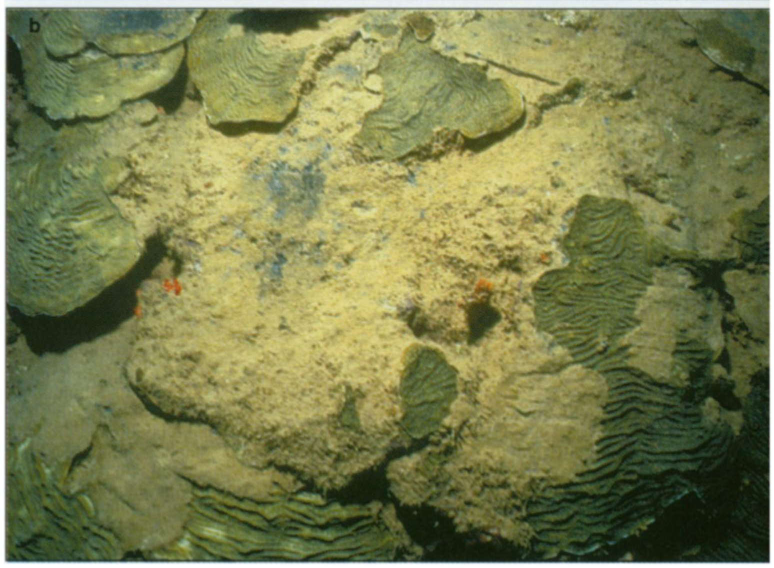
Report

Joshua Sladek Nowlis, Callum M. Roberts, Allan H. Smith and Erkki Siirila

# Human-enhanced Impacts of a Tropical Storm on Nearshore Coral Reefs

Land development ranks among the most significant human threats to coral reefs, causing damage by promoting the erosion and transport of soil—called sediment once suspended in water. We studied the impacts of sediment on the coral communities of St. Lucia following a tropical storm. We found more sediment and coral damage on reefs closest to the mouths of large rivers. Coral mortality exceeded 50% at some sites, and the degree of coral mortality and bleaching depended on the amount of sediment at the site. Despite exemplary efforts by engineers to reduce erosion rates, we found more sediment at sites near a road under construction at the time of the storm. Collectively, our data demonstrated a major negative impact of land development on coral reefs, a problem likely to grow in scale given the growing demands for developed land and the recent frequency of large storms in the tropical Atlantic.



(a) The West Coast Road Project and (b) sediment smothering a coral head. The road project, despite exemplary erosion control practices by the engineer, promoted the erosion and transport of soils onto coral reefs where they caused coral mortality and bleaching.
Photos: (a) C.M. Roberts; (b) E. Siirila.

## INTRODUCTION

Coral reefs hold the highest number of species in the ocean (1) and the highest number of taxonomic families, orders, or any higher classification on the entire planet (2). This diversity benefits us directly through harvestable food, medicines, raw materials, and coastline protection, and indirectly by sustaining the ecological processes that provide these resources. Coral reefs are also highly productive ecosystems and support large populations of organisms, whether measured in numbers or biomass (3–5). For these reasons, coral reefs are of great conservation and economic importance. Developing tropical countries, especially small island states, depend heavily on their coral-reef resources for food from reef fisheries (6–8) and for economic benefits from visiting scuba divers and snorkelers (9, 10). Environmental degradation from increasing worldwide exploitation of coral reefs and nearby terrestrial and marine ecosystems has provoked international concern over the fate of reefs as a global resource (11–13), similar to the apprehension over tropical rainforest destruction.

Coral reefs are generally perceived as fragile systems because of the large numbers of delicate invertebrates they support and their sensitivity to human-induced damage (14, 15). However, discoveries over the last two decades suggest that reefs may be more physically robust than previously understood. In many regions, they are periodically subjected to severe storm damage from which they can rapidly recover (16, 17), if the primary effect of the storms is physical damage to corals caused by waves. A potentially more damaging effect is sediment-laden freshwater runoff. In coastal areas, storms can produce large volumes of sediment carried by runoff, depending on the condition of the watershed from which it comes. Storm inputs from pristine watersheds are generally small and dispersed rapidly, causing little permanent damage. For example, historic patterns of flood runoff onto the Australian Great Barrier Reef have been detected in the growth rings of very old coral colonies which repeatedly survived such events (18).

As pristine watersheds have become more developed, sediment runoff has become a greater problem (19). High rates of sedimentation degrade reefs by inhibiting coral growth, survival, reproduction, and settlement of coral larvae (20–23). A recent meeting of coral reef scientists identified increased sedimentation as one of the three greatest causes of reef degradation worldwide (11, 12). International concern about coral reef health has not yet matched the level of concern about rainforests, despite the sediment link between the two. The clearing of rainforests increases erosion rates, and much of the resulting sediment is carried to the sea where it can cause damage to nearshore coral reefs. As an example, high rates of rainforest clearing in certain parts of Costa Rica have led to severe degradation of coral reefs (24, 25).

In this paper we describe the impacts of a tropical storm with low winds, but high rainfall, on the coral reefs of St. Lucia, an island in the Lesser Antilles chain of the West Indies. The storm introduced large quantities of fine sediment onto nearshore reefs and we argue that human development activities in nearby watersheds greatly increased the severity of storm impact upon these reefs. The damage carries a potentially large economic cost and highlights the importance of integrating land-based activities into comprehensive coastal zone management strategies to ensure the long-term conservation of coral reef ecosystems. Despite its potentially severe effects, the relationship between sediment input and coral mortality has only been established previously in a qualitative sense, where damage is noted under extreme conditions (24) or through small-scale experiments (22, 26–29). We were able to look at reef damage over a continuum of sediment input intensities in generally natural conditions and over a large spatial scale, allowing us to provide one of the clearest assessments to date of the negative consequences of sediment deposition on coral reefs.

## STORM DESCRIPTION

On the evening of 9 September 1994, a tropical depression began to affect the weather of St. Lucia. The heaviest rains persisted from about 3 a.m. to 7 a.m. on 10 September, during which time the tropical depression was upgraded to Tropical Storm Debbie. These rains fell on ground already saturated from previous rainfall. In total, Debbie dropped over 20 cm of rain at each of St. Lucia's two airports, located at the north and south ends of the island. According to plantation records, rainfall is typically twice as high in the interior of the island (30). Debbie's primary impact was through heavy rainfall, as wind gusts never exceeded 75 km $hr^{-1}$ and steady winds never exceeded 52 km $hr^{-1}$ at either airport.

In the past 50 years, only one other storm—Tropical Storm Beulah in 1967—brought as much rain to St. Lucia. Much of Debbie's rain fell during just a few hours at an intensity which rivals any storm recorded in St. Lucia's past, according to limited historical records (30). In contrast, many storms brought higher seas and stronger winds, including Hurricane Allen in 1980. Allen caused a great deal of damage, but less erosion and flooding than Debbie.

