

Land use, water quality, and the history of coral assemblages at Bocas del Toro, Panamá

Richard B. Aronson^{1,2,*}, Nancy L. Hilbun^{2,3}, Thomas S. Bianchi⁴, Timothy R. Filley⁵, Brent A. McKee⁶

¹Department of Biological Sciences, Florida Institute of Technology, 150 West University Boulevard, Melbourne, Florida 32901, USA

²Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528, USA

³Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36688, USA

⁴Department of Geological Sciences, University of Florida, Gainesville, Florida 32611, USA

⁵Department of Earth, Atmospheric, and Planetary Sciences and the Purdue Climate Change Research Center, Purdue University, West Lafayette, Indiana 47907, USA

⁶Department of Marine Sciences, The University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27599, USA

ABSTRACT: As human activities have intensified along tropical coastlines, the anthropic influence on adjacent coral reefs has become increasingly deleterious. Changes in land use generally degrade water quality, but controversy persists over the degree to which reduced water quality affects the ecology of reef communities. We cored reef frameworks at 4 sites in Bahía Almirante, a semi-enclosed, coastal lagoon in northwestern Panamá, to explore the historical relationship between turnover in coral-species dominance and terrigenous input. The coral constituents of the cores were analyzed in tandem with lignin-phenol concentrations. Chronologies and sedimentation rates were determined from ²¹⁰Pb profiles in the cores. Increased terrigenous input from agricultural development and expansion of the human population degraded water quality in Bahía Almirante over the last century. Documented episodes of heavy rainfall after 1970 accelerated a phase shift from dominance by branching corals of the genus *Porites* to dominance by the lettuce coral *Agaricia tenuifolia* at water depths of 5 to 10 m by increasing runoff, increasing sediment and nutrient loads, and lowering light levels. The phase shift in coral dominance was unprecedented on a millennial time scale and the degree to which it occurred varied along a gradient of terrigenous input to the Bahía.

KEY WORDS: Coral reefs · Phase shift · *Agaricia tenuifolia* · Land use · Eutrophication · Nutrient loading · Water quality · Bocas del Toro

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INTRODUCTION

Coastal ecosystems worldwide have been altered over the last century by increased human population sizes, increased agriculture and urbanization, and the accompanying changes in land-use practices (Filoso et al. 2006). Land-use changes can alter the hydrologic regime, which in turn can affect inputs of terrestrially-derived organic matter, or T_{err}OM, to coastal systems

(Dittmar et al. 2001, Sampere et al. 2011). Conversely, organic-matter concentrations in sediments can provide a historical record documenting nutrient input, increased primary production, and concomitant deterioration of water quality (Corredor et al. 1999, Zimmermann & Canuel 2000, Bianchi 2007).

Of all the local, regional, and global factors that are currently degrading coral reefs, none is more controversial than declining water quality (Szmant 2002,

Fabricius 2005, Burkepile & Hay 2006, D'Angelo & Wiedenmann 2014). The localized impacts of nutrient loading and increased sedimentation are well-documented (e.g. Bell & Tomascik 1994, Hunter & Evans 1995, Lapointe et al. 1997), as are the geographic- and geologic-scale importance of terrigenous inputs to coral reefs (Hallock & Schlager 1986, Ginsburg & Shinn 1994, D'Olivo et al. 2013). Some level of nutrient input is normal—or even salutary—for most coral populations (Rougerie et al. 1992, Leichter et al. 2007), but disagreement persists over how recent changes in water quality might translate to reef degradation on large spatio-temporal scales (e.g. Brodie et al. 2005, Sandin et al. 2008, Gilmour et al. 2013).

In this study we reconstructed the near-term history of inputs of $T_{err}OM$ and sediment to Bahía Almirante, a coastal lagoon in Caribbean Panamá. We tested the hypothesis that changing patterns of land use created conditions that ultimately precipitated a recent phase shift in coral dominance, which was unprecedented on a millennial time scale. By exploring the relationship of terrigenous input to the composition of coral assemblages along a hydrographic gradient, we were able to discern the importance of both $T_{err}OM$ and inorganic sediment in driving the phase shift.

