder tool, to calculate sediment from different sources that reach the marine environment. It was modified from STJ-EROS (Ramos-Scharrón and MacDonald 2007a, Ramos-Scharrón 2009) to reflect the differences between Saint John and Saint Lucia. I obtained a version of STJ-EROS that had been modified for the islands of Culebra and Vieques in Puerto Rico from its author (Ramos-Scharrón 2009). STJ-EROS calculates sediment erosion and delivery from three main land features: unpaved roads, streambanks/treethrow, and hillslopes. In SLU-EROS, sediment erosion and delivery from the former two elements were calculated in the same way as in STJ-EROS. The main modification for Saint Lucia was in the calculation of sediment production and delivery from hillslopes, which in STJ-EROS was limited to natural (undisturbed) hillslopes because most land area in Saint John is protected by a national park (MacDonald et al. 1997). In Saint Lucia, hillslopes were divided into six land uses: undisturbed, densely vegetated, farmed, grasslands, urban, and exposed soil.

Routines

The SLU-EROS model is composed of four separate routines, each created as a separate model in ArcInfo (Figure 6.2). It begins with the sediment delivery routine, which asks the user to select sediment delivery ratio (SDR) values for areas of high, moderate and low sediment delivery potential in the watershed. These areas have been predefined as polygons in a data layer and represent, respectively, areas draining directly to the coast, to a coastal wetland (e.g. mangroves) and to a pond with no pathway to the marine environment (Ramos-Scharrón and MacDonald 2007a). The sediment delivery ratio represents the proportion of eroded sediment that is moved to the basin outlet, rather than re-deposited along the way. The SDR is influenced by a multitude of factors and is difficult to measure, but it tends to decrease with basin size; small (15-20 km^2) watersheds, such as those in Saint Lucia, have been estimated to have SDRs between 35-100% (Walling 1983). In SLU-EROS, as in STJ-EROS, the user can choose values between 50-100% for high sediment delivery potential areas, and between 0-50% for those with moderate sediment delivery potential. Areas of low sediment delivery potential are automatically assigned an SDR of 0. This routine creates a polygon data layer that incorporates the user-defined SDRs into the sediment delivery layer; this new layer is called SDR. The SDR layer is used in subsequent routines to calculate sediment delivery to the coast based on sediment production within each polygon. Since there were no ponds or wetlands in the two watersheds of interest, the entire watershed was designated as having a high sediment delivery potential.

The Road Sediment Delivery routine calculates the production of sediment for each unpaved road segment (between two drains) based on its surface type (graded, ungraded or abandoned), slope, length and width, and rainfall. Paved roads were considered to contribute no sediment as observations and measurements on Saint John indicate that their cutbanks and fillslopes contribute relatively little sediment compared to unpaved roads (Ramos-Scharrón and MacDonald 2007a). Each road segment is associated with a drainage point, and the amount of eroded sediment delivered to the coast from each drainage point is calculated based on the SDR where the drainage point is located. This routine requires the input of watershed boundaries, roads and drains and creates a polygon data layer which stores the calculated sediment delivery value of each road segment. The Hillslope Sediment Delivery routine calculates sediment erosion within polygons of the six defined land uses (undisturbed, densely vegetated, farmed, grasslands, urban, and exposed soil) based on the erosion function (see below) and rainfall. The Streams Sediment Delivery routine calculates total annual erosion produced by streams, from both erodible banks as well as treethrow. Stream sediment delivery is calculated per amount of time, rather than as a function of rainfall. All calculations were done for one year and mean annual rainfall.

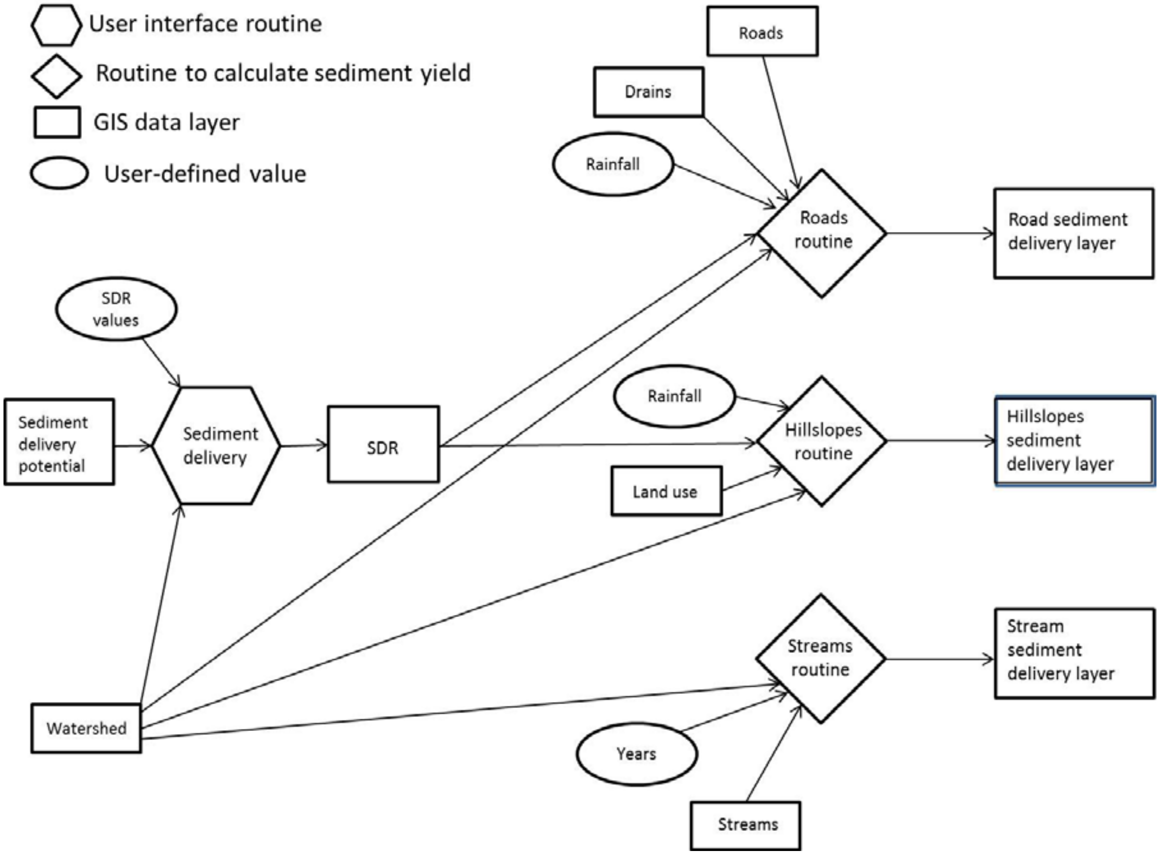

Figure 6.2. Flowchart of the SLU-EROS model

Calculations of sediment yield

Erosion functions in the model were the same as STJ-EROS, or modified from erosion functions for those land use types not present in STJ-EROS, based on field measurements in Puerto Rico and Saint Lucia (Table 6.1). Erosion from unpaved roads and streams was calculated in the same way as STJ-EROS. In the Hillslope Sediment Delivery routine, the erosion function for undisturbed hillslopes is the same as STJ-EROS and is based on the amount of rainfall from large storms (> 6 cm during the storm event), which is the minimum amount of rainfall necessary to initiate surface erosion in undisturbed catchments in Saint John (Ramos-Scharrón and MacDonald 2007a). In Saint John, those storms represent 14% of total rainfall amount and therefore in the erosion function, the total rainfall is multiplied by 0.14. Data were not available in the detail necessary to calculate the amount of rainfall attributable to storms producing more than 6 cm of rainfall at my study sites, but the available data suggest that this proportion is larger than 6 % (Saint Lucia Water Resources Department, based on rainfall data from 1997 to 2009). In the absence of data suggesting otherwise, I used the same proportion as Saint John. Densely vegetated areas in Saint Lucia were assumed to produce the same as undisturbed hillslopes in Saint John. Soil erosion for grasslands, farm areas and exposed soil were calculated as a factor of erosion from undisturbed hillslopes, based on differences in sediment production between undisturbed forest and these land use types measured in Puerto Rico (Gellis et al. 2006), where soil erosion was found to be 30.0, 23.1 and 1.7 times greater for exposed soil, farmlands and grasslands, respectively, than for undisturbed forest. The farmland factor appears to be appropriate for Saint Lucia: soil erosion in an agricultural watershed in the northern part of the island was measured as being 20 times greater than in an adjacent, forested watershed (Cox et al. 2006). Urban areas, which were dominated by pavement, were considered to contribute no sediment. The sediment yields from hillslopes in each polygon were obtained by multiplying the calculated sediment production rate by the assigned SDR.