In total, four people died, 24 were injured, and 300 left temporarily homeless by Debbie. These casualties resulted primarily from flooding and landslides. The high waters washed out eight bridges and left 5 cm of silt on airport runways. They also caused massive landslides, flooding, and erosion.

The damage on land gained most of the public attention, but the damage to marine communities may have been equally severe, costly, and lasting. One clear indicator of the storm damage was the large amount of sediment trapped in giant barrel sponges (*Xestospongia muta*), many of which still contained sediment three months after the storm. Another clear indicator was the amount of dead and bleached hard coral (31).

## METHODS

We set out to document coral reef damage caused by Tropical Storm Debbie and to determine whether this damage was related to land-use practices. We did so by measuring the quantity and quality of sediment deposits as well as type and degree of coral damage at 15 sites in both deep (15 m) and shallow (5 m) water. We chose locations at varying distances from the mouths of three rivers which differed in size and in the land-use practices within their catchment basins. Our goals were *(i)* to document the overall damage to nearshore coral reefs attributable to sediment runoff from the storm; *(ii)* to establish relationships between river size, distance from river mouth, site depth, and coral death; and *(iii)* to make inferences about the effects of various land-use practices on the marine environment.

We studied reefs near the mouths of three different river systems: Soufrière, Anse Galet/Anse La Raye, and Anse Mamin (Fig. 1). The Soufrière River basin was characterized by three prominent land-use features at the time of the storm: it was the most heavily settled of the three; it was the most heavily farmed; and it contained 2.7 km of the large-scale West Coast Road Project (32). The West Coast Road Project ran through a region of high rainfall and steep topography between the villages of Soufrière and Canaries. At the time of the storm, the road cutting had exposed soil over the entire distance between these villages. In comparison, the Anse Galet and Anse La Raye River basins had intermediate levels of settlement and agriculture, and the West Coast Road was completed in these basins in 1993 (32). Finally, the Anse Mamin River basin had the least settlement and agriculture, but did contain 2.4 km of the West Coast Road Project (32). The Soufrière River is the largest of the three, containing 44.1 $hm^3$ (1 hm = 0.1 km) of water. Anse Mamin is the smallest , containing only 8.2 $hm^3$ of water. The Anse Galet and Anse La Raye Rivers are intermediate in size, containing approximately 12.7 and 37.2 $hm^3$ of water each (32). For analyses, we had to integrate the effects of the Anse Galet and Anse La Raye Rivers, whose mouths emerge within 800 m of each other. Doing so gave us an effective river size of 29.3 $hm^3$ (33).

We collected data from three locations near each of the Soufrière and Anse Mamin rivers, and from two locations near the Anse Galet/Anse La Raye rivers. At each location, with one exception, we collected information at 5 and 15 m depth. We were unable to survey both depths at the location 500 m from the mouth of the Anse Mamin River because this location only had deep reef. At each site (defined as one depth at a given lo-

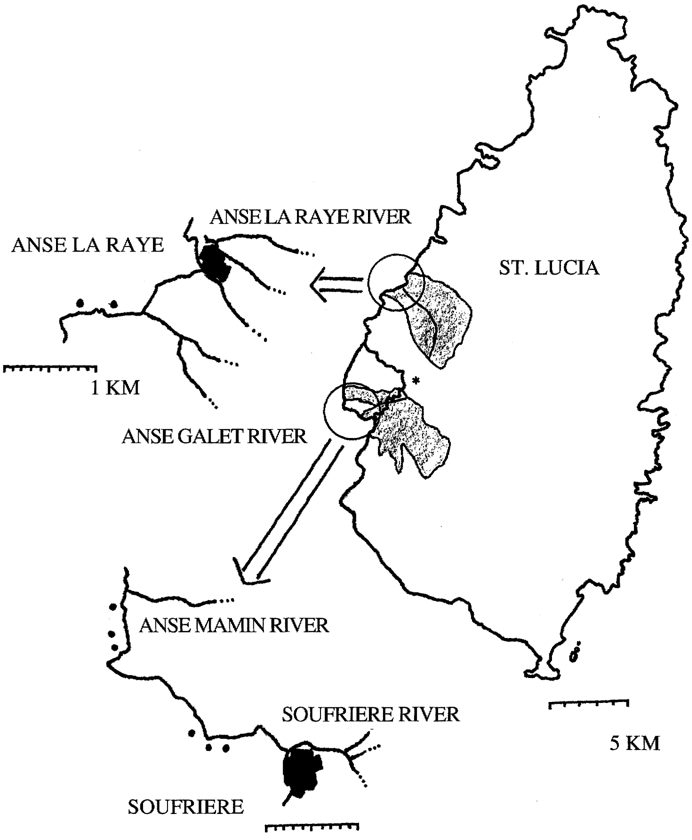



**Figure 1. Survey sites on St. Lucia (32). The enlargements show survey locations (•) relative to villages (dark shaded) and river systems. The map of St. Lucia shows the West Coast Road Project (*) and the drainage basins of, from north to south, the Anse La Raye, Anse Galet, Anse Mamin, and Soufrière Rivers, indicated by light shading. Island map survey locations, rivers, and their drainage basins.**

cation), we collected the following data: mud thickness, sediment texture and organic content, and indices of coral mortality and bleaching.

### Sediment Deposition

In early December 1994, approximately two months after the storm, we measured the thickness of the fine clay-like mud layer, if present, in at least 10 'hollows' per site. These hollows formed from the structure of the reef, and served as natural sediment traps. At most sites, a clay-like layer overlaid a coarser sand-like sediment, which probably originated on the reef. We measured the thickness of the mud to the nearest millimeter using a pencil probe and ruler. We gently pressed the blunt side of the pencil into the sediment until feeling an abrupt increase in resistance, and then measured the depth to which the pencil had been pushed. This method worked better than cores taken with clear plastic straws because the coring technique clearly compressed the mud.

At every second hollow, we collected a sediment sample to be analyzed for texture and organic content. We pressed a plastic bag (15 x 17 cm) with small holes in its bottom into the sediment to core out a consistently-sized sample. This bag was then immediately placed in a labeled bag for storage. The samples, which included sand-like as well as clay-like sediments, were analyzed for soil texture and organic content.

Soil texture can be quantified as the proportion of soil mass made up of sand, silt, and clay particles—defined as 2.0 to 0.05, 0.05 to 0.002, and 0.002 or fewer mm in diameter, respectively. Silt and clay particles indicate a land-origin of sediments. Similarly, even low levels of organic material indicate land-originated sediments. We measured texture using a standard hydrometer technique (34–36), and organic content using sodium dichromate and a colorimeter (37).