Geography and hydrography

Bahía Almirante (hereafter 'the Bahía'; Fig. 1), a coastal lagoon in north-western Panamá, is delimited by the archipelago of Bocas del Toro. The Bahía has a surface area of ~446 km² and a maximum natural depth of 29 m. Most of Bahía Almirante is <10 m deep, but there is a ship channel dredged to 30 m depth.

The Bahía is partially isolated from the Caribbean Sea by 3 large islands: Colon, Bastimentos, and Popa. Small mangrove islets occur throughout in conjunction with beds of the seagrass *Thalassia testudinum*. Sediments within the Bahía include bioclastic-carbonate sands and muds, with the mud fraction consist-

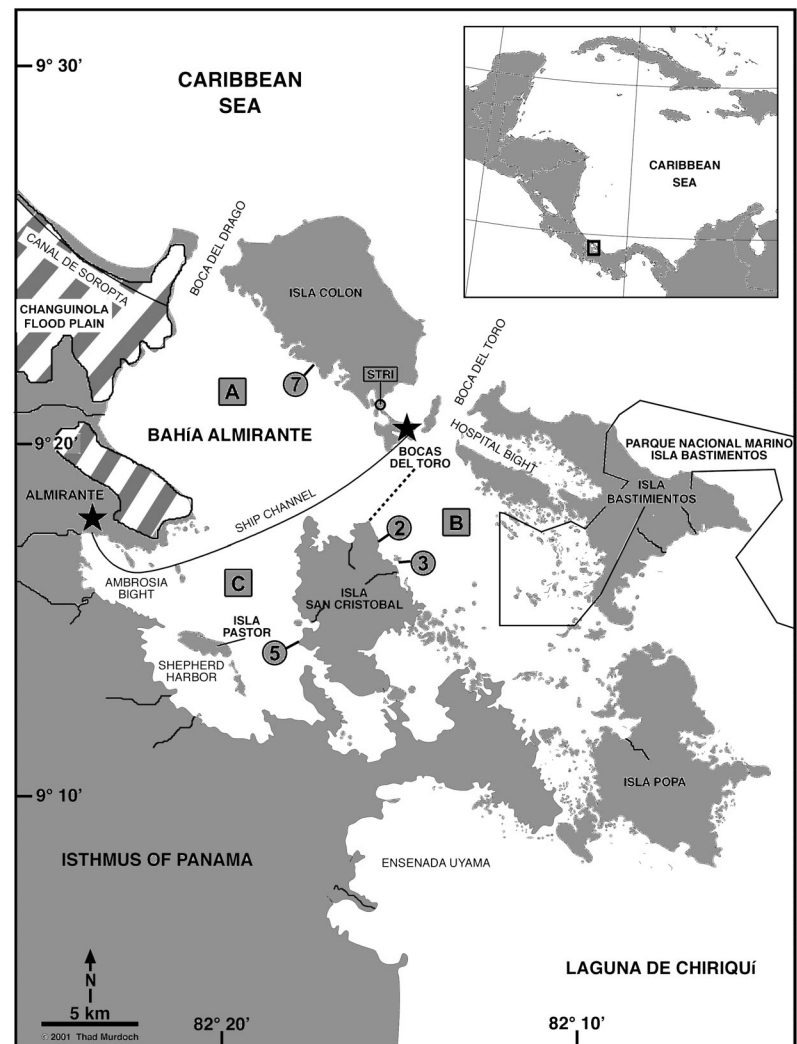


Fig. 1. Map of Bahía Almirante, showing major geographic and physiographic features, and locations of the numbered sites where the cores were extracted. Dashed line separates the 2 hydrographic regimes recognized by Guzmán & Guevara (2002), and boxed letters identify the 3 hydrographic sectors. Streams are represented by irregular black lines. The Canal de Soropta (upper left; also known as the Changuinola Canal and the United Fruit Company Canal) was dug in 1903. STRI: Smithsonian Tropical Research Institute's Bocas del Toro Research Station. Stars: urban centers; gray/white striped area: Changuinola flood plain

ing of >75% carbonate (Macintyre & Aronson 2006). Uncemented coral-reef frameworks, capped by living coral assemblages, occur along shoals within the Bahía and around its margins (Guzmán & Guevara 1998, Aronson et al. 2004, 2005).