Table 6.1. Sediment production functions for unpaved roads, streams and hillslopes in SLU-EROS. Distances are in m, area is in m^2, time is in years, slope is a decimal, and rainfall is in centimeters. Resulting sediment production is in Mg. Erosion functions for roads, streams, undisturbed hillslopes and densely vegetated hillslopes are based on Ramos-Scharron and MacDonald (2007a), and those for farms, grasslands and exposed soils are calculated as a ratio of erosion in those land uses compared to undisturbed forest (Gellis et al. 2006). Variables that are derived from GIS layers are in italics

Sediment source	Sediment production function
Graded roads	[-0.432+4.73*(_slope_$^{1.5}$)*rainfall]*_length_*_width_*1.204/1000
Ungraded roads	[-0.432+1.88*(_slope_$^{1.5}$)*rainfall]*_length_*_width_*1.136/1000
Abandoned roads	0.071*_slope_*rainfall*_length_*_width_*1.0034/1000
Streambanks	10*2*_channel length with erodible banks_*_bank height_*years/1000
Treethrow	0.17*_channel length_*years/1000
Undisturbed	0.000064*14% rainfall*_area_*1.0136/1000
Densely vegetated	0.000064*14% rainfall*_area_*1.0136/1000
Farmland	23.1 *(0.000064*14% rainfall*_area_*1.0136/1000)
Grasslands	1.71 *(0.000064*14% rainfall*_area_*1.0136/1000)
Exposed soil	29.95 *(0.000064*14% rainfall*_area_*1.0136/1000)
Urban areas	0

GIS layer acquisition and modification

I ran the SLU-EROS model for current conditions (2010) as well as for 1995 conditions and for a completely undisturbed watershed (no roads, and 100% undisturbed forest), to compare sediment yield estimates at different time periods. The following GIS data layers were obtained from the Saint Lucia government: coastline, watershed boundaries, streams, roads and land use. Roads, streams and land use layers were modified from those obtained from the government to reflect 2010 conditions and to have all the attributes necessary for the model (Table 6.2), based on field surveys (November 2010 & June 2011) as well as high-resolution 2010 satellite photos (GeoEye Foundation) and 2009 aerial photos (Saint Lucia Government). A data layer of road drains was created based on 2010 field surveys, when we recorded the location of culverts, stone drains and any other drainage structure using a handheld GPS device. Data layers representing 1995 conditions were modified from government data and based on 1992 aerial photos (Saint Lucia Government). The same drain data layer as 2010 was used. I chose to estimate yield from 1995 rather than 1992, as road construction which occurred between 1991 and 1994 would have resulted is short-term increases in sediment yield. Sediment delivery estimates for undisturbed conditions involved a modified hillslopes layer composed of only undisturbed areas and streams. The roads routine was not used in that iteration of the model.

Table 6.2. List of GIS data layers necessary to run the SLU-EROS model, along with feature type, list of attributes needed and routine in which is it used

Layer	Feature Type	Attributes	Routine
Sediment delivery potential	Polygon	Delivery potential (High, moderate, low)	Sediment delivery
Watershed	Polygon	Area	Sediment delivery, roads, streams, hillslopes
Roads	Line	Length, width, slope, drain ID, surface type (graded, ungraded, abandoned)	Roads
Drains	Point	Drain ID	Roads
Land use	Polygon	Land use (undisturbed, densely vegetated, farmland, grassland, exposed soil, urban), area	Hillslopes
Streams	Line	Length, bank height	Streams

Results

Changes in sediment accumulation rates over coral reefs

The top ~5cm of both the Anse La Raye (ALR) and the Soufriere (SOU) cores formed a visually distinct layer (Figures 6.3 and 6.4). This top layer had finer sediment (Figures 6.3d and 6.4d) and a higher proportion of terrigenous material (Figures 6.3c and 6.4c) than underlying layers, suggesting that the layer was entirely associated with recent deposition from Hurricane Tomas, which occurred three weeks prior to sampling. The SLR profiles confirmed this scenario. The large decrease in ^{210}Pb activity in the top ~3cm in both cores (Figure 6.3a and 6.4a) is likely the result of very high accumulation rates which diluted the radioisotope (Holmes 2001). ^{7}Be was detected in the top 1 cm of ALR but was not detected in SOU. Dilution from high accumulation rates associated with the hurricane in the upper core may also be responsible for the lack of detectable ^{7}Be in SOU (Figure 6.4a), and ^{234}Th levels which were only slightly higher than background in both cores (Figure 6.3a and 6.4a). Neither core showed detectable levels of ^{137}Cs, which indicates that they are either too modern to have been exposed to the ^{137}Cs peak in 1963, or that the ^{137}Cs in these sediments is below detectable levels. Mass accumulation rates (MAR) and deposition dates therefore had to be estimated with ^{210}Pb alone.

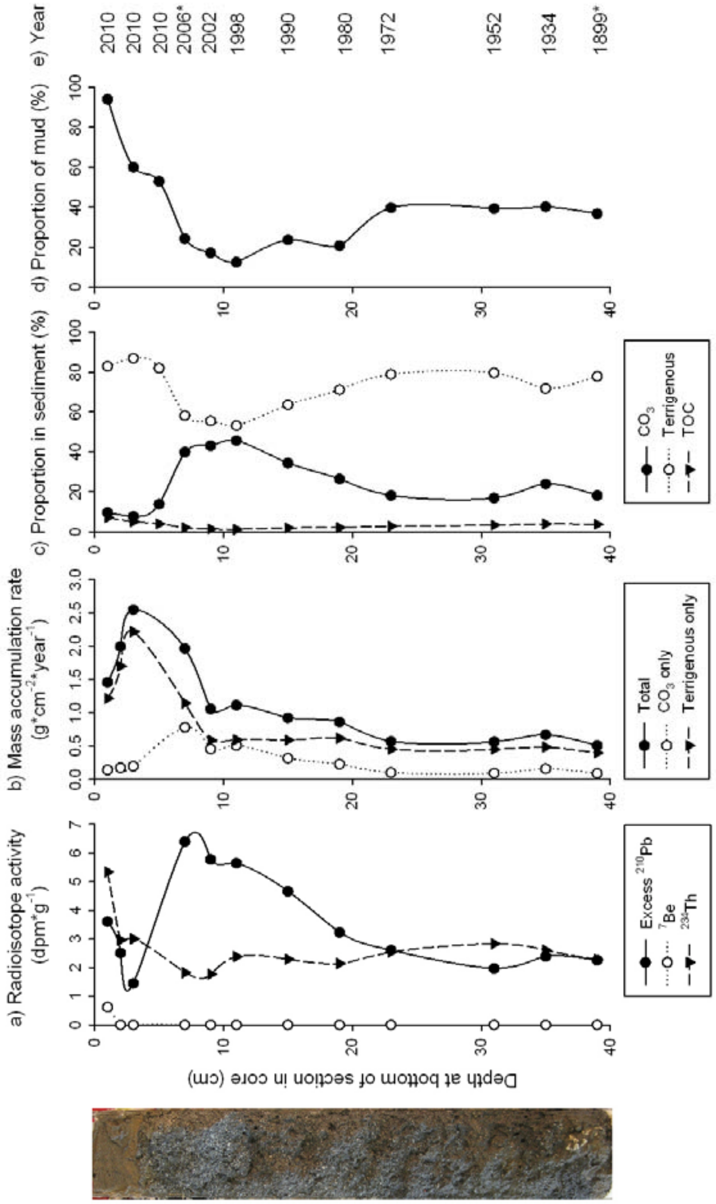

Figure 6.3. ***Results of analysis of the Anse La Raye core, Saint Lucia, eastern Caribbean. (a) Activity of three radioisotopes, (b) mass accumulation rates (estimated by CRS model) of total sediment, calcareous fraction and terrigenous fraction , (c) proportion of carbonates, terrigenous material, total organic content (TOC), (d) proportion of mud (grain size < 63μm) and (e) approximate year deposited, in relation to depth along the core. Depth = 0 represents the top (surface) of the core. The photograph to the left of panel (a) shows the core, scaled to match the depth axis. Year deposited is estimated based on the CRS model, and years with high uncertainty are marked with an asterisk. The location of the coring site is shown in Figure 6.1***

