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PLEASE ADD TO TITLE THE WORD Historical Decline...

Decline in Coral Reef Growth After the Panama Canal

?1 The Panama Canal is near its vessel size and tonnage handling capacity, and Panamanians have decided to
?2 widen it. However, broadening the canal may have long-lasting pervasive impacts on marine coastal habitats, particularly on sensitive coral reefs. These potential impacts were never discussed during the national referendum as were other equally important issues, such as its effects on forests, watersheds, and water supply. Coral growth rates provide a direct measure of coral fitness and past environmental conditions comparable to analyses of tree rings. We examined stable isotopes, metal geochemical tracers, and growth rates on a century-long (1880–1989) chronology based on 77 cores of the dominant reef-building coral *Siderastrea siderea* collected near the Caribbean entrance to the canal. Our results showed a gradual decline in coral growth unrelated to changes in sea surface temperature but linked to runoff and sedimentation to coastal areas resulting from the construction and operation of the Panama Canal.

INTRODUCTION

Caribbean coral reefs are rapidly degrading and changing due to widespread natural and anthropogenic disturbances. Two problems plague the particular assessment of human effects on coral reefs: separation of the signal of human disturbance from the noise of natural environmental variation (1–3) and choice of appropriate measures of the health of coral populations and communities (3–6). The first detailed ecological description of Caribbean coral reefs is less than 45 years old, and the longest quantitative records extend back less than 35 years (7). However, generation times and longevities of reef corals, as well as the frequency of severe disturbances to the environment, are commonly measured in decades to centuries (4, 8–12). Thus, long-term measures of community composition and response to natural and anthropogenic environmental change require paleontological time series extending back thousands of years (13–15). Moreover, coral cover or abundance alone is a static measure of the health of reef corals that may be insensitive to decline in coral fitness due to pervasive stress (4, 16, 17) that is subsequently manifest in outbreaks of coral disease, overgrowth by algae, or coral bleaching. Coral growth rates, incidence of injuries, and rates of regeneration provide more direct measures of coral fitness comparable to vital signs measured by physicians to assess human health (3, 18, 19).

The coral reefs along the central Caribbean coast of Panama have been heavily exploited for the construction of forts since the 16th century (20), but human disturbance was greatly increased by the excavations for the French Canal in 1880; the American Canal in 1900; and intensive clearing and draining of land for settlement, mosquito control, and industrial activity (see Study Area). In contrast, the first ecological observations of coral reefs in the region began in the 1960s, and quantitative census of reef communities began only in the 1980s (17, 20). Coral communities in the 1960s were depauperate both in numbers of species and live coral cover compared with other localities along the coast (20), but it is difficult to say whether these differences reflect anthropogenic disturbance or naturally unfavorable conditions for coral community development (3, 20). One way to resolve the question of the possible effects of earlier human disturbance is by excavations through time to determine earlier (Holocene) community composition (13–15). However, the results for Panama are equivocal, because decreases in coral abundance may reflect growth of the reef to approximate sea level that obviously limits upward coral growth (21, 22). We chose instead to assess changes in coral fitness over time by historical analyses of rates of coral growth coupled with multiple geochemical tracers, to describe recent environmental changes in central Caribbean Panama.

Coupling coral growth patterns with C^{13}/C^{12} and metal tracers provides a robust approach to studying the effects of environmental stresses on reef corals and communities (23–27). Given that zooxanthellar photosynthesis increases the C^{13} concentration in the coral skeleton, increasing temperature or decreasing light weakens the isotopic signal (27–30). A decline in coral metabolism and growth and $\delta^{13}C$ indicates reduced photosynthesis and calcification due to increasing water turbidity or nutrients (28–30). Similarly, measuring Ba in coral skeletons has been successfully used as a proxy for runoff or river floods and lower salinity for being abundant in rivers and estuaries in relation to surface seawater (23, 26, 31). Indeed, seasonal Ba concentrations recorded in corals from Barbados were related to variations in water discharge from the Amazon River (23). Commonly abundant elements, such as Fe and Al, may also serve as terrigenous runoff indicators in coastal areas (32).