These sediment analyses complemented a time-series of sediment deposition at two of the locations in our study. We measured sediment rates at these sites from the quantity of sediment that accumulated in cylindrical vessels (sediment traps) fixed to the reef over a known period of time. Each sediment trap consisted of a PVC tube with an internal diameter of 41 mm and a height of 160 mm, capped at the base. The aspect ratio of our traps fell within values of maximal efficiency (38). At each station, we placed traps into two PVC sockets cemented to the reef 2.0 mm apart. We established two stations at 15 m depth 500 m from the mouth of the Anse Mamin River, and two at 6 m depth 650 m from the mouth of the Anse Mamin River. We periodically capped and removed traps, replacing them with new units immediately. Thus, we were able to sample continuously. We filtered trap contents with suction through Whatman No. 1 paper. We then dried the paper plus sediment at 70°C to constant weight before weighing. After subtracting the weight of the paper, we divided the sediment weight by the area of the sediment trap's cross-sectional area and by the number of days it had been in the field to convert it to a sedimentation rate (mg $cm^{-2}$ $d^{-1}$).

### Coral Damage

In early October, less than a month after the storm, we performed photo transects at 15 m depth at three of our locations—400 and 800 m from the mouth of the Anse Galet River, and 1000 m from the mouth of the Soufrière River (Fig. 1) (31). A transect consisted of 20 photographs, spaced one meter apart, each covering an area of 1.3 $m^2$ on average. We manually digitized each photograph to measure the percentage cover in four categories: nonbleached hard coral, bleached hard coral, mud-covered hard coral, and other. These initial results were compared with findings from surveys conducted at a greater number of locations in November and December.

From 24 November through 11 December 1994, we measured composition of the coral community and signs of damage using a random 1 $m^2$ quadrat method. At all sites but one (where only deep reef existed, as explained above), we surveyed 10 quadrats along both 5 and 15 m depth contours. We computer-generated random numbers between one and nine to determine the distances (in m) before the first and between subsequent quadrats, always moving in the same direction along the depth contour. Within each quadrat, we used visual techniques to estimate percent cover of massive (nonbranching) hard coral, branching hard coral, other organisms, rubble (loose rocks and other dead material) and sediment (including clay-like and sand-like varieties). Additionally, we measured the percent cover of recently killed and bleached massive hard coral. Coral bleaching is a sign of colony stress where symbiotic algal cells—zooxanthellae—either leave or are ejected from colonies (39), and is easy to identify by the white appearance of the colony region. We recognized recent hard coral mortality using two indicators: *(i)* well-preserved corallite detail without significant overgrowth; and *(ii)* flat borders between dead and living regions of the same colony. The first indicator demonstrated that insufficient time had passed for corallite detail to be eroded and for microorganisms to colonize the dead coral surface. The second indicator showed that insufficient time had elapsed for the live coral regions to grow above adjacent dead regions—if a coral colony region had died a longer time ago, the live region would have grown higher than the adjacent dead region. We assumed that the region had been killed recently only if both indicators were present. When we could not distinguish whether a colony region was bleached or extremely recently killed, we assumed it was bleached to make our estimates of coral mortality conservative rather than inflated.

We then calculated damage indices to correct for overall massive hard coral percent cover. To determine the proportion of coral that had been killed recently, we divided the percent cover of dead hard coral at a site by the percent cover of living plus recently dead hard coral. To ascertain the proportion of living coral showing signs of bleaching, we divided the percent cover of bleached hard coral by the percent cover of living hard coral.

Finally, we conducted statistical analyses on our data. We primarily used multiple regression analysis, a technique that tests the significance of several factors independently of each other. Thus, we could contrast the coral community or sediment at various sites and both assess and factor out the size of the nearest river, the distance of the site from the river mouth, the depth of the site, and other differences among the three rivers. For all multiple regression analyses, we treated each sample or quadrat as a separate replicate.

We used standard linear regression when examining the relationships between the thickness of the mud layer and coral damage. We did not require a multiple regression model for these analyses because we were interested in only a single independent variate. Because mud thickness and coral damage data were collected in separate surveys, a replicate from one data set did not correspond to a replicate from the other. Consequently, we averaged the replicates within sites and treated each site as a replicate. This process sacrificed statistical power but eliminated the problem of correspondence among our replicates. We used a significance level of 0.05 for all statistical tests, but also noted marginally significant results with a significance between 0.05 and 0.1.

## RESULTS

### Sediment Deposition

The thickness of the clay-like sediment layer varied predictably with size of the nearest river to the site, distance of the site from the river mouth, and depth of the site (40). As would be expected, sediment levels were higher at sites closer to river mouths (Fig.

2a) and near big rivers (Fig. 2b) (40). In addition, sediment levels were higher at 15 than 5 m depth (Fig. 2c) (40). Moreover, several interaction terms were significant, including the three-way interaction between river size, distance from river mouth, and depth (40). However, the pattern of sediment levels remained consistent across river size, distance from river mouth, and depth. Once these factors were taken into account, a river effect was still able to explain a marginally significant portion of the residual remaining from this analysis (41), suggesting that there were differences among the rivers in how much sediment they carried. Specifically, the Anse Mamin and Soufrière sites had more mud than the Anse Galet/Anse La Raye sites once patterns based on river size, distance from river mouth, and depth were accounted for (41) (Fig. 2d). In other words, all other things being equal, sediment levels were higher on reefs in the vicinity of the Soufrière or Anse Mamin rivers than in the vicinity of the Anse Galet/Anse La Raye rivers.

Our sediment traps confirmed the dramatic increase in sedimentation rates following the storm. During the six days after Debbie, sediment traps at two of our less-impacted sites accumulated sediment at average rates of 11.71 and 64.32 mg $cm^{-2}$ $d^{-1}$. These rates exceeded average rates from 1989 through 1994, which were generally below 2 mg $cm^{-2}$ $d^{-1}$, and also exceeded typical yearly maximums of 7 to 9 mg $cm^2$ $d^{-1}$ (42). We used these two estimates along with the corresponding mud thickness measurements at each site to generate the following formula relating sedimentation rate to the thickness of the mud layer at the time of our survey.

$$R = 50.545 \cdot D^{0.769},$$

where $R$ is the rate of sediment deposition in mg $cm^{-2}$ $d^{-1}$, and $D$ is the depth in cm of clay-like sediment found at a location during our surveys. This formula was statistically untestable because it was based on only two points. If we use this formula to extrapolate other mud thickness measurements, we find that sedimentation rates met or exceeded 100 mg $cm^{-2}$ $d^{-1}$ at six sites with the highest rate topping 260 mg $cm^{-2}$ $d^{-1}$. We find these estimates intriguing, but caution that they are based on a formula that remains untested and that they all fall above the values used to generate the formula.

As with sediment quantity, the proportion of sediment falling into silt and clay categories increased with increasing proximity to the river mouth (Fig. 3a), river size (Fig. 3b), and depth (Fig. 3c) (43). There was a significant statistical interaction between river size and site depth (43). The interaction term suggested that deep sites near large rivers received relatively more silt and clay. Once these factors were accounted for, there were no significant differences among rivers in the amount of silt and clay.