Water exchange with the Caribbean Sea occurs through 2 inlets, Boca del Toro and Boca del Drago, resulting in a damped tidal range of 2 to 15 cm. Prevailing winds from the north and northeast drive currents of <40 cm sec⁻¹ (Greb et al. 1996). Water temperature and salinity remain stable throughout the

year. The mean water temperature was 28.6°C at 2 m depth near Site 7 (Fig. 1) from 1999 to 2004, and salinity generally ranged from 30 to 34‰ during that period (Kaufmann & Thompson 2005).

Rains occur year-round, with the wet season extending from May through December and the 'less-wet' season from January through April. Mean values of annual rainfall were 3277 mm at Bocas del Toro for 1972 to 2004, and 2615 mm at the nearby town of Changuinola for 1926 to 2004 (Kaufmann & Thompson 2005). Kaufmann & Thompson (2005) identified years of increased precipitation at Bocas del Toro in 1973, 1997, and 2002 (all >4000 mm yr⁻¹); and 1975, 1986, 1990–1991, 1994 and 1996 (all >3500 mm yr⁻¹). Average precipitation from 1950 to 1969 at Changuinola was ~2500 mm yr⁻¹, and from 1970 to 2002 precipitation increased to an average of ~3000 mm (Hilbun 2009). Mean annual runoff is 1600 mm. Water flowing into the Bahía is rich in organic matter, inorganic nutrients, and fine-grained, siliciclastic sediments (Phillips & Bustin 1996, D'Croz et al. 2005, Guzmán et al. 2005).

Guzmán & Guevara (2002) divided the Bahía into lower- and higher-runoff regimes (Fig. 1). The north-western Bahía, which comprises the higher-runoff sector, is closer to the mountains of the mainland and is influenced by rivers and streams near the city of Almirante, as well as the Changuinola flood plain near Boca del Drago (Fig. 1; Phillips & Bustin 1996, Guzmán & Guevara 1998). The lower-runoff, south-eastern sector of the Bahía is not in proximity to mountains and as a result has few freshwater inputs.

Subsequent analyses (D'Croz et al. 2005, Collin et al. 2009) suggest a more nuanced hydrographic gradient in the Bahía, maintained primarily by exposure to runoff from the Changuinola flood plain. A northern basin (Sector A in Fig. 1), which includes the southwest-facing coastline of Isla Colon, is directly exposed to runoff from the flood plain. Water quality is poor relative to other areas of Bahía Almirante, although it is better than in the Laguna de Chiriquí as a result of oceanic input to the Bahía through the pass of Boca del Drago. Between the east-facing coastline of Isla San Cristobal and the southwest-facing coastline of Isla Bastimentos (Sector B), runoff from the flood plain and input from the town of Bocas del Toro apparently mix with oceanic water coming through the pass of Boca del Toro. A western basin (Sector C) is partially isolated from flood-plain runoff and partially shielded from the town of Bocas del Toro, but near the city of Almirante. Water quality tends to be most degraded in Sector A, intermediate in Sector B, and least degraded in Sector C.

History of land use

Heckadon-Moreno (1997) and Cramer (2013) reviewed the agricultural history of the region. Bananas were the major crop in the area surrounding Bahía Almirante beginning in the late nineteenth century, and agricultural development continued through the twentieth century. In addition to recent rises in cattle and teak tree farming (Collin 2005), some coastal areas are currently being deforested for the construction of roads and hotels to accommodate increasing tourism (Guzmán & Guevara 1998). In summary, the area has undergone significant alterations in land use over the last century, all of which are likely to have increased terrigenous input to Bahía Almirante.