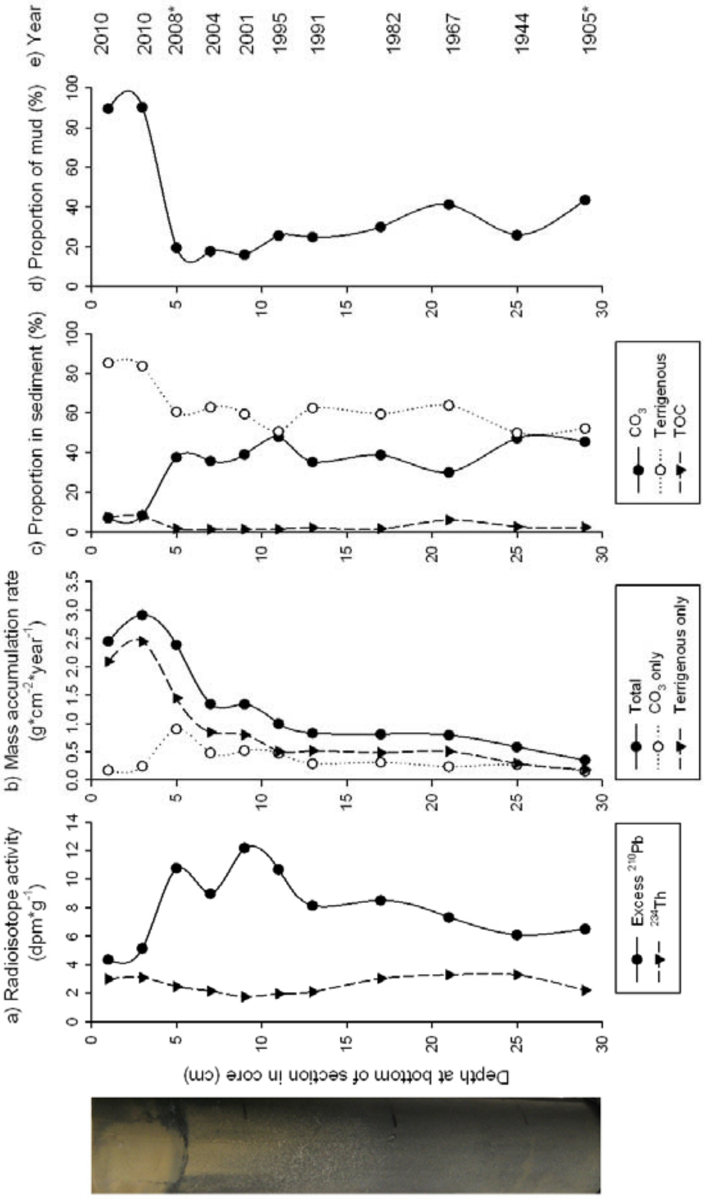

Figure 6.4. Results of analysis of the Soufriere core, Saint Lucia, eastern Caribbean. (a) Activity of three radioisotopes, (b) mass accumulation rates (estimated by CRS model) of total sediment, calcareous fraction and terrigenous fraction , (c) proportion of carbonates, terrigenous material, total organic content (TOC), (d) proportion of mud (grain size < 63µm) and (e) approximate year deposited, in relation to depth along the core. Depth = 0 represents the top (surface) of the core. The photograph to the left of panel (a) shows the core, scaled to match the depth axis. Year deposited is estimated based on the CRS model, and years with high uncertainty are marked with an asterisk. The location of the coring site is shown in Figure 6.1

In the ALR core, ^{210}Pb background levels were not found throughout the core, resulting in a loss of CRS model accuracy; thus, age at the very deepest point sampled (39cm) tends to be unreliable (Holmes 2001). Age at the next deepest sampling point, 35 cm deep, was estimated at 75 years (~1936). Mass accumulation rates, as estimated by CRS, increased (from ~0.56 g*cm^{-2}*year^{-1} to ~0.86 g*cm^{-2}*year^{-1}) from the bottom of the core to around 20 cm deep (late 1970s), mostly driven by an increase in terrigenous MAR (from ~0.46 g*cm^{-2}*year^{-1} to ~0.60 g*cm^{-2}*year^{-1}). The increase in total MAR from ~20 cm to 9 cm (late 1970s to just before hurricane Tomas in 2010; from ~0.86 g*cm^{-2}*year^{-1} to ~1.06 g*cm^{-2}*year^{-1}), however, was caused largely by an increase in calcareous MAR. Between 1990 (15 cm) and 2002 (9 cm; the most recent year where MAR can be measured without being affected by deposition from Hurricane Tomas), there was a 15% increase in total MAR, which was entirely due to increase calcareous MAR; terrigenous MAR remained stable around 0.58 g*cm^{-2}*year^{-1} (Figure 6.3b). The relative proportions of calcareous and terrigenous sediment reflect these trends (Figure 6.3c). Finally, total MAR increased by a factor of 2.4 in surface layers associated with hurricane Tomas (from 1.06 g*cm^{-2}*year^{-1} to 2.56 g*cm^{-2}*year^{-1}), due to a 3.8-fold increase in terrigenous MAR (from 0.58 g*cm^{-2}*year^{-1} to 2.22 g*cm^{-2}*year^{-1}; Figure 6.3b).

In the SOU core, sediment at 25 cm (the second deepest sampling point) was estimated to have been deposited around 1945. There was an increase over time in overall MAR (Figure 6.7b), but in contrast to ALR, the increase in the last two decades can be ascribed to an increase in terrigenous MAR. The proportion of terrigenous sediment generally increased over time throughout the core (Figure 6.4c). Total accumulation rates for SOU, as estimated from the CRS model, increased by a factor of ~3.5 (from 0.35 g*cm^{-2}*year^{-1} to 0.83 g*cm^{-2}*year^{-1}) from 29 cm deep (~1945) to 13 cm deep (~

1991) (Figure 6.4b). Total MAR from 11 cm (~1995) to 7 cm (between 2004 and 2010, the last data point before influence from Hurricane Tomas) increased by ~35 % (from 0.99 $g*cm^{-2}*year^{-1}$ to 1.34 $g*cm^{-2}*year^{-1}$), which was due to a ~62% increase in terrigenous MAR (from 0.5 $g*cm^{-2}*year^{-1}$ to 0.84 $g*cm^{-2}*year^{-1}$). By comparison, calcareous MAR increased by less than 1%, and the proportion of calcareous sediment declined by 25% over the same period (Figures 6.4b, c). In the surface layers, total mass accumulation rate increased by a factor of 2.2 (1.34 $g*cm^{-2}*year^{-1}$ to 2.91 $g*cm^{-2}*year^{-1}$), due almost exclusively to accumulation of terrigenous sediment (Figure 6.4b).

Predicted sediment yields

SLU-EROS estimated that the 2010 sediment yield for both the Soufriere and Anse La Raye watersheds was produced largely by roads (95 % and 83 % of total sediment yield, respectively, in 2010) (Figure 6.5, Tables 6.3 & 6.4). Anse La Raye, with more rivers than Soufriere, had a more important contribution from streams (15 % vs 4 %). For both watersheds, the estimated sediment yield from hillslopes was very small (1.1 % of total yield in Soufriere, 2.1% in Anse La Raye; Figure 6.5). The model estimated 2.2 times greater yields per area in the Soufriere watershed than in the Anse La Raye watershed, which was mostly driven by higher inputs from roads in Soufriere (Figure 6.5).

Estimated sediment yields for 1995 in Anse La Raye were very similar to 2010 estimates (Figure 6.5, Table 6.3). Over this period, Anse La Raye had more important increases than Soufriere in the land uses expected to produce the most sediment, with a three-fold increase in farmland (from 0.19 km^2 to 0.57 km^2) and 12-fold increase in exposed areas (from 0.01 km^2 to 0.12 km^2) (Figure 6.6, Table 6.5). This was reflected in a larger predicted contribution from hillslopes in 2010 (1.48 $Mg*km^{-2}$) compared to 1995 (1.19

Mg*km^{-2}) but made little difference to the overall predicted sediment yield (2010.4 Mg in 2010 vs 2007.4 Mg in 1995).

In the Soufriere watershed, on the other hand, the predicted sediment yield in 2010 was 18.5% higher than that of 1995 (Figure 6.5, Table 6.4). The increase in predicted yield during that time period was mostly driven by new roads and previously paved roads that have been degraded and are now unpaved (Figure 6.7, Table 6.4). The total length of unpaved roads in the Soufriere watershed increased by 29% between 1995 and 2010, from 17.11 km to 22.06 km (Table 6.5). During this period, there was only a small increase in farmland (9%, from 1.12 km^2 to 1.20 km^2) and no change in exposed areas (Figure 6.6, Table 6.5).