Organic content in sediments also increased with proximity to river mouth (Fig. 4a), increasing river size (Fig. 4b), and depth (Fig. 4c) (44). No interactions among these effects were significant. As with the amount of silt and clay, once river size, distance from river mouth, and depth were accounted for, there were no significant differences among rivers in organic content.

Sediment deposition was an important indicator of reef condition because it explained significant variation in both the dead and bleached massive hard coral indices. We found higher coral mortality (Fig. 5a) and bleaching (Fig. 5b) at sites with thicker mud layers (45). Mud thickness explained coral mortality particularly well, demonstrating the strong link between sedimentation and reef degradation.

## Coral Damage

In our October survey, less than a month after the storm, we found a great deal of mud covering three reefs (Table 1), with some coral showing signs of bleaching (31). Most coral, however, was buried. Thirty to 55% of the reef was covered in mud in October, and this resulted in 5 to 32% dead coral cover in

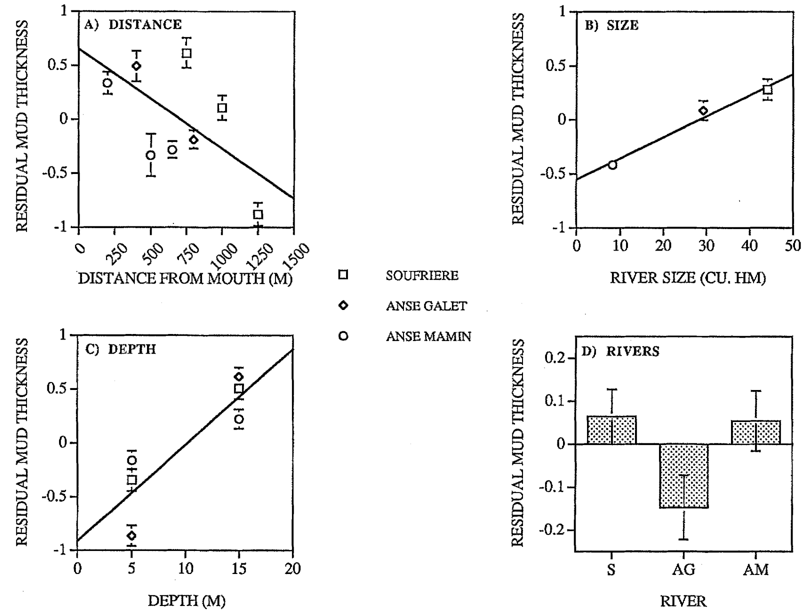



**Figure 2. Thickness of mud layer. Mud thickness increased with proximity to; river mouth (a); river size (b); and depth (c) (40). For these three graphs and all subsequent graphs, excepting only Figure 5, data points represent statistical residuals, and error bars represent one standard error. The residuals are generated by mathematically adjusting each point to remove the effects of other factors. The residual data values then illustrate the effect of the factor of interest in the absence of other factors. Once all three factors and their interactions were accounted for, we found differences among the three river basins, with less sediment at sites near the Anse Galet River mouth (d) (41).**

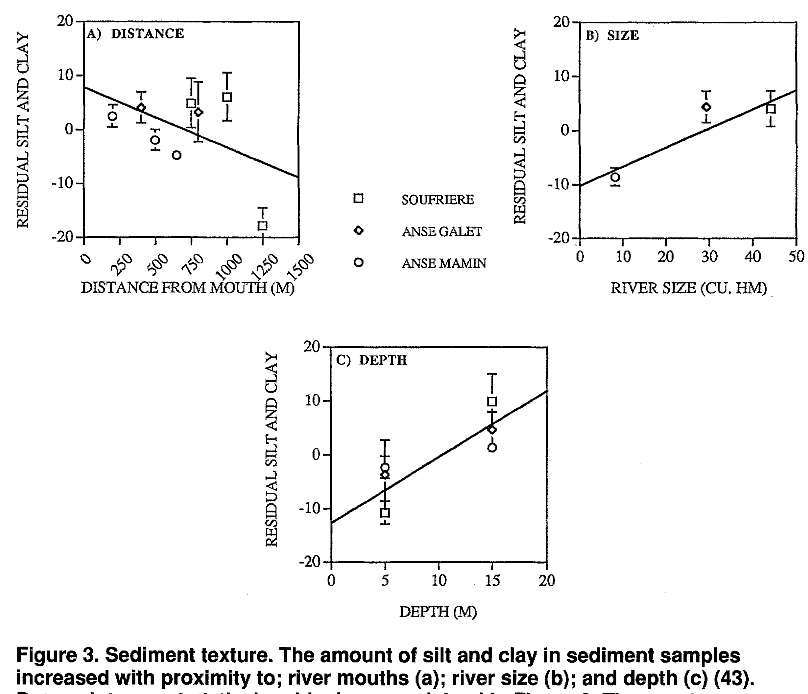



**Figure 3. Sediment texture. The amount of silt and clay in sediment samples increased with proximity to; river mouths (a); river size (b); and depth (c) (43). Data points are statistical residuals, as explained in Figure 2. These patterns closely resembled those of sediment deposition (Fig. 2), suggesting that sediments originated on land.**

November and December (equal to 14.2 to 53.9% coral mortality). The mud cover decreased from October to November and December, exposing dead coral (Table 1). However, the decrease in mud corresponded with an increase in live coral (Table 1). These results suggest either *(i)* that the polyps survived burial for the month between the storm and our first survey; or *(ii)* that the coral colonies were able to repair/regrow damaged regions in the two months between our first and second surveys.

Our November and December surveys revealed that coral mortality increased with proximity to river mouths (Fig. 6a), size of the river (Fig. 6b), and depth of the site (Fig. 6c) (46). There were many significant interactions, but the overall pattern was quite similar to that of mud thickness (Fig. 2). Differences among the rivers did not explain a significant amount of the residual after the analysis of the three main effects.

The relationship between coral bleaching and river size, distance from river mouth, and depth below sea level was more variable. Only the size by depth interaction term was statistically significant with distance from river mouth showing marginal significance (47). Generally speaking, these terms suggested an increase in bleaching with proximity to river mouths (Fig. 7a) and at greater depths (Fig. 7b). We had expected bleaching to show less clear patterns since so much coral died, leaving only coral that got mildly stressed to fall into this category.

## DISCUSSION

We found considerable damage to the nearshore reefs of St. Lucia's southwest coast after Tropical Storm Debbie, with coral mortality exceeding 50% at the most-heavily impacted site in our survey. This degree of damage will take years to offset, given the slow growth rates of corals (48) and the fact that, for modular organisms like coral, overall growth rate is slower when less exists (49). Recovery will also be inhibited by the continued presence of clay-like sediments on the reefs. The small particle size of these sediments will cause chronic stress to existing corals and will reduce rates of recolonization by settling corals (21, 22).