Study Area

The study area covers the central Caribbean coast of Panama in Bahia Las Minas, about 5 km off from the entrance to the Panama Canal (Fig. 1). Two marine protected areas including coral reef habitats are located downstream and easterly from the Panama Canal: Paisaje Protegido Isla Galeta (4 km) and Parque Nacional Portobelo (50 km).

Shallow fringing coral reefs occur along the central coast of Panama, rarely extending below 12 m and with maximum coral growth shallower than 6 m (17). After decades of environmental changes in the study area (see below), *Siderastrea siderea* is the solely dominant massive coral species that has thrived with greater abundance and development. Living coral reef cover has averaged 6% in the area since 1986, and no major recovering has occurred due to chronic pollution (17, 19, 20).

Historically, disturbances along this coastal zone began in the 1870s with excavation, dredging, landfilling, spraying of mangroves for mosquito control, and erosion due to the construction of the Panama Canal and the City of Colón. At the Caribbean entrance to the Panama Canal, about 20 million m^3 of terrigenous sediment, corals, and sand were excavated or dredged during 1882–1885 by the French Company, and the American Company removed 33 million m^3 during 1904–1907. Islands were transformed into peninsulas, and the town of Cristobal, the terminal basin of the Panama Canal, breakwaters, and 7 military bases were built on reefs. Several hectares of mangroves were dredged and filled with more than 1.9 million m^3 (underestimation due to missing records) of excavated coral

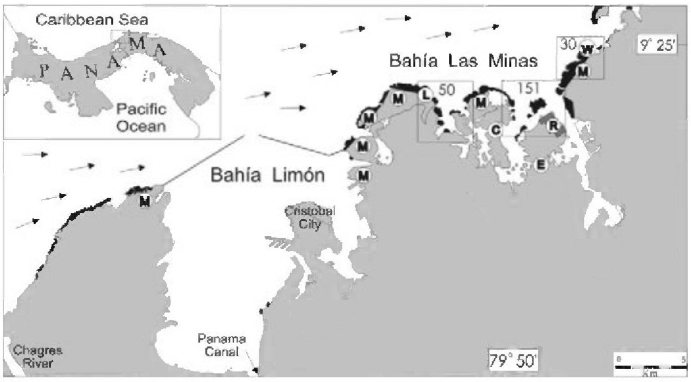

Figure 1. Map of the study area in central Caribbean Panama (upper-left insert). Bahía Las Minas is located approximately 5 km from the Caribbean entrance to the Panama Canal. Numbers represent total coral colonies drilled at reefs (shaded coastal areas) and used for developing master growth chronology (n = 231). Core samples (n = 3) used for isotope and metal analyses were each selected from 1-framed subareas. The *M, L, C, E, R,* and *W* show military sites developed after 1911, the Galeta Marine Laboratory, cement factory, electrical power plant, oil refinery, and *Witwater* tanker wreck, respectively. Arrows represent the direction of prevailing easterly marine currents.

rock and sand between 1904 and 1928 (20). Furthermore, between 1958 and 1974, more than 5 million m^3 of reef corals were dredged, 80 ha of mangroves were destroyed and filled, and ~~runways~~ were erected to construct a coastal refinery (17, 20). Oil spills affected beyond recovery coral reefs in the area in 1968 and 1986 (17, 19).

MATERIALS AND METHODS

We chose the massive coral *S. siderea* to obtain a proxy high-resolution measurement of local reef growth based on established criteria for a bioindicator species (25): outstanding temperature and salinity tolerance; low growth rates and considerably longevity; and resistance to sedimentation, oil pollution, and other pollutants. In addition, *S. siderea* is the dominant reef-builder species in the central coast of Panama (20). To develop an absolute time chronology for coral growth and geochemical tracers, sufficient extant specimens are required (27, 30). Massive colonies of the coral *S. siderea* with a size range from 1.0 to 2.5 m in diameter were drilled (n = 231 cores of 1 m × 9 cm) using a lightweight, hydraulically powered underwater drill from Bahía Las Minas (Fig. 1). Average coral depth was 2.1 m (range 1.5–3.0 m). Standard methods were used to process the cores (17, 33, 34), and the best 77 cores were selected by examining X-radiographs. Annual growth extension rates were measured from the previous year's outermost high-density band (e.g., 1989) from each colony using a Sigma-Scan 3.90 digitizer at a 0.001-mm resolution. Annual growth patterns were previously calibrated for the locality (17, 25). Major spills and chronic pollution thereafter (1990) killed most large colonies, precluding further analysis to the present (17).