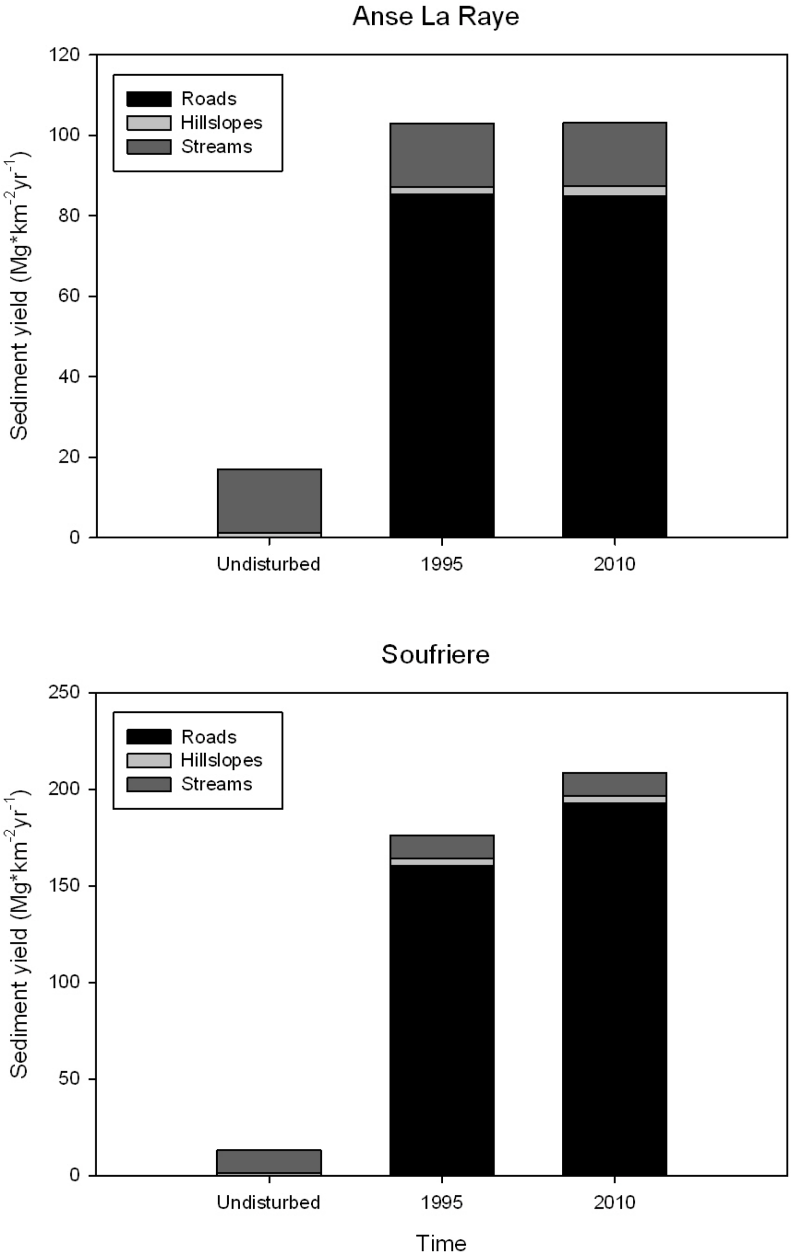

Figure 6.5. Sediment yields from different land uses calculated by SLU-EROS for two watersheds in Saint Lucia, eastern Caribbean, for undisturbed watersheds, and conditions in 1995 and 2010. Note the smaller Y-axis scale for Anse La Raye than Soufriere

Table 6.3. Sediment yields estimated by SLU-EROS for the Anse La Raye watershed in 1995 and in 2010, and percent change between the two time periods

Routine Category	1995		2010		1995-2010 Change (%)
	Watershed yield (Mg*year^{-1})	Area yield (Mg*km^{-2}*yr^{-1})	Watershed yield (Mg*year^{-1})	Area yield (Mg*km^{-2}*yr^{-1})	
Roads					
Total	1670.50	85.62	1659.60	85.06	-0.7
graded	403.94	20.70	403.94	20.70	0.0
ungraded	1248.49	63.99	1237.65	63.44	-0.9
abandoned	18.04	0.92	18.04	0.92	0.0
Hillslopes					
Total	28.95	1.48	42.80	2.19	47.8
Undisturbed	12.40	0.64	12.26	0.63	-1.1
Densely vegetated	9.46	0.48	9.12	0.47	-3.6
Grasslands	1.68	0.09	1.52	0.08	-9.5
Farming	5.17	0.26	15.58	0.80	201.4
Exposed	0.26	0.01	4.30	0.22	1553.8
Streams					
Total	307.96	15.78	307.96	15.78	0.0
Total	2007.41	102.89	2010.36	103.04	0.1

Table 6.4. Sediment yields estimated by SLU-EROS for the Soufriere watershed in 1995 and in 2010, and percent change between the two time periods

Routine Category	1995		2010		1995-2010 Change (%)
	Watershed yield ($Mg*year^{-1}$)	Area yield ($Mg*km^{-2}*yr^{-1}$)	Watershed yield ($Mg*year^{-1}$)	Area yield ($Mg*km^{-2}*yr^{-1}$)	
Roads					
Total	2483.00	160.92	2983.20	193.34	20.1
graded	40.87	2.65	40.87	2.65	0.0
ungraded	2439.15	158.08	2880.42	186.68	18.1
abandoned	2.99	0.19	61.90	4.01	1968.4
Hillslopes					
Total	49.64	3.22	51.90	3.36	4.6
Undisturbed	3.04	0.20	3.04	0.20	0.0
Densely vegetated	11.84	0.77	11.30	0.73	-4.6
Grasslands	2.93	0.19	3.65	0.24	24.6
Farming	31.83	2.06	33.90	2.20	6.5
Exposed	0.00	0.00	0.00	0.00	0.0
Streams					
Total	183.50	11.89	183.50	11.89	0.0
Total	2716.14	176.03	3218.60	208.59	18.5

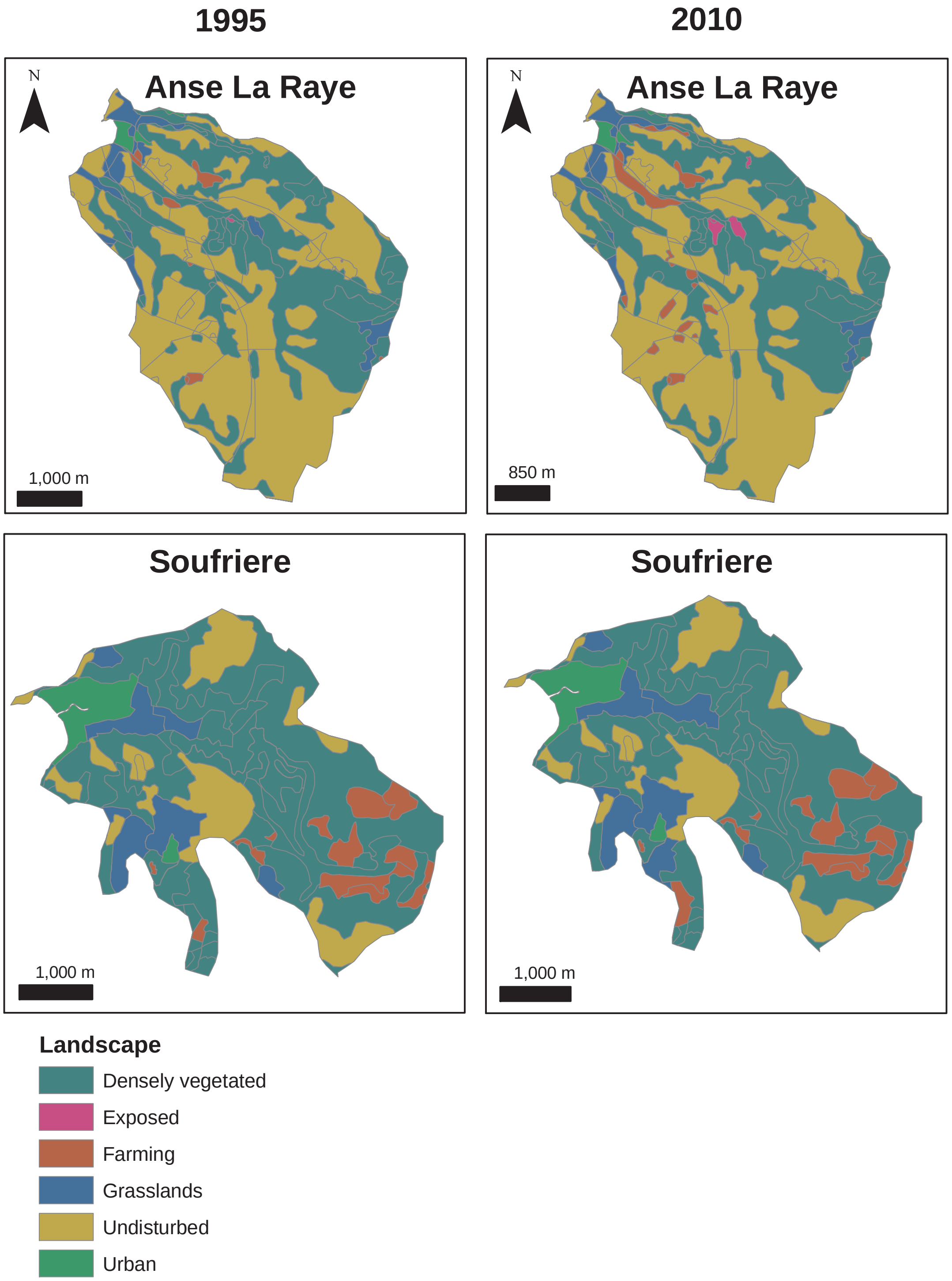

Figure 6.6. Maps of Anse La Raye (top panels) and Soufriere (bottom panels) watersheds in Saint Lucia, eastern Caribbean, in 1995 (left panels) and 2010 (right panels), showing land cover/land use in each time period

Table 6.5. Length of unpaved roads (in km) and area (in km^2) of each land use for Anse La Raye and Soufriere in 1995 and 2010.