Four pieces of evidence show that sediments from land caused the bulk of the damage. First, we observed large quantities of clay-like sediments shortly after the storm in areas where this type of sediment is usually absent (Table 1). Second, patterns of sediment deposition indicated that sediment came from land via the rivers (Fig. 2). Third, soil texture and organic content analyses point towards a land-based origin of the clay-like sediments (Figs 3 and 4). Finally, we found higher levels of dead and bleached coral in areas with thicker layers of clay-like sediment (Fig. 5), strongly suggesting that the sediment was primarily responsible for the damage.

We believe that intensive land-use practices in each of the river basins contributed to erosion, landslides, and flooding, all of which increased sediment deposition on reefs. The west coast of St. Lucia is in a phase of rapid development, including construction and intensive agriculture. These practices have been shown to contribute to erosion elsewhere (19), and the rugged topography of St. Lucia made the land all the more susceptible to soil loss.

Moreover, our data show that a road construction project taking place in the drainage basins of the Anse

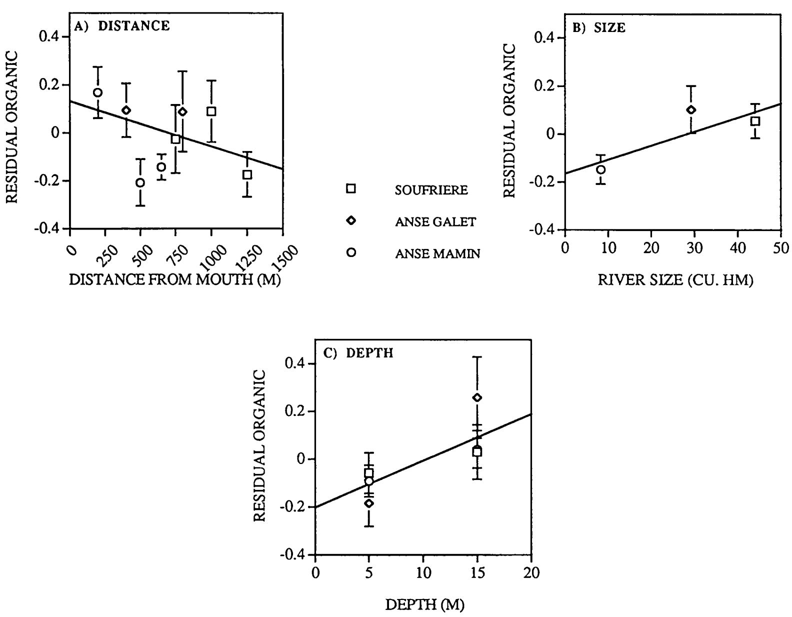



**Figure 4. Organic content. The organic content in sediment samples increased with proximity to; river mouths (a); river size (b); and depth (c) (44). Data points are statistical residuals, as explained in Figure 2. These patterns closely resembled those of sediment deposition (Fig. 2), suggesting that sediments originated on land.**

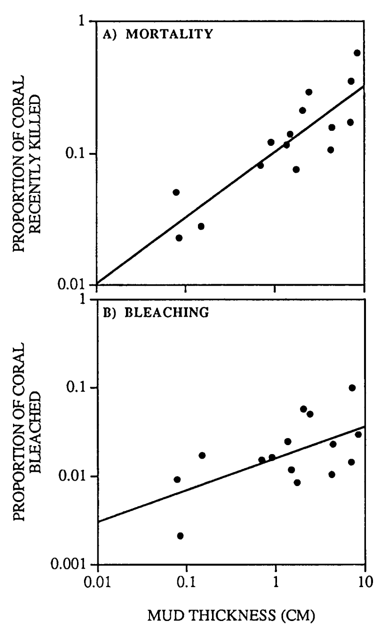



**Figure 5. Coral damage and mud thickness. We found more coral mortality (a) and bleaching (b) at sites with thicker mud layers (45). Each data point represents the average coral damage and mud thickness at a site. Log-log plots represent statistical transformations used in analyses.**

**Table 1. Changes in mud cover and coral death through time. Comparison of data collected in early October (31) and in November and December at three locations, indicated by the name of the closest river and the distance of the location from the river mouth. "Live %" represents the percent cover of healthy hard corals (branching and nonbranching). "Bleach %" represents the percent cover of bleached hard coral, an indication of stress. "Mud %" represents mud cover in October, and mud and rubble cover in November and December. "Dead %" represents the percent cover of recently killed hard coral. "Mud + dead" is the sum of these two numbers in November and December, and is presented to facilitate comparison with what had been buried in October. Finally, "other %" represents the percent cover of any other organisms or bare space.**

| Site | Anse Galet (400 m) | | Anse Galet (800 m) | | Soufrière (1000 m) | |
|---|---|---|---|---|---|---|
| Date | Oct | Nov/Dec | Oct | Nov/Dec | Oct | Nov/Dec |
| Live % | 23.8 | 27.4 | 29.9 | 34.5 | 35.6 | 43.7 |
| Bleach % | 0.9 | 0.7 | 0.8 | 0.7 | 0 | 0.56 |
| Mud % | 54.3 | 14.0 | 33.4 | 15.9 | 36.0 | 20.6 |
| Dead % | — | 32.0 | — | 5.7 | — | 8.0 |
| Mud + Dead | 54.3 | 46.0 | 33.4 | 21.6 | 36.0 | 28.6 |
| Other % | 21.0 | 25.9 | 36.3 | 43.2 | 28.6 | 27.1 |

Mamin and Soufrière rivers increased overall sediment deposition onto reefs. Sediment levels, once corrected for river size, distance from river mouths, and site depths below sea level, were higher at sites near the mouths of the two rivers whose basins contained the road project. Since this project involved blasting, landscaping, and clearing of vegetation, it was an obvious source of sediment. The road builder used conscientious erosion control practices, including revegetation of denuded slopes, establishment of catchment dams below the road, and careful choices of sites for sub-base sources and soil disposal (50). These measures maintained normal sediment deposition rates onto nearshore reefs 650 m away from the Anse Mamin River during periods of normal rainfall and prevented any landslides along the road project from Tropical Storm Debbie. However, this study shows that even a responsibly conducted major road project can cause significant increases in sediment deposition, especially if the project coincides with a storm bringing heavy rainfall. Our results complement another recent study which identified unpaved roads as a major contributor to erosion and transport of soils (51).

The economic impacts of Debbie will continue to grow through negative effects on tourism and fisheries. Eco-tourism, including snorkeling and SCUBA diving, has become big-business on St. Lucia and grows every year. Anbaglo, St. Lucia's Diving Association, estimates that 3000 to 4500 dives took place each month during 1994, almost all in the areas of our study. Mud, reduced coral cover, and a decline in underwater visibility at impacted sites decrease their attractiveness for diving, and will continue to do so well into the future due to slow recovery. Moreover, the damage will reduce the capacity of the reefs to sustain heavy visitation. Divers and snorkelers can inadvertently degrade reef communities by physically damaging colonies or by resuspending sediments, and heavily-dived reefs show clear signs of damage (9, 10). If St. Lucia is to pursue a policy of sustainable tourism development based around the carrying capacity of reefs for tourism, then a cap on tourism growth will soon be reached and that level will be lower as a result of storm damage.