Coral reef ecology

Aronson et al. (2004) extracted push-cores in triplicate from reef frameworks at 12 sites in Bahía Almirante at intermediate water depths (5 to 10 m). Identification, taphonomic analysis, and radiocarbon-dating of the skeletal material in the cores revealed that branching *Porites* spp. (*P. furcata* and *P. divaricata*; hereafter referred to as *Porites*) had dominated the coral assemblages for the last 3000 years or more. Recently, the foliose coral *Agaricia tenuifolia* (revised in some recent sources to *Undaria tenuifolia*; hereafter referred to as *Agaricia*) abruptly rose to dominance at most of the sites.

Based on observed rates of framework deposition in lagoonal environments of the Caribbean, Aronson et al. (2004) estimated that the turnover in dominance occurred around 1970. They attributed the transition to deteriorating water quality over the preceding century, and they suggested that episodes of unusually heavy rainfall around 1970 had driven the coral assemblages across a threshold beyond which branching *Porites* could not persist at those depths. The shift in dominance from one coral taxon to another was mediated by populations of the herbivorous echinoid *Echinometra viridis*, which suppressed the recruitment and growth of macroalgae. In a subsequent study, Aronson et al. (2005) showed that reef frameworks in shallower water (0 to 2 m depth) did not undergo the transition from *Porites* to *Agaricia*, perhaps because of the consistently greater availability of light at those shallow depths.

Interestingly, even some of the intermediate-depth sites studied by Aronson et al. (2004) did not display the transition to *Agaricia*. The extent of the phase

shift varied along the hydrographic gradient in the Bahía. In Sector A, 12 of 12 cores from 4 sites (100%) displayed the transition from *Porites* to *Agaricia*; in Sector B, 9 of 12 cores from 4 sites (75%) showed the transition; and in Sector C, 2 of 6 cores from 2 sites (33%) displayed the transition (Aronson et al. 2004). The contemporary, living coral assemblages in the 3 sectors reflected their histories as revealed in the cores: *Agaricia* was most abundant at intermediate depths in Sector A, more interspersed with *Porites* in Sector B, and least abundant in Sector C. Thus, poorer water quality was associated with a more complete, spatially more uniform phase shift.

MATERIALS AND METHODS

Coring procedure

Field operations were based at the Smithsonian Tropical Research Institute's Bocas del Toro Research Station (STRI–Bocas). One core was extracted from each of 4 sites in 5.7 to 6.4 m water depth (Fig. 1). Sites 2, 3, 5, and 7 correspond to Sites N, S, P, and O in Aronson et al. (2004).

The coring operation has been described in detail elsewhere (Dardeau et al. 2000, Aronson et al. 2002). In brief, segments of aluminum irrigation tubing, 2.3 m long and 7.6 cm in diameter, were manually forced into the uncemented, lagoonal reef framework using adjustable core slips with handles. Teeth cut into the bottom of each tube aided in penetration. A weighted, fiberglass measuring tape was dropped down the open tube to verify that material was entering the tube continuously. Once the tube had penetrated at least 60 cm, the top was covered with a plastic cap and sealed with electrical tape. Divers then carefully pulled the core from the sediment and capped and sealed the bottom of the tube.

The extracted cores were returned to STRI–Bocas, where they were extruded. They were sectioned into the thinnest possible intervals, which were 2 to 7 cm thick. Each interval was partitioned into sedimentary matrix and coral material. The samples were then transported, frozen and in the dark, to the Dauphin Island Sea Lab, Dauphin Island, Alabama (DISL). They were stored at DISL frozen and in the dark.