	Anse La Raye		Soufriere	
	1995	2010	1995	2010
Unpaved roads				
Total	11.71	11.62	17.11	22.06
graded	0.48	0.48	0.53	0.53
ungraded	10.09	10.00	15.41	17.52
abandoned	1.14	1.14	1.17	4.01
Land uses				
Total	19.51	19.51	15.43	15.43
Undisturbed	10.40	10.28	2.48	2.48
Densely vegetated	7.94	7.65	9.65	9.24
Grasslands	0.82	0.75	1.40	1.74
Farming	0.19	0.57	1.12	1.20
Exposed	0.01	0.12	0.00	0.00
Urban	0.15	0.15	0.78	0.78

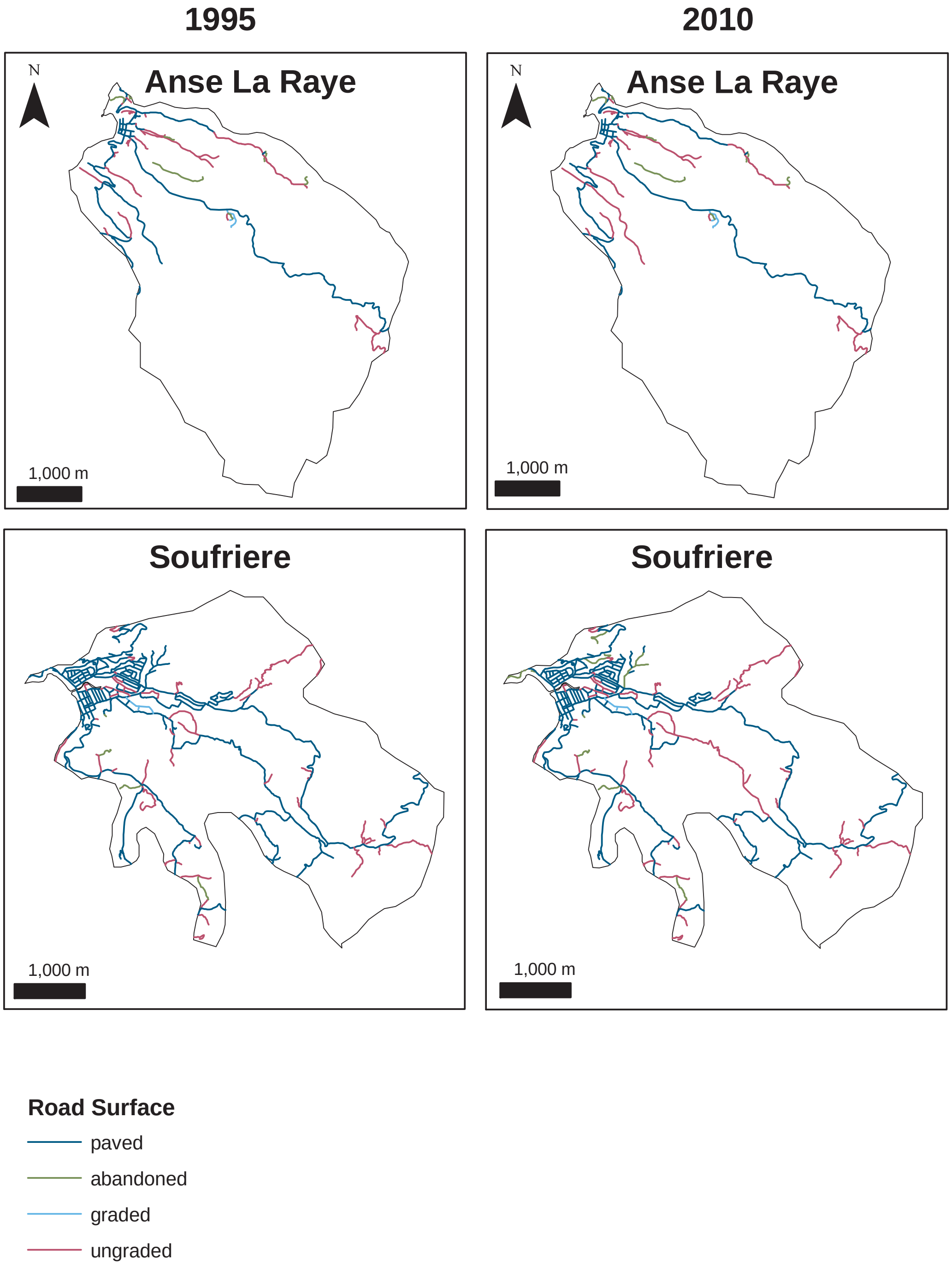

Figure 6.7. Maps of Anse La Raye (top panels) and Soufriere (bottom panels) watersheds in Saint Lucia, eastern Caribbean, in 1995 (left panels) and 2010 (right panels), showing the extent of the road network and road surface types in each time period

Comparison between SLU-EROS sediment yield estimates and core-derived sediment accumulation rates

Changes in sediment yield calculated with the SLU-EROS model and sediment accumulation rates measured from the cores between 1995 and 2010 were very similar for Anse La Raye but less so for Soufriere. SLU-EROS calculated a stable sediment yield (0.01% increase) for Anse La Raye from 1995 to 2010. During this period, there were essentially no modifications to the road system (Figure 6.7, Table 6.5) but there were increases in exposed soil and farming areas in the watershed (Figure 6.6, Table 6.5). SLR analyses of the ALR core similarly indicate no increase in terrigenous sediment accumulation from 1992 to the latest estimate prior to the 2010 hurricane (Figure 6.3b). In Soufriere, SLU-EROS estimated an increase in sediment yield of 19% from 1995 to 2010, due to increases in the road network and the degradation of previously paved roads (Figure 6.7, Table 6.5), as few changes in other land uses occurred in this watershed over that time (Figure 6.6, Table 6.5). Core analyses show a 62% in terrigenous sediment mass accumulation over the same period, from 1995 to the latest data available prior to Hurricane Tomas.

Current major sources of sediment yields

I used the SLU-EROS model to identify the most important anthropogenic sources of sediment in each watershed. Estimates from the model suggested that in the Soufriere watershed, five roads segments, measuring a total length of 2.5 km, are responsible for ~50% of all current sediment yield from roads (1525 Mg*km^{-2} out of 2983 Mg*km^{-2}) and 47% of sediment yield from all sources (1525 Mg*km^{-2} out of 3219 Mg*km^{-2}; Figure 6.8). Similarly, model calculations suggested that in the Anse La Raye watershed, the four most important road segments in terms of sediment production have a combined length of 2.3 km and together produce 61% of all sediment yield from roads (938 Mg*km^{-2} out of 1521 Mg*km^{-2}) and 47% of all sediment yield (938 Mg*km^{-2} out of 2007 Mg*km^{-2}). These road segments represent only 13% (Soufriere) and 19% (Anse La Raye) of the road network in length. Based on SLU-EROS calculations, the most important sediment contributors in hillslopes are exposed soil areas and farmlands; however, my data suggest that their contribution may not be as important roads. For example, the quarry that was developed in Anse La Raye between 2007 and 2010 is estimated to have increased sediment yield from hillslopes by 4.04 Mg, which represents ~9 % of watershed land use contributions in 2010, but only 0.2 % of all watershed contributions.