Coral reef fish stocks in St. Lucia are already heavily overfished, reducing fishery productivity to well below maximum levels (52). Reef degradation will further undermine the productive capacity of reefs (22, 53). St. Lucia's reef fisheries provide a livelihood and food for large numbers of people, especially the poor. Reef degradation from the storm will exacerbate the problem of dwindling stocks faced by these fishers.

In this study, we have shown how land development can increase the risk of severe damage to coral reefs by sediment runoff during storms. Although not many storms bring as much rain as Debbie, St. Lucia has experienced such storms twice in the past 50 years (30). Furthermore, global warming may contribute to more frequent and severe storms (54, 55). If land development continues at its current pace, the reefs of St. Lucia are in peril, as 25 years is probably inadequate for the most severely damaged reefs to recover fully—even under favorable conditions. And yet, the conditions are not favorable. Smaller storms, occurring several times yearly, can carry sediments to nearshore reefs and cause chronic stress, adding to the stress from fishing and tourism. Loss of soil causes economic impacts on land and underwater (19, 56) and stemming these losses represents both an urgent conservation priority and economic imperative.

## References and Notes


1. Reaka-Kudla, M.L. 1995. The global biodiversity of coral reefs: a comparison with rainforests. In: *Biodiversity II: Understanding and Protecting Our Resources.* Reaka-Kudla, M.L., Wilson, D.E. and Wilson, E.O. (eds). National Academy/Joseph Henry Press.
2. Thorne-Miller, B. and Catena, J.G. 1991. *The Living Ocean.* Island Press, Washington, DC.
3. Williams, D.M. and Hatcher, A.I. 1993. Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser. 10,* 239–250.
4. McAllister, M.K. and Peterman, R.M. 1992. Experimental design in the management of fisheries: a review. *N. Am. J. Fish. Mgmt 12,* 1–18.
5. Roberts, C.M. and Polunin, N.V.C. 1994. Hol Chan: demonstrating that marine reserves can be remarkably effective. *Coral Reefs 13,* 90.
6. Munro, J.L. and Williams, D.M. 1985. Assessment and management of coral reef fisheries: biological, environmental, an socio-economic aspects. In: *5th International Coral Reef Congress.* Tahiti, pp. 545–581.
7. Johannes, R.E. and MacFarlane, J.W. 1991. *Traditional Fishing in the Torres Strait Islands.* Commonwealth Scientific and Industrial Research Institute, Hobart.
8. Polunin, N.V.C. and Roberts, C.M. (eds). 1997. *Tropical Reef Fisheries.* Series in Fish

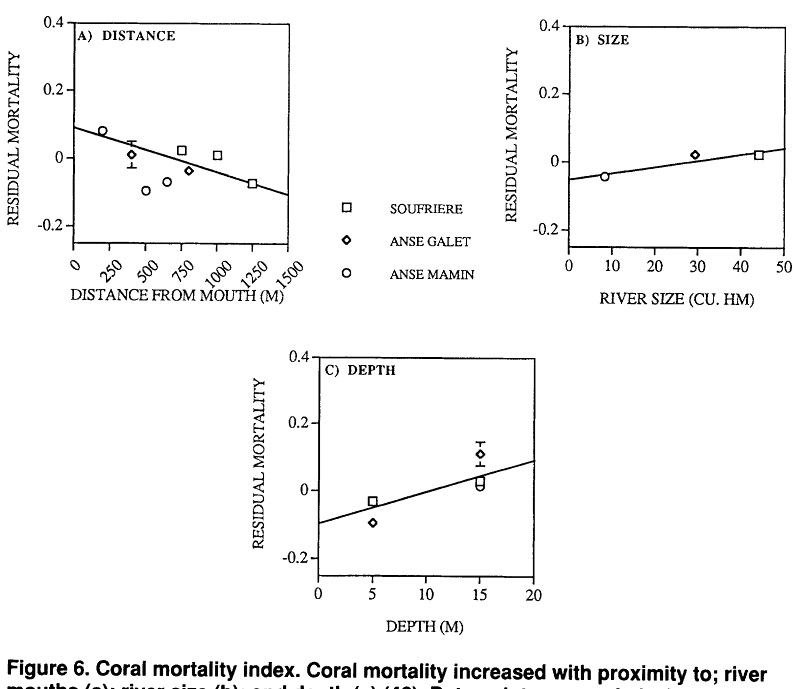




**Figure 6. Coral mortality index. Coral mortality increased with proximity to; river mouths (a); river size (b); and depth (c) (46). Data points are statistical residuals, as explained in Figure 2. These patterns closely resembled those of sediment deposition (Fig. 2), suggesting that land-based sediments kill corals.**

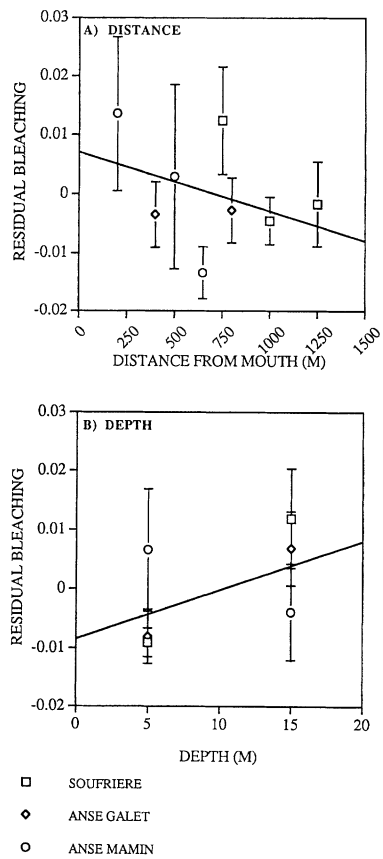



**Figure 7. Bleached coral. Coral bleaching increased with proximity to; river mouths (a); and depth (b). Data points are statistical residuals, as explained in Figure 2. These patterns are much less clear than others from this study, as exemplified by the lack of statistical significance for many of the patterns (47) and by the large error bars.**