Annual growth extension rates were analyzed following standard statistical procedures to construct a master-index chronology (33–35). Annual raw data for each colony were normalized (index) by dividing yearly growth increments by the overall time series average. Master growth chronology was constructed by averaging all individual series by year and suppressing random variation and emphasizing common patterns without affecting the lifetime growth trend of the time series (33). Three- and thirteen-year moving averages were used as smoothing filtering techniques to reduce undesirable variance and high- and low-frequency variances, respectively (34–36). Sublethal changes in growth rates for *S. siderea* under stress can be detected after their occurrence (17, 19), with potential 1- to 2-y delay in the dating of chronology.

Three colonies of *S. siderea* were analyzed for stable isotope composition ($\delta^{13}C$) as minimum level of replication suggested for geochemical tracers (27). Annual growth was determined from the positive prints (17, 33, 34), and yearly sampling along the coral slice was performed using a hand drill fitted with a 7-mm (diameter) diamond bit. Annual samples were finely pulverized and weighed (1 ± 0.3 mg) before analysis. Samples were reacted at 9°C with 100% orthophosphoric acid and analyzed using a VG Isogas Prism mass spectrometer and following a protocol previously established (25). The instrument was calibrated within and between runs with an internal aragonite standard (COR1B), and resulting values were converted into the conventional delta (δ) notation relative to PDB (Peedee Belemnite carbonate). Precision for $\delta\ ^{13}C$ was 0.05‰, based on 16 replicate samples. The isotope concentration was defined according to the notation (‰ from the international standard, PDB):

$$\delta^{13}C = (C_{13_{13}}/C_{12_{12}} - C_{13_{13}}/C_{12_{12}})/C_{13_{13}}/C_{12_{12}} \times 1000\ (25) \qquad \text{(Eq.1)}$$

Three different colonies of *S. siderea* were analyzed for Ba, Fe, and Ca concentrations as an indicator of runoff (23, 31, 32). Sampling along the coral slice was performed at 1- to 2-y intervals using a hand drill fitted with a 10-mm (diameter) diamond bit. Samples were drilled in areas of the skeleton void ?3 of possible bioerosion to avoid contamination from trapped sediments inside injuries. Samples were prepared following a modified cleaning procedure (23, 37, 38). A detailed flow chart diagram showing the protocol for chemical analyses is available elsewhere (38). Samples (±1.5 g) were externally cleaned by repeated washing with distilled deionized water in an ultrasonic bath for 10 min, followed by rinses with clean 0.2 N HNO_3 for 5 min in an ultrasonic bath. Whole samples were coarsely crushed (<5 mm), and a secondary cleaning was performed. A second and final fine crushing was made, samples were sieved (280–700 μm), and a final ultrasonic cleaning was done with distilled water and 0.15 N HNO_3. Oxidative, reductive, and coprecipitation procedures were not considered during this study. Therefore, mechanical losses during the preparation of samples were negligible (38). Weighed subsamples (120 mg ± 0.5) were dissolved in 2 mL 3N HNO_3 and diluted in distilled water to 120 mL. Just prior to analysis, a further fivefold dilution factor was carried out and the solution made up to a final volume of 10 mL. All samples were analyzed for each element by inductively coupled plasma mass spectrometry (model ICP-2500). Procedural blanks were prepared in duplicate for each routine analysis, and samples were analyzed against artificial standards. Standards with concentrations of 10, 20, and 30 ppb were prepared and used to calibrate the instrument and to assess analytical accuracy. A 10-ppb internal standard was continuously run (every 5 samples) to compensate for variations in instrument sensitivity. However, to optimize the internal precision of the chronology (100 y), a complete core was run on a single day (38). Precision (1Φ) was approximately 1.7 for Ba, 4.6 for Fe, and 5.5 for Ca.