Chronologies and sedimentation rates

To establish chronological and depositional models for the cores, sedimentation rates and degrees of

mixing were determined from ^{210}Pb profiles. Down-core activities of the particle-reactive radiotracer ^{210}Pb were determined by gamma spectrometry using Canberra low-background Germanium planar detectors (Cutshall et al. 1983). Aliquots of sediment were ground, packed, and sealed into 70 mm diameter petri dishes, and counted for 24 to 48 h after at least 21 d (to allow ^{210}Pb activities to in-grow to secular equilibrium). Total ^{210}Pb activity was determined from the 46-keV photopeak, and supported ^{210}Pb activities were determined by using averaged activities of the ^{226}Ra daughters ^{214}Pb (295 and 352 keV) and ^{214}Bi (609 keV). Detector efficiencies for this geometry were calculated using a natural sediment standard (IAEA-300 Baltic Sea sediment); detector background at each energy level of interest was determined using petri-dish blanks. Gamma data were corrected for self-adsorption by counting a ^{210}Pb source placed on the top of the sample for 2 min and comparing it to a 2 min count placed on top of an empty petri dish. To determine sedimentation rates and derive age models for the cores, a constant-initial-concentration model of steady-state sediment accretion was applied to the derived excess ^{210}Pb values as they changed with depth (Appleby 2001). Sediment-radionuclide analyses were conducted at Tulane University (New Orleans, Louisiana).

Coral analysis and sedimentary petrology

The coral material from each interval was rinsed of all sediment and retained on a 5 mm sieve. Constituents of the coral samples were identified and sorted to the lowest taxonomic level possible. The sorted coral skeletons were dried to a constant weight at 80°C and weighed to the nearest milligram (Aronson et al. 2004). The corals were analyzed at DISL.

To differentiate depositional environments in Bahía Almirante, grain size analyses were conducted on Cores 5 and 7 at the University of South Alabama (Mobile, Alabama). Sand (grain sizes 63 to 2000 μm) was separated from fine sediments (<63 μm) using sieves. Settling tubes were used to separate the fine sediments.

Lignin-phenol analysis

Geochemical proxies have recently come into use for tracking inputs of $T_{\text{err}}\text{OM}$ to coral reef ecosystems (Patchineelam & Smoak 1999, McCulloch et al. 2003).

Bahía Almirante has no history of hurricanes, at least on a centennial time scale (Phillips et al. 1997, Lovelock et al. 2004), and the undisturbed sedimentary record allowed us to reconstruct its biogeochemical history on a decadal scale. Lignin polymers are found in the cell walls of all vascular plants, making lignin-phenols (vanillyl, syringyl, and cinnamyl phenols) excellent biomarkers for vascular plant matter (Hedges & Ertel 1982, Gough et al. 1993, Bianchi et al. 1997). Ratios of vanillyl, syringyl, and cinnamyl phenols make it possible to distinguish among inputs of $T_{err}OM$ from different sources—agricultural plants, trees and shrubs, and mangroves—and distinguish them from seagrass, which also contains lignin (Benner et al. 1990, Bianchi et al. 1999, Dittmar et al. 2001).

The cupric-oxide oxidation method (Hedges & Ertel 1982) was used to extract lignin-phenol monomers from lignin macromolecules in sediment samples from Cores 2, 5, and 7. Eight lignin-phenol monomers were investigated: the vanillyl compounds vanillin, acetovanillone, and vanillic acid; the syringyl compounds syringaldehyde, acetosyringone, and syringic acid; and the cinnamyl compounds *p*-hydroxycinnamic acid and ferulic acid. Sigma-8, or Σ_8 , defined as the aggregate concentration of the 8 lignin-phenol monomers relative to the dry weight of sediment (Gough et al. 1993), was used as a relative indicator of terrestrial input. Total cinnamyl:vanillyl (C:V) and syringyl:vanillyl (S:V) abundances were used to differentiate plant sources. Ratios of vanillic acid to vanillin [(Ad:Al)_v] and syringic acid to syringaldehyde [(Ad:Al)_s] were used as proxies for lignin degradation (Hedges et al. 1988a,b). The vanillyl ratio is a more robust indicator of lignin decay than the syringyl ratio (Bianchi & Canuel 2011).