Biology and Fisheries. Chapman and Hall. London. (In press).
9. Dixon, J.A., Fallon Scura, L. and van't Hof, T. 1993. Meeting ecological and economic goals: marine parks in the Caribbean. *Ambio 22*, 117–125.
10. Hawkins, J.P. and Roberts, C.M. 1994. The growth of coastal tourism in the Red Sea: present and future effects on coral reefs. *Ambio 23*, 503–508.
11. Roberts, C.M. 1993. Coral reefs: health, hazards and history. *Trends Ecol. Evol. 8*, 425–427.
12. Ginsburg, R.N. (ed.). 1994. *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History.* Rosenstiel School of Marine and Atmospheric Science, University of Miami. Miami.
13. Sebens, K.P. 1994. Biodiversity of coral reefs: what are we losing and why? *Am. Zool. 34*, 115–133.
14. Kühlmann, D.H.H. 1988. The sensitivity of coral reefs to environmental pollution. *Ambio 17*, 13–21.
15. Wells, S.M. and Hanna, N. 1992. *The Greenpeace Book of Coral Reefs.* Blanford, London.
16. Shinn, E.A. 1976. Coral reef recovery in Florida and the Persian Gulf. *Environ. Geol. 1*, 241–254.
17. Rogers, C.S. 1993. Hurricanes and coral reefs: the intermediate disturbance hypothesis revisited. *Coral Reefs 12*, 127–137.
18. Isdale, P. 1984. Fluorescent bands in massive corals record centuries of coastal rainfall. *Nature 310*, 578–579.
19. Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R. and Blair, R. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science 267*, 1117–1123.
20. Edmunds, P.J. and Spencer Davies, P. 1989. An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. *Coral Reefs 8*, 37–43.
21. Hodgson, G. 1990. Sediment and the settlement of larvae of the reef coral *Pocillopora damicornis. Coral Reefs 9*, 41–43.
22. Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser. 62*, 185–202.
23. Te, F.T. 1992. Response to higher sediment loads by *Pocillopora damicornis* planulae. *Coral Reefs 11*, 131–134.
24. Cortés, J. and Risk, M.J. 1985. A reef under siltation stress: Cahuita, Costa Rica. *Bull. Mar. Sci. 36*, 339–356.
25. Hands, M.R., French, J.R. and O'Neill, A. 1993. Reef stress at Cahuita Point, Costa Rica: anthropogenically enhanced sediment influx or natural geomorphic change? *J. Coastal Res. 9*, 11–25.
26. Rice, S.A. and Hunter, C.L. 1992. Effects of suspended sediment and burial on scleractinian corals from west central Florida patch reefs. *Bull. Mar. Sci. 51*, 429–442.
27. Stafford-Smith, M.G. and Ormond, R.F.G. 1992. Sediment rejection mechanisms of 42 species of Australian scleractinian corals. *Aust. J. Mar. Freshwater Res. 43*, 683–705.
28. Stafford-Smith, M.G. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. *Mar. Biol. 115*, 229–243.
29. Riegl, B. 1995. Effects of sand deposition on scleractinian and alcyonacean corals. *Mar. Biol. 121*, 517–526.
30. Devaux, R.J. 1994. *A Century of Rain Storms Over St. Lucia, 1894-1994.* St. Lucia National Trust. Castries, St. Lucia.
31. Siirila, E. 1995. *Coral Cover on Four Reef Sites in St. Lucia After Tropical Storm Debbie: An Assessment.* ENCORE-Local Site Management Team, Ministry of Planning. Castries, St. Lucia.
32. Laboratory for Computer Information Mapping and Analysis of the University of Pennsylvania. 1984. *Saint Lucia Development Maps.* Organization of American States, Philadelphia.
33. We used the decreasing relationship of sediment input as seen in the Soufrière and Anse Mamin Rivers to determine the extent to which sediment from the Anse La Raye River would have dissipated by the time the water mass reached the Anse Galet River (the Anse Galet River was closer to our sampling locations). This analysis gave us a dissipation factor of 0.444. To determine the effective size of the combined Anse Galet and Anse La Raye Rivers, we multiplied the size of the Anse La Raye River by the dissipation factor and added this product to the size of the Anse Galet River, yielding an effective river size of 29.3 $hm^3$.
34. Soil analyses were conducted by the Cooperative Extension Service's Diagnostic Laboratory for Soil, Plant and Water Analyses at the University of the Virgin Islands. Stoke's Law of particles moving through viscous fluids allow the use of a hydrometer to measure the relative amounts of sand, mud, and clay particles in a given sample. First, they weighed out 49.9 g dry weight of each soil sample, after it had been ground in a grinder, and divided this amount equally among four 250 mL flasks. The grinder was used to break up clots and does not split individual sediment grains into smaller pieces. They then added 25 mL of calgon solution and 75 mL of deionized water to each flask, and agitated them for 30 minutes on an electronic shaker. Next, they emptied the contents of all four flasks into a texture cylinder, filled the cylinders with deionized water to 7.7 cm below a 1 L mark, placed a hydrometer into the cylinder, and filled the cylinder fully to the 1 L mark. They recorded the temperature of the solution and suspended the sediment with three inversions of the cylinder (with the hydrometer temporarily removed), noting the exact time when the third inversion was completed. They then read the hydrometer after 40 seconds and after 2 hours. At two hours, they also recorded the temperature of the solution. These temperature and hydrometer readings correlate with specific proportions of clay, silt, and sand particles according to specific formulae (35, 36). After 40 seconds, all the sand particles should have settled out, and only silt and clay remained. After 2 hours, negligible amounts of silt particles remained, so the reading indicated the amount of clay.
35. Bouyoucos, G.H. 1951. A recalibration of the hydrometer for making mechanical analysis of soils. *Agron. J. 43*, 434–438.
36. Day, P.R. 1953. Experimental confirmation of hydrometer theory. *Soil Sci. 75*, 181–186.
37. Soil analyses were conducted by the Cooperative Extension Service's Diagnostic Laboratory for Soil, Plant and Water Analyses at the University of the Virgin Islands. In this technique, the soil lab placed 1 mL of soil, 6 mL of a 100g $L^{-1}$ sodium dichromate solution and 4 mL of concentrated sulfuric acid solution into a beaker. After the solution had cooled, they added 25 mL of Superfloc™ 127 solution (50 mg $L^{-1}$), mixed it thoroughly by swirling, and let stand for 30 minutes. Finally, they combined 2 mL of supernatant from the resulting mixture with 10 mL of water, and read percent transmittance in a colorimeter set at 650 nm using a 2 cm cuvette. This reading was converted into percent organic matter using a standard curve (Dale Morton, Soil Analysis Laboratory, University of the Virgin Islands, personal communication).
38. Gardner, W.D. 1980. Field assessment of sediment traps. *J. Mar. Res. 38*, 41–52.
39. Glynn, P.W. 1991. Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol. Evol. 6*, 175–179.
40. Multiple regression on mud thickness transformed to ln(depth + 1) for normality. Whole model: adjusted $r^2 = 0.623$; $F_{7,146} = 37.1153$, $p < 0.0001$. Distance: $F_{1,146} = 21.2457$, $p < 0.0001$. River size: $F_{1,146} = 2.7816$, $p < 0.10$. Depth: $F_{1,146} = 3.4117$, $p < 0.07$. River size x Distance x Depth: $F_{1,146} = 14.2923$, $p < 0.0002$.
41. One-way ANOVA of river basin on the residual sediment thickness: $F_{2,144} = 2.7481$, $p < 0.07$. Tukey Honestly Significant Difference Method, Anse Galet/Anse La Raye versus Anse Mamin: $p \approx 0.05$; Anse Galet/Anse La Raye versus Soufrière: $p < 0.04$.
42. Smith, A. 1994. *Sedimentation Rates on Coral Reefs at Anse Chastinet, St. Lucia, 1989–1994.* Caribbean Natural Resources Institute. Vieux Fort, St. Lucia.
43. Multiple regression analysis on silt plus clay. Whole model: adjusted $r^2 = 0.453$; $F_{4,59} = 14.0322$, $p < 0.0001$. Distance: $F_{1,59} = 13.2000$, $p < 0.0006$. River size: $F_{1,59} = 1.7204$, $p > 0.19$. Depth: $F_{1,59} = 0.0457$, $p > 0.8$. River size X Depth: $F_{1,59} = 6.2293$, $p < 0.02$.
44. Multiple regression analysis on organic content transformed to ln(org+1) for normality. Whole model: adjusted $r^2 = 0.126$; $F_{3,71} = 4.5400$, $p < 0.006$. Distance: $F_{1,71} = 4.3797$, $p < 0.04$. River size: $F_{1,71} = 9.4770$, $p < 0.003$. Depth: $F_{1,71} = 5.1690$, $p < 0.03$.
45. Standard linear regression analyses on mud thickness and coral damage ln-ln transformed for normality. Coral mortality: adjusted $r^2 = 0.737$, $F_{1,13} = 40.1707$, $p < 0.0001$. Coral bleaching: adjusted $r^2 = 0.315$, $F_{1,13} = 7.4496$, $p < 0.02$.
46. Multiple regression analysis on coral mortality transformed to ln(mort+1) for normality. Whole model: adjusted $r^2 = 0.486$; $F_{7,136} = 20.3054$, $p < 0.0001$. Distance: $F_{1,136} = 6.8072$, $p < 0.02$. River size: $F_{1,136} = 8.2438$, $p < 0.005$. Depth: $F_{1,136} = 0.0391$, $p > 0.1$. Distance X Size X Depth: $F_{1,136} = 6.7947$, $p < 0.02$.
47. Multiple regression analysis on coral bleaching transformed to ln(bleach+1) for normality. Whole model: adjusted $r^2 = 0.069$; $F_{4,138} = 3.6149$, $p < 0.008$. Distance: $F_{1,138} = 2.9238$, $p < 0.09$. River size: $F_{1,138} = 3.4043$, $p < 0.0672$. Depth: $F_{1,138} = 1.6780$, $p > 0.1$. Size X Depth: $F_{1,138} = 5.2681$, $p < 0.025$.
48. Buddemeier, R.W. and Kinzie, R.A.I. 1976. Coral growth. *Oceanogr. Mar. Biol. Ann. Rev. 14*, 183–225.
49. Harvell, C.D., Caswell, H. and Simpson, P. 1990. Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea* L.). *Oecologia 82*, 227–237.
50. Halcrow Fox. 1994. *St. Lucia West Coast Road Project: Erosion Control Measures for Mamin River and Anse Chastinet Catchments.* British Development Division of the Caribbean, Overseas Development Administration. UK.
51. Anderson, D.M. 1994. *Analysis and Modeling of Erosion Hazards and Sediment Delivery on St. John, U.S. Virgin Islands.* Master's Thesis, Department of Earth Resources, Colorado State University, Ft. Collins, CO.
52. Roberts, C.M., Sladek Nowlis, J. and Hawkins, J.P. 1995. *Status of Reefs and Reef Fish Stocks in St. Lucia.* Eastern Caribbean Center, University of the Virgin Islands. St. Thomas, U.S. Virgin Islands.
53. Hatcher, B.G., Johannes, R.E. and Robertson, A.I. 1989. Review of research relevant to the conservation of shallow tropical marine ecosystems. *Oceanogr. Mar. Biol. Ann. Rev. 27*, 337–414.
54. Wendland, W.M. 1977. Tropical storm frequencies related to sea surface temperatures. *J. Appl. Meteor. 16*, 477–481.
55. Emmanuel, K.A. 1987. The dependence of hurricane intensity on climate. *Nature 326*, 483–485.
56. Hodgson, G. and Dixon, J.A. 1988. Measuring economic losses due to sediment pollution: logging versus tourism and fisheries. *Trop. Coast. Area Mgmt 3*, 5–8.
57. We wish to acknowledge the U. S. Agency for International Development's Historically Black Colleges and Universities Research Fund which provided the funding to carry out this research. We also wish to thank the Fisheries Department of St. Lucia, the Soufrière Foundation, and especially Jean-Thierry Winstel for assistance and logistical support. We are grateful to Dale Morton and Frank Drigo of the Cooperative Extension Service's Diagnostic Laboratory for Soil, Plant and Water Analyses at the University of the Virgin Islands for conducting sediment analyses, and to Julie Hawkins for her valuable help in the field. Finally, we are indebted to Rebecca Sladek Nowlis for her insightful comments on the manuscript.
58. First submitted 7 February 1996. Accepted for publication after revision 18 June 1996.