Annual water discharge during lockages was used here as a reliable indicator to estimate water runoff into the Caribbean during the operation of the Gatun Locks (39). Yearly total Panama Canal traffic, including all vessels and toll categories that have transited the canal, was used as an alternative to runoff at the locks (39). Annual rainfall from 7 meteorological stations representing the Gatun Lake drainage basin was analyzed (40).

Sea surface temperature (SST) data (1885–1997) of a region extending 2° latitude and 2° longitude within 12°N–78°W and

10°N–80°W were obtained from the International Comprehensive Ocean-Atmosphere Data Set, Release 2.2 (41). We calculated annual SST averages and a time series of the absolute values of their first differences (FD) (1915–1997). Values before 1915 were not used because their variance was predominantly larger than that of the remaining FD series ($p < 0.000$, $F = 0.05$, 1-tailed F-test $_{(27,\ 80)}$), suggesting strong nonhomogeneity (42). Discontinuities were flagged in those intervals in which values of FD exceeded the average + 2 standard deviations of their standardized distribution of frequencies. Starting from 1997, the average of the SST values before each discontinuity was equaled to the average of the values after it, following 3 steps: *i)* the SST average within the 2 most recent discontinuities was subtracted from that of the immediately previous homogeneous subset of the series, *ii)* this average difference was added to the whole data set values before the most recent discontinuity, *iii)* the position with the most recent discontinuity was unflagged. These steps were repeated along the SST series until no discontinuities remained. Detection and correction of discontinuities were repeated on the data set until no discontinuities were found or subset averages were equal. Discontinuities were found in 1915 (1.0°C), 1941 (0.85°C), 1945 (–0.16°C), 1946 (0.53°C), 1957 (0.17°C), 1958 (–0.08°C), 1968 (–0.06°C), and 1986 (0.17°C). A CUSUM chart of the first principal component of the SST average grid data revealed inhomogeneities also occurring in 1942–1943, 1945–1946, 1957–1958, 1968–1969, 1982–1983, 1986–1987, and 1994–1995 (43). The century-long trend of the inhomogeneous and corrected SST series is similar to that reported for global inhomogeneous and corrected SST anomalies between 1856 and 1981 (44, 45).

Trends in the data were described using polynomials fitted to the raw data, following standard procedures (46, 47). The polynomial order was determined by the significance ($\alpha = 0.05$) of the parameters and never exceeded 2. Only larger p values are shown. Overall trend correlations of variables (r) and of their 13-y moving averages (r_{13}) were calculated using Pearson product-moment coefficients.

RESULTS AND DISCUSSION

Coral growth decreased ($b_1 = -5.0 \cdot 10^{-3}$; $p < 0.001$; $R^2 = 0.30$) (Fig. 2a) during canal excavations (1903–1914), dredging, deforestation, construction of military facilities (1920s), and industrial development thereafter. Signals of increasing runoff and turbidity in coral growth bands throughout the century, as measured by 2 separate techniques, were congruent with increasing sedimentation, the most likely cause of the negative coral growth trend (20).