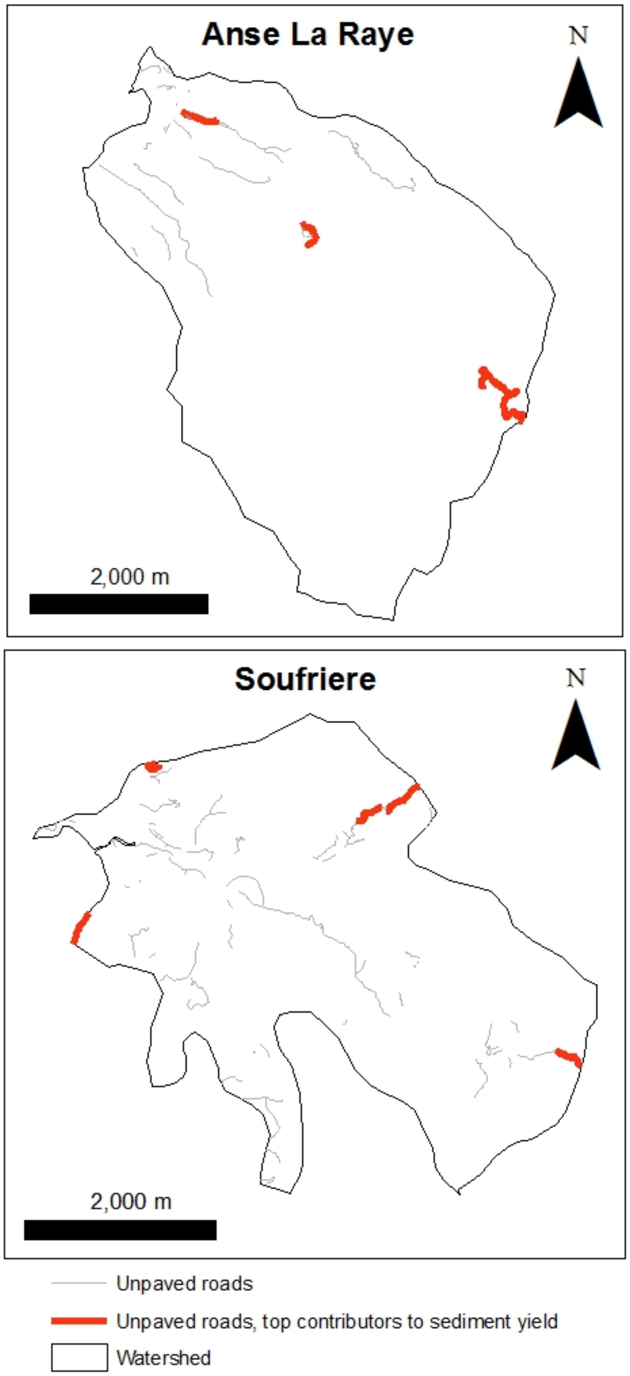

Figure 6.8. Maps of (a) Anse La Raye and (b) Soufriere watersheds in Saint Lucia, eastern Caribbean, showing all unpaved roads in 2010. The road segments highlighted in red together contribute 50% (Soufriere) and 61% of Anse La Raye of sediment yield from roads, based on SLU-EROS

Discussion

This study represents the first in-depth look at changes in sediment accumulation rates in the coastal zone of Saint Lucia in relation to changes in upstream watersheds. Short-lived radioisotope analyses showed a 2-3 fold increase in sedimentation rate over the past several decades, due to increases in the accumulation of both terrigenous and calcareous sediment. The model developed, SLU-EROS, suggested that the most important contribution of terrigenous sediment in two watersheds currently comes from unpaved roads. Increases in accumulation of calcareous sediment may be caused by the loss of coral cover and break down of reef framework.

Total sediment accumulation rates estimated from short-lived radioisotope analyses were very similar for both watersheds examined. Accumulation rates estimated in this study (0.35-1.34 $g*cm^{-2}*year^{-1}$, prior to the deposition event associated with Hurricane Tomas) were consistent with another core previously analyzed in the Soufriere region (Chapter 4) and are high for a coral reef environment. By comparisons, accumulation rates derived from cores were estimated at 0.15 $g*cm^{-2}*year^{-1}$ in Coral Bay, St John (Brooks et al. 2007), and 0.24 $g*cm^{-2}*year^{-1}$ on a fore reef in Puerto Rico (Ryan et al. 2008). Both of the analyzed cores showed slow increases in accumulation rates in the past six to eight decades and a large peak in sedimentation associated with Hurricane Tomas in 2010. There was a shift to higher levels of terrigenous sediment accumulation rates in the late 1970s/early 1980s, most likely due to development in the upstream watersheds. The cores also show increasing levels of calcareous sediment from the early 1980s to the present, probably due to increased availability of calcareous material associated with coral mortality and erosion of the reef framework. Coral cover at sites close to these cores were located has been declining steadily over the past 15 years (Chapter 5), and possibly earlier like many other Caribbean sites (Gardner et al. 2003).

Sediment yields from each watershed were calculated using a simple GIS-based model adapted from the island of Saint John. Comparisons of the changes in terrigenous sediment yield estimates from the model with terrigenous sediment accumulation rates measured in cores near downstream reefs showed agreement with core data in one watershed and some discrepancy in the other. SLU-EROS predicted no change in sediment yield in Anse La Raye from 1995 to 2010, and the cores indeed showed a stable rate of terrigenous sediment accumulation over that period. In the Soufriere watershed, SLU-EROS accurately predicted an increase in sediment yield for the same period, lthough it underestimated its magnitude (19% increase in predicted yield vs 62% increase in terrigenous sediment mass accumulation rate measured on the reef). It is difficult to compare this performance to other models since model performance, if evaluated at all, is usually measured against different measures of sediment yield or accumulation (e.g. yield at catchment input, or sedimentation rate measured by sediment traps; Ramos-Scharrón and MacDonald 2007a, Boomer et al. 2008). However the discrepancy between predictions and measured values in this study is comparable to that of other erosion models (Warren et al. 2005, Ramos-Scharrón and MacDonald 2007a).

Different changes occurred in the two watersheds over the study period. In Anse La Raye, the road network remained the same but several forested areas were converted to farms or quarries. In Soufriere, land use remained similar while new roads were developed and several previously paved roads were degraded so much that they were re-classified as unpaved, either as “abandoned” or “ungraded”. While it may be surprising that the conversion of forest to farming and quarries seen in Anse La Raye does not increase sediment yield substantially, this result was found both for model-predicted yields and core-measured accumulation rates. In contrast, increases in the extent of unpaved road network in the Soufriere watershed were associated with increased sediment yields (both as predicted by the model and as measured in sediment cores). It may be that the increase in sediment accumulation rate recorded in sediment cores in Soufriere was caused, at least partly, by changes in the watershed other than those that were used in the model (e.g. changes in the stream network and associated alterations to sediment erosion and transport caused by increased impervious surfaces). Further research is needed to address this question and better assess the relative importance of unpaved roads to sediment production, and whether the calculations of SLU-EROS (which indicate a large relative impact of unpaved roads) are substantiated by field measurements of erosion in Saint Lucia. It should be remembered that roads on steep slopes are predicted to produce more sediment (Table 6.1) than those on more gentle inclines, and many roads in the two watersheds studied are quite steep. By contrast, farms and quarries are likely to be on relatively flat ground and slope was not used in the erosion functions associated with these land uses. The stable rate of terrestrial sediment accumulation downstream of the Anse La Raye watershed (Table 6.3, Figure 6.3) during a time where increased watershed area was developed into farms and quarries (Figure 6.4) supports the idea that little sediment produced from those land uses was carried to the coastal zone. However, this result should not be taken to mean that increased deforestation for farms and quarries has no effect on sediment yield. It is possible that these land uses produced little sediment under normal rain conditions but have the potential, even if they are occur on relatively flat land, to produce much higher sediment yield than undisturbed areas during large storms. It could also be that the new quarries in Anse La Raye, which were developed around 2007, are too recent for their effect to have been detected in the sediment core before the large accumulation associated with Hurricane Thomas.

The fact that predicted changes in sediment yields calculated with SLU-EROS generally agreed with changes in accumulation rate recorded in cores for both Anse La Raye and Soufriere shows its potential to be developed into predictive tool. However, the model still has several weaknesses and more field data will be necessary to test and improve its predictions. Most obviously, field measurements of erosion rates in Saint Lucia would be preferable over estimates derived from other islands. Moreover, the hillslope erosion functions used in this chapter do not take account of slope. Better field data on erosion rates of all landscapes at various slopes may allow the incorporation of a slope variable for hillslopes, which would improve model accuracy. The Sediment Delivery Ratio used in this model is a simplification of sediment re-deposition and storage in the watershed (Walling 1983, Ramos-Scharrón and MacDonald 2007a). All paved areas (urban areas and paved roads) are estimated to contribute no sediment, when in fact these impervious surfaces can alter flow patterns (Lee et al. 2006) and increase erosion (Sidle et al. 2011) and the risk of landslide (Larsen and Parks 1997, Holcombe and Anderson 2010). The effect of large storms is also difficult to predict as the model cannot account for landslides that are often associated with those storms. Besides increasing sediment yield during storms, landslides can significantly alter land cover and the sediment yield from the watershed for months afterwards. These limitations must be remembered when using and interpreting the results from this model; for example, it may be worthwhile to examine the effects of roads and land use in separate analyses to avoid downplaying the potential contribution of land use to overall yield, which may only be evident during large storm events. However, my initial results show that the model is promising, and its simplicity may allow its application to other islands. The accuracy of the model can be tested further in coming years, as land use and roads change and additional sediment accumulation data become available.