**Joshua Sladek Nowlis received his doctorate in ecology and evolutionary biology from Cornell University. He uses quantitative techniques to study several forms of human impacts on marine communities, including fishing and land development. His affiliation during the research was the University of the Virgin Islands, St. Thomas. His address: Northeast Fisheries Science Centre, NMFS-NOAA, 166 Water Street, Woods Hole, MA 02543, USA.**

**Callum Roberts is a lecturer in ecology at the Department of Environmental Economics and Environmental Management at the University of York, England, but worked at the University of the Virgin Islands during this study. He gained his PhD in reef-fish ecology from the University of York. He has broad interests in tropical coastal management and conservation, with a specialty in the design and function of marine reserves. His address: Dept. of Environmental Economics and Environmental Management, University of York, York, YO1 5DD, UK.**

**Allan Smith is a research scientist at the Caribbean Natural Resources Institute. He earned an MSc from McGill University in phycology and oceanography. Primary interests include ecology and cultivation of marine algae, and research that involves collaboration with resource users for the development of management strategies for artisanal fisheries, mangroves and coral reefs. His address: Caribbean Natural Resources Institute, Clarke Street, Vieux Fort, St. Lucia, West Indies.**

**Erkki Siirila is a technical advisor to the USAID-financed Environment and Coastal Resources (ENCORE) Project in the Eastern Caribbean. He received his MSc in tropical coastal management from Newcastle University. Before his current assignment in the ENCORE/WWF-US Project Office, Mr. Siirila worked as a staff member and consultant of UNDP, FINNIDA, and IUCN. His address: ENCORE/WWF, P.O. Box 1383, Castries, St. Lucia, West Indies.**