The stable carbon isotope ($\delta^{13}C$), an indicator of physiological condition, light, and turbidity, became lighter ($b_1 = 0.3$, $b_2 = -7.9 \cdot 10^{-5}$; $p < 0.000$; $R^2 = 0.69$) from the 1920s to 1990, with an average reduction of –0.4‰ (Fig. 2b). This downward trend, correlated with coral growth ($r = 0.38$; $r_{13} = 0.74$; $p < 0.001$), depicts a population of corals living under degrading physiological conditions during most of the century. Similarly, changes in the concentration of Ba and Fe suggest an increase of runoff and sedimentation since 1915 (Fig. 2b), when canal operations began, and especially between 1930 and 1990 ($b_1 = -2.6$, $b_2 = 10^{-3}$; $p < 0.01$; $R^2 = 0.65$ and $b_1 = 1.45$; $p < 0.000$; $R^2 = 0.79$, respectively). Indeed, as traffic increased through the century, locks opened more frequently. Runoff (fresh water spilled into the ocean through locks), strongly correlated with Ba/Ca ($r = 0.72$; $r_{13} = 0.91$; $p < 0.05$) and Fe/Ca ($r = 0.84$; $r_{13} = 0.98$; $p < 0.05$), was also correlated with vessel transit through Gatun Locks ($r = 0.98$; $p < 0.000$ for Ba and $r = 0.82$; $p < 0.05$ for Fe) and showed an upward trend from 1914 to 1990 (Fig. 2c). All of these correlations are evidence of the canal's role in coral reef decline.

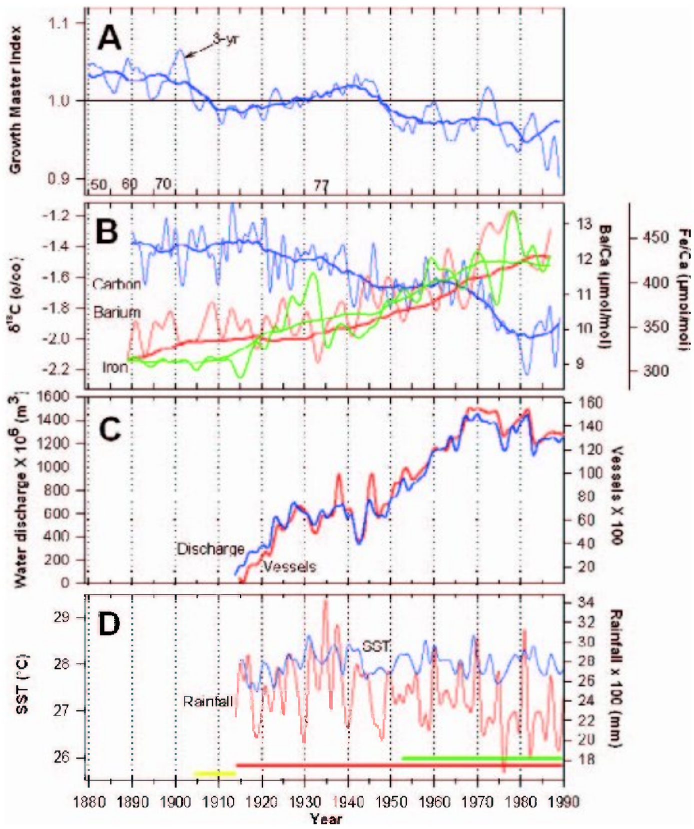

Figure 2. Time series of coral growth and environmental variables at the Caribbean entrance to the Panama Canal. Plots show raw data unless otherwise indicated; left axis for blue plots and right axis for red and green plots. Trend lines are 13-y moving averages. a: 110-y proxy 3-y moving average growth chronology for *Siderastrea siderea*, showing a significant decreasing trend ($b_1 = -5.0 \cdot 10^{-3}$; $p < 0.001$; $R^2 = 0.30$). X axis shows number of cores. b: Yearly carbon isotope chronology with significant trend ($b_1 = 0.3$, $b_2 = -7.9 \cdot 10^{-5}$; $p < 0.000$; $R^2 = 0.69$) and biannual Ba/Ca and Fe/Ca chronologies with an overall significant increasing trend ($b_1 = -2.6$, $b_2 = 10^{-3}$; $p < 0.01$; $R^2 = 0.65$ and $b_1 = 1.45$, $p < 0.000$; $R^2 = 0.79$, respectively). c: Runoff/water discharge through Gatun Locks ($b_1 = 1.6 \cdot 10^7$; $p < 0.000$; $R^2 = 0.85$) and transit of vessels ($b_1 = 5666$, $b_2 = -1.4$; $p < 0.001$; $R^2 = 0.88$). d: Rainfall measured in Gatun Lake basin and sea surface temperature monthly averages showing no significant trend. Rainfall was negatively correlated to Ba/Ca ($r = -0.44$; $p < 0.01$), Fe/Ca ($r = -0.46$; $p < 0.05$), and Gatun Locks discharge ($r = -0.229$; $p \leq 0.045$). Color bars at the bottom indicate the construction period without runoff (yellow), operation period with runoff (red), and industrialized era (green) at the Panama Canal.