In evaluating the accuracy of SLU-EROS, I compared sediment yields calculated from the model to sediment accumulation rates measured on reefs near river mouths. I assumed that the relative proportion of the sediment yield accumulating near reefs would be consistent, so that a two-fold increase in yield would be recorded as a two-fold increase in accumulation rate. However, this may not necessarily be the case. Changes in energy levels and current patterns may affect where sediment is ultimately deposited in the coastal zone (Brooks et al. 2007), resulting in some discrepancy between sediment yield and sediment accumulation rate at one site. However, in the absence of data to quantify the link between yield and deposition, accumulation rates from these cores are the best estimates available, and a good starting point evaluate the accuracy of SLU-EROS.

My study shows that there have been marked increases in sedimentation accumulation rates over coral reefs at two sites in Saint Lucia over the past several decades. Increased sediment loads have been an on-going threat to coral reefs in Saint Lucia and corals in and out of MPAs have declined in the past 15 years (Chapter 5). Reducing sediment loads to reefs has been an important management concern in the country. My results indicate that SLU-EROS has the potential to be a helpful predictor of crude sediment yields under various roads and land use scenarios. For example, it can identify specific landscape features or road segments that are the most likely major contributors to sediment yields, thereby facilitating priority ranking for remedial action.

SLU-EROS is not site-specific and may be used in other watersheds as the required data layers become available. Further research, including the application of SLU-EROS to other watersheds and field estimates of erosion for various landscapes in Saint Lucia, will continue to improve it as a useful management tool.

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Chapter 7.

General Conclusion

Multiple factors have contributed to the substantial degradation of coral reefs in the past few decades (Gardner et al. 2003; Bruno and Selig 2007) and management action to mitigate those factors is needed promptly in order to slow this decline and promote coral recovery. Of all the threats to coral reefs, increased sedimentation is an especially important issue on reefs surrounding tall and steep islands (Richmond et al. 2007), and a logical one to focus efforts and resources on, as it can realistically be ameliorated with local action. However, despite a significant amount of research effort, there is still surprisingly little quantitative data on temporal changes in sedimentation rate over coral reefs occurring concurrently with development upstream, and associated impacts on coral communities (Wolanski et al. 2009). My thesis addressed these significant knowledge gaps using islands of the eastern Caribbean as focal sites.

General methodological considerations: improving measurement and prediction of sedimentation

Anthropogenic activities that clear natural vegetation lead to increased sediment erosion (Walling 1997; Wilkinson and McElroy 2007). However, the complexities of sediment transport and re-deposition in a watershed make it difficult to predict how these changes affect sediment deposition in downstream ecosystems (Walling 1983; Rawlins et al.

1998). Models that require local field measurements and incorporate more parameters may yield more accurate predictions of sediment transport and deposition, but the added complexity likely reduces the application of such models, especially in areas with low capacity and limited pre-existing GIS data. Simple sediment budget models have the potential to estimate relatively accurately the changes in sediment delivery to the coastal zone that occur with anthropogenic development (e.g. Ramos-Scharrón and MacDonald 2007; Chapter 6) and have the added benefit of requiring less data input—therefore can be readily used in more locations.

Little information is available on temporal changes in sedimentation rates in coral reef environments, in large part because reef ecologists have typically measured “sedimentation rate” on reefs with sediment traps. The limitations of these traps have been clear for many decades (Bloesch and Burns 1980; Gardner 1980), and recent research has highlighted their inaccuracies, misuse and misinterpretations when used in the high-energy environment of coral reefs (Storlazzi et al. 2011). Indeed, the lack of significant association between sedimentation rate and coral cover at a global scale in the meta-analytical review I conducted in Chapter 2 may be caused by inaccurate estimates of “sedimentation rate”, which was measured by sediment traps in all but one study. Sediment cores stand out as the only method to obtain accurate records of changes in terrigenous sedimentation input. Short-lived radioisotopes (SLR) are a powerful tool to estimate age of sediment (from which one can derive accumulation rate at various times) and my research shows that ^{210}Pb, ^{7}Be and ^{234}Th can all be detected in the relatively coarse sediment that accumulates near coral reefs and used to date sediment and derive accurate accumulation rates. The accumulation rates I measured in Saint Lucia using SLR were about twice those recorded in Saint John and Puerto

Rico in cores taken in similar (though likely lower-energy) environments (Brooks et al. 2007; Ryan et al. 2008). By contrast, accumulation rates estimated from sediment traps and reported in Chapter 2 were considerably larger than rates estimated from cores, either in this thesis or in other Caribbean studies. For example, the highest accumulation rates reported from traps were an order of magnitude larger than the highest rates estimated here with SLR (which included the very intense depositional event associated with a hurricane). Average accumulation rates reported from traps in Chapter 2 (all Caribbean sites combined) were about four times higher than the rates measured in Saint Lucia in this thesis. These figures support the statement that accumulation rates measured by sediment traps are not representative of sediment accumulation rate on the reef and should not be reported as such (Storlazzi et al 2011). While SLR analyses are a powerful tool to investigate changes in sedimentation regimes, their high cost limits their widespread use.

Sediment cores may also be used to investigate changes in sediment composition over time, which can be linked to the amount of sediment running off from land. In coral reef environments located next to volcanic or continental land masses, calcareous sediment is produced *in situ* from the degradation of the reef framework and from other calcareous organisms, and non-calcareous sediment can be assumed to have originated on land. Assuming a relatively constant supply of calcareous material at a given location, increases in the proportion of non-calcareous material (e.g., Chapter 4) should indicate a rise in the input of terrigenous sediment. Similarly, the proportion of terrigenous material in surface sediment is expected to increase closer to an input source (Subba Rao 1958; Maxwell and Swinchat 1970; Perry and Taylor 2004; Badran and Al Zibdah 2005; Ryan et al. 2008; Alonso-Hernandez et al. 2011) and this was also shown at several sites in the eastern Caribbean (Chapter 3). Composition analysis of surface sediment may therefore be a simple and crude proxy of terrestrial sediment load to a site, and a better alternative to sediment traps. Clearly, simple surface sediment analyses have limitations and results of such analyses are influenced by recent rain and deposition events (e.g., large hurricanes). However, since a sample may represent sediment deposited over several years, this method can give a rapid and inexpensive measure of spatial variability in terrestrial influence on reefs, integrated over recent years.

Linking land use, sediment load and coral communities in the eastern Caribbean

I showed in this thesis a significant link between surface sediment composition (used as a proxy for terrestrial sediment input) and several metrics of coral health. This pattern was found at two different scales. In Chapter 3, in which I surveyed varied sites on 11 islands throughout the eastern Caribbean, I found significantly different coral communities as well as lower coral cover at sites with higher levels of terrigenous sediment. Chapter 5 focused on sites in Saint Lucia, and showed lower coral cover and larger coral declines over a decade at sites which had a higher proportion of terrigenous sediment. Such a clear link between sediment load and various aspects of coral communities has not been shown before in un-manipulated field conditions.

My thesis also highlighted significant changes in the sedimentation regimes over several eastern Caribbean reefs. Simple composition analyses over the length of sediment cores showed significant increases in proportion of terrigenous material deposited over time, at several reefs in the eastern Caribbean that were located close to a clear source of terrigenous sediment (Chapter 4). Such an increase was not seen near reefs further from sources of sediment and therefore this trend is most likely a consequence of development on the nearby islands (as opposed to further sources of large sediment inputs such as the Orinoco or Amazon rivers). Short-lived radioisotope analyses were conducted on three cores from Saint Lucia (Chapters 4 and 6) and showed that sediment accumulation rates over coral reefs in Saint Lucia have been increasing over the past several decades. This increase in sediment in the coastal zone has occurred concurrently with the increasing extent of unpaved roads and reduction in undisturbed forest in the watersheds.

Chapter 6 established that a simple GIS-based model modified from one initially developed for another island may give crude but relatively accurate estimates of sediment produced under different land scenarios in Saint Lucia. This information can in turn be used for land use planning. The results from the sediment budget model in this thesis, as well as in Saint John where it was initially developed, highlight that a few road segments in the watershed can be responsible for a large proportion of the sediment delivered to the coastal zone. This model can be a very useful tool to establish priorities in management actions that should be taken to reduce sediment runoff. However, successfully reducing sediment loads on the coral reefs of Saint Lucia will require the co-operation of agencies responsible for land and marine jurisdictions. Such initiatives towards integrated planning were recently outlined by the government of Saint Lucia in the National Sustainable Development Strategy, but the project did not proceed as planned due to a lack of political will, financial support, and backing from key institutions (Tulsie 2006). Similar problems of inadequate legislation, enforcement, and stakeholder support remain a challenge for long-term environmental stewardship in many areas (Richmond et al. 2007).

Further work and management implications

While the research presented in this thesis is an important step towards a better understanding of the changes in coastal sedimentation and associated effects on coral reefs communities in response to development, further research will help answer several remaining important questions. The sediment budget model developed here would be improved with added data on sediment erosion and delivery, in particular to better understand how the contributions of unpaved roads and various land uses change with various rain regimes. Moreover, the model was only used with two watersheds in Saint Lucia and it would be worthwhile to study its application to other watersheds and islands. With added data to improve its accuracy, this model may be useful to understand how sediment yields may vary in the future with changing rain regimes associated with climate change. More work is also needed to better understand the effects of added sediment on coral communities. Many field studies that monitor changes in coral over time measure total percent cover and lump all coral species together. Laboratory and experimental field studies clearly show that some species are more tolerant to sediment than others (e.g. Hubbard and Pocock 1972; Rogers 1983), yet it is not clear how increased terrigenous sediment affects community dynamics in non-experimental settings. A better understanding of community effects could lead to the identification of "indicator species" that could help managers better assess sediment stress on their reefs.

It is becoming clear that successful management in many ecosystems must be more comprehensive than it has been in the past. We need to move beyond single-species and sectorial management to consider entire ecosystems (Froese et al. 2008; Norse 2010), and multiple disciplines may be required to better understand how we affect our environment (Fowler 1999). This thesis endeavored to embrace this management philosophy for coral reefs of Saint Lucia and the eastern Caribbean. Research presented here surveyed both the marine and terrestrial worlds and integrated concepts and techniques from the fields of ecology, geology and geography, in order to better understand past changes and start identifying future solutions to help the recovery of corals in the region. However, much more work is needed to fully understand the complex interactions at play on eastern Caribbean coral reefs. While excess sedimentation is an important threat that needs to be addressed in this region, successful conservation of corals must ultimately also address the global-scale environmental issues that can affect reefs regardless of the quality of local management plans.

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Appendix 1: SLU-EROS Sensitivity Analysis

The goal of this appendix is to provide an assessment of the relative effect of various parameters of SLU-EROS on the sediment yield calculated by the model. Specifically, I investigate the effect of varying the total amount of rainfall, the proportion of rain that fell during events yielding over 6 cm of rain, and the sediment delivery ratio (SDR).

Rainfall and Proportion of Rainfall from Large Storms

Both the “rainfall” and “proportion of rainfall over 6 cm” parameters are simple multipliers in the Roads and Hillslopes routines (Table 1, Chapter 6). There is therefore a direct relationship between these parameters and the sediment production estimates (e.g., a doubling in rainfall would yield twice the sediment production). Modifying the rainfall input by one standard deviation would lead to an increase or decrease in the estimated sediment production from roads and hillslopes of 26% in Soufriere, and of 18% in Anse La Raye. There are limited data to accurately estimate the proportion of rain that fell as part of large (> 6 cm) storms and it is therefore difficult to estimate the error on this parameter, but the available data suggest that this proportion is at least 6%. Using this value instead of the 14% used in our analysis would decrease sediment production estimates for roads and hillslopes by 57%.

Sediment Delivery Potential

Sediment yields are obtained by multiplying estimated sediment production by the SDR. SDR for high delivery potential areas can be chosen between 50-100%, and I systematically used 75% as the SDR value in my analysis. Choosing instead the lower or higher end of the allowed values (50% and 100%, respectively) would result in sediment yields 33% lower or higher, respectively, than the values obtained in my analysis.

Effects on overall sediment yield

Taking into consideration the potential relative changes brought about by modifying the above variables, I calculated the total sediment yield for both the Anse La Raye and the Soufriere watersheds (2010 conditions) for low estimates, high estimates and original calculations (Figure 1). High estimates were calculated using the mean + 1 standard deviation for total rainfall, 14% as the proportion of rain in events greater than 6 cm, and a sediment delivery ratio of 100%. High estimates were 48% (Anse La Raye) and 64% (Soufriere) higher than original estimates. Low estimates were calculated using mean - 1 standard deviation as total rainfall, 6% as the proportion of rain higher than 6 cm and a sediment delivery ratio of 50%. Low estimates were 65% (Anse La Raye) and 74% (Soufriere) lower than original calculations. Since the calculated sediment yield from streams does not vary with either SDR or rainfall variables, changing these values affects the relative contribution from streams, which is more important for low estimates (Figure 1). It should also be noted that while changing the three variables considered here together can have a substantial effect on overall predicted sediment yield, none of the three variables taken individually has a disproportionate effect on the yield. Moreover, unless the error occurs in different directions for each time periods, then the error should have minimal consequences on our calculations of relative change in sediment yield over time.

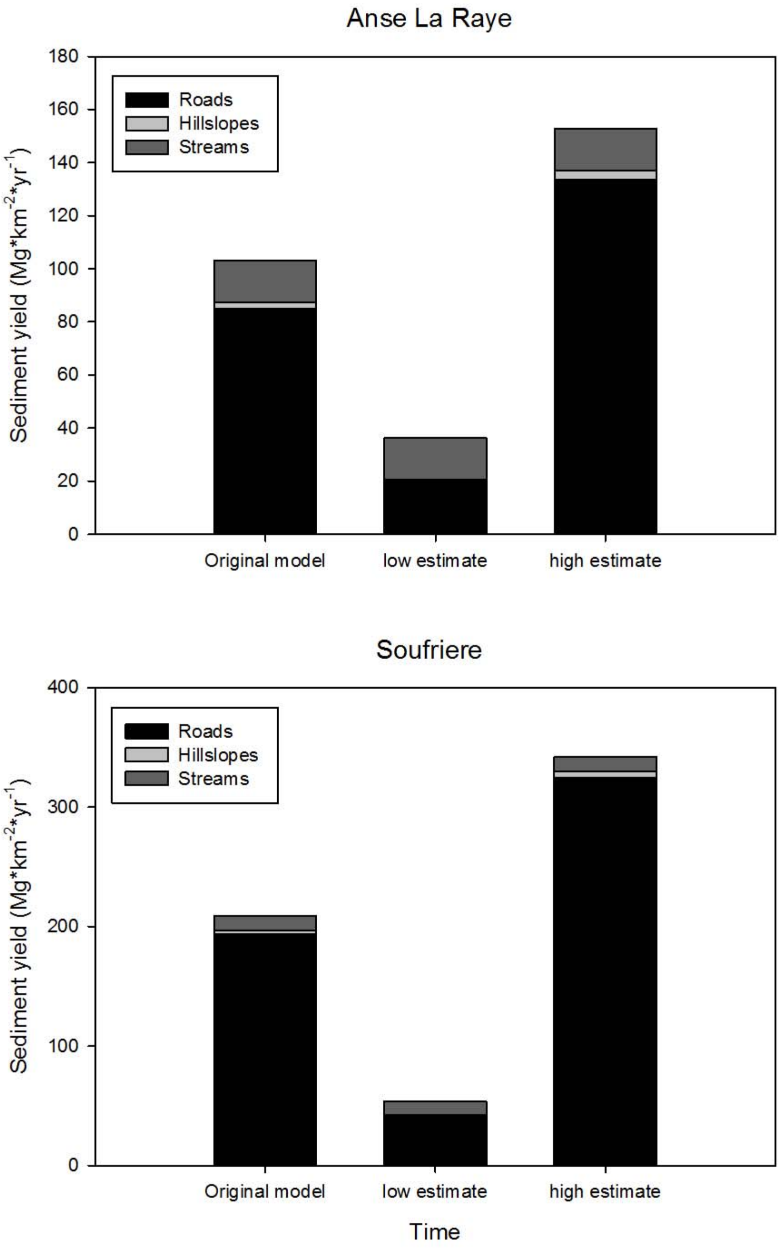

Figure A-1. Sediment yields from different land uses calculated by SLU-EROS for two watersheds in Saint Lucia, eastern Caribbean, calculated with original functions, and lower and higher estimates for 2010 conditions. High estimates: total rainfall = mean + 1 standard deviation; proportion of rain higher than 6 cm = 14 %; Sediment delivery ratio: 100%. Low estimates: total rainfall = mean - 1 standard deviation; proportion of rain higher than 6 cm = 6 %; Sediment delivery ratio: 50%. Note the smaller Y-axis scale for Anse La Raye than Soufriere