Lyophilized sediment samples from the cores extracted at Sites 2, 5, and 7 were analyzed in duplicate for lignin-phenol content using cupric-oxide oxidation, following the modified protocol of Dalzell et al. (2007). The low organic content of the sediments necessitated sample weights of at least 200 mg to yield 1 to 3 mg of organic carbon. Each sample was placed into a 10 ml Monel stainless-steel reaction vessel, or bomb, with approx. 330 mg CuO powder and purged with nitrogen gas for a minimum of 4 h. The bomb was then filled with 2N NaOH and heated to 150°C for 3 h at a rate of 4.2°C min⁻¹. Ethyl vanillin (6000 ng) was added as an internal recovery standard. The sample was extracted in diethyl ether, reduced to 1 ml via rotoevaporation, and purged dry with nitrogen. Each sample was re-diluted in pyri-

dine with 3,4-dimethoxy-benzoic acid as an absolute recovery standard. Subsamples were mixed with bis(trimethylsilyl)trifluoroacetamide (BSTFA), a silylating agent, and then heated to 70°C for 20 to 30 min to aid in the derivitization process. Lignin-phenol compositions and concentrations were determined using a Hewlett–Packard 5890 Series II/5971 GC/MS at Purdue University (West Lafayette, Indiana). Data from the duplicate samples were averaged.

Data analysis

Age models for Cores 2, 5, and 7 were calculated by regressing excess ²¹⁰Pb (in disintegrations min⁻¹) on depth in-core (in cm). For each core, a least-squares regression was calculated using the statistical package SPSS®. The residuals were tested for normality using the the Shapiro–Wilk test, and they were normal in all 3 cases.

The temporal novelty of the recent transition from *Porites* to *Agaricia* in Bahía Almirante was supported statistically by Aronson et al. (2005) with a larger sample size. Associations among composition of the coral assemblages, lignin profiles, and sedimentation rates were examined qualitatively. The likely autocorrelation of data within cores precluded regression analysis (a general problem in coring studies), and the brevity of the time intervals represented precluded time-series analysis. The interpretive basis of this study, therefore, is necessarily descriptive.

RESULTS

Chronologies and sedimentation rates

²¹⁰Pb geochronologies for the 3 cores verified that little to no mixing from physical resuspension or bioturbation had occurred down-core. Regressions of excess ²¹⁰Pb on depth in-core yielded R² values of 0.669, 0.702, and 0.595 for Cores 2, 5, and 7, respectively. The regression coefficients for Cores 2 and 5 were significantly different from zero at $p = 0.004$ and $p = 0.001$, respectively. Although the regression coefficient for Core 7 was marginally non-significant at $p = 0.072$ because of low sample size, the 95% confidence interval of the regression coefficient was entirely negative (as it was for the other 2 cores). The relationship, therefore, was well-enough constrained to calculate an age model for Core 7.

In Core 5, excess ²¹⁰Pb was detected down to 38 cm, and the estimated date at that level was 1949.

Excess ^{210}Pb was detected down to 26 cm in Core 7, yielding an estimated date of 1975, and it was detected down to 45 cm in Core 2, yielding an estimated date of 1969 (Table 1). The age model for Core 2 was applied to Core 3, which was extracted nearby.

Rates of accumulation varied with location in the Bahía. Site 5, which is furthest from Bocas del Toro and the Changuinola flood plain, yielded the lowest sedimentation rate in-core, 0.70 cm yr^{-1} . Site 7, which is closest to the flood plain, had a higher rate of 0.97 cm yr^{-1} . Site 2 yielded the highest sedimentation rate, 1.10 cm yr^{-1} .

Coral analysis and petrology

The skeletal material within the cores was packed in a muddy-sand to silty-sand matrix, in which >93% of the weight was coral. The upper 30 cm of Cores 3 and 7 consisted of a layer of *Agaricia tenuifolia*, which was deposited after 1975 (Fig. 2B,D). Branching *Porites* spp. dominated below the *Agaricia* layer, although the pattern was clearer in Core 3 than in Core 7. Cores 2 and 5 were dominated by *Porites* throughout (Fig. 2A,C). All sites exhibited at least a minor increase in *Agaricia* beginning in the interval 1970 to 1986. These results are fundamentally in agreement with those of Aronson et al. (2004).

Core 7, which was extracted closest to the Changuinola flood plain in Sector A, contained a higher percentage of fine sediments than Core 5 (Table 1). The upper 20 cm of sediment in Core 7 was 13.5% clay (<2 μm grain size), compared to 1.6% clay in the upper 20 cm of Core 5 from sector C. The highest percentages of clay and silt (2 to 20 μm grain size) in the cores were observed at a depth of 15 cm in core 7—17.6 and 15.4%, respectively—reflecting increased rainfall recorded in 1986 (see Discussion). The percentages of clay and silt were also high within Core 5 (although lower than in Core 7) at a depth of 4 cm—2.0 and 5.3%, respectively—corresponding to increased rainfall in 1997.

Lignin-phenol analysis

The clear transition from *Porites* to *Agaricia* in Core 3 (Fig. 2B) coincided with a peak in the Σ_8 profile of Core 2 (Fig. 2A), which was extracted nearby. Cores 2 and 5 did not exhibit an obvious transition from *Porites* to *Agaricia*; nevertheless, in each of these cores there was an increase in *Agaricia* and a decrease in *Porites* in the early 1990s, which correlated

Table 1. Age models based on sedimentation rates derived from ^{210}Pb and grain-size analysis of sediments in the cores from Bahía Almirante. Grain-size analyses were conducted on Cores 5 and 7. Dashes: no data

Core ID	^{210}Pb date	Depth in-core (cm)	Sedimentary % total fines (<63 μm)	Composition % sand (63–2000 μm)
2	2003 ^a	0	–	–
	1999	7	–	–
	1994	12	–	–
	1990	17	–	–
	1986	22	–	–
	1981	27	–	–
	1977	32	–	–
	1973	37	–	–
	1969	42	–	–
5	2003 ^a	0	21.54	78.08
	1997	4	27.50	72.50
	1992	8	30.67	69.33
	1984	13	28.82	71.18
	1977	18	27.94	72.06
	1974	20	–	–
	1972	22	27.19	72.81
	1969	24	28.06	71.94
	1966	26	29.13	70.87
	1963	28	–	–
	1956	33	26.49	73.51
	1949	38	24.05	75.96
	7	2003 ^a	0	34.84
1998		5	37.12	61.97
1992		10	34.53	63.67
1987		15	35.08	60.86
1981		20	34.99	64.41
1979		22	32.46	67.17
1977		24	37.30	61.03
1975		26	24.10	75.26

^aSurface samples from the cores

with a peak in Σ_8 (Fig. 2A,C). The interval of Core 7 in which lignin-phenols were detectable (corresponding in time to 1979–2003) was deposited after the transition from *Porites* to *Agaricia* (cf. Aronson et al. 2004) and was characterized by high values of Σ_8 (Fig. 2D).

Cores 2, 5, and 7 all showed increases in Σ_8 after 1968 (Fig. 2). The highest Σ_8 values at Sites 2 and 5 occurred in 1986 and around 1990, which corresponded to increased rainfall at Changuinola (Note, however, that the peak value of Σ_8 in Core 7 dated to 1980, for which there was no independent evidence of increased rainfall.) A secondary increase in Σ_8 was observed in Cores 2 and 5 from 1968 to 1975, probably associated with flooding in 1970.

The ratios of vanillic acid to vanillin (Ad:Al)_v and syringic acid to syringaldehyde (Ad:Al)_s indicate the