Average annual rainfall was found to be negatively correlated to Ba/Ca ($r = -0.44$; $p < 0.01$) and to Fe/Ca ($r = -0.46$; $p < 0.05$). Gatun Locks discharge was marginally and negatively correlated to rainfall ($r = -0.229$; $p \leq 0.045$).

Changes in rainfall and SST may also have negative effects on corals. However, although rainfall declined over the century ($b_1 = -4.53$; $p < 0.01$; $R^2 = 0.1$), neither rainfall nor SST (Fig. 2d) were correlated with declining coral growth, nor was SST correlated with $\delta^{13}C$, Ba/Ca, and Fe/Ca.

Our results indicate that environmental conditions in central Caribbean Panama were relatively favorable to coral growth for much of the last quarter of the 19th century, until the construction of the waterway and the disturbances that accompanied it. Such disturbances continue today: more than 2 million m^3/y of sediments are dredged to maintain both entrances of the Panama Canal and about 14 million m^3/d of water and silt are discharged into the Caribbean Sea through the locks (Fig. 3). Our results also suggest that disturbances attributed to human population growth and coastal development, such as runoff and sedimentation, might represent a

Figure 3. Gatun Locks aerial view looking southwest from the Caribbean entrance to the Panama Canal. This is the largest set of locks (approximately 2 km) with 3 levels and 6 functional chambers designed to raise or lower vessels by 26 m above sea level (photo by Marco Guerra).

greater threat to reefs and coastal areas at local and regional levels than more evenly distributed and gradual climatic changes (12). Even if anthropogenic stresses and long-term climatic changes have sublethal effects on corals, these perturbations can affect their community dynamics and that of the entire ecosystem (12, 18).

A century ago, the marine environment was of negligible importance to governments and coastal developers. Today, however, environmental impact assessments are mandatory in most countries, and environmental awareness issues are
?4 increasingly important to society. Construction and operation of the canal inadvertently affected coral reefs and coastal areas in the past, and future expansion is likely to ~~make the situation worse~~. The Panama Canal Authority states that "It has been found that all possible adverse environmental impacts can be mitigated through existing procedures and technology and no immitigable or permanent adverse impacts on the population or the environment are anticipated" (48). However, priorities in the design and construction of the new waterway emphasize the conservation and sustainable use of water resources, soil, primary forest, and archeological sites (48) and minimizes a myriad of harmful effects on coastal ecosystems derived from enlarging port facilities; coastal landfilling and dredging; and increasing runoff, pollution, and vessel transit. All those detrimental disturbances are not unique to Caribbean Panama and are commonly reported as affecting coastal areas in the entire region with most of the degradation of coral reefs by increased influx of terrigenous sediments (32, 5~~0~~). Indeed, similar scenarios but at smaller scales have been described for mainland's Mexico and Central America. In Costa Rica, an excess of terrigenous sedimentation associated with human activities several kilometers upstream has polluted the coastal zone since the 1970s and is considered the most important anthropogenic impact on Caribbean coral reefs (5~~1~~). In Nicaragua, Belize, and Mexico several reef areas are affected by river waters carrying silt and fertilizers (~~49, 52–54~~).

The amount of excavated or dredged material at the Caribbean entrance of the new upcoming canal is unknown, but there is a clear intention of depositing it in the northern side of Bahia Limon and outside the west breakwater (48). Two protected areas located downstream, within 4 and 50 km away, ~~will~~ be potentially affected because the easterly sea surface currents (32) ~~will~~ continue the chronic transport and distribution of sediments and pollutants through the central coast of Panama. Thus, the century-old impact on coral reefs may prevail.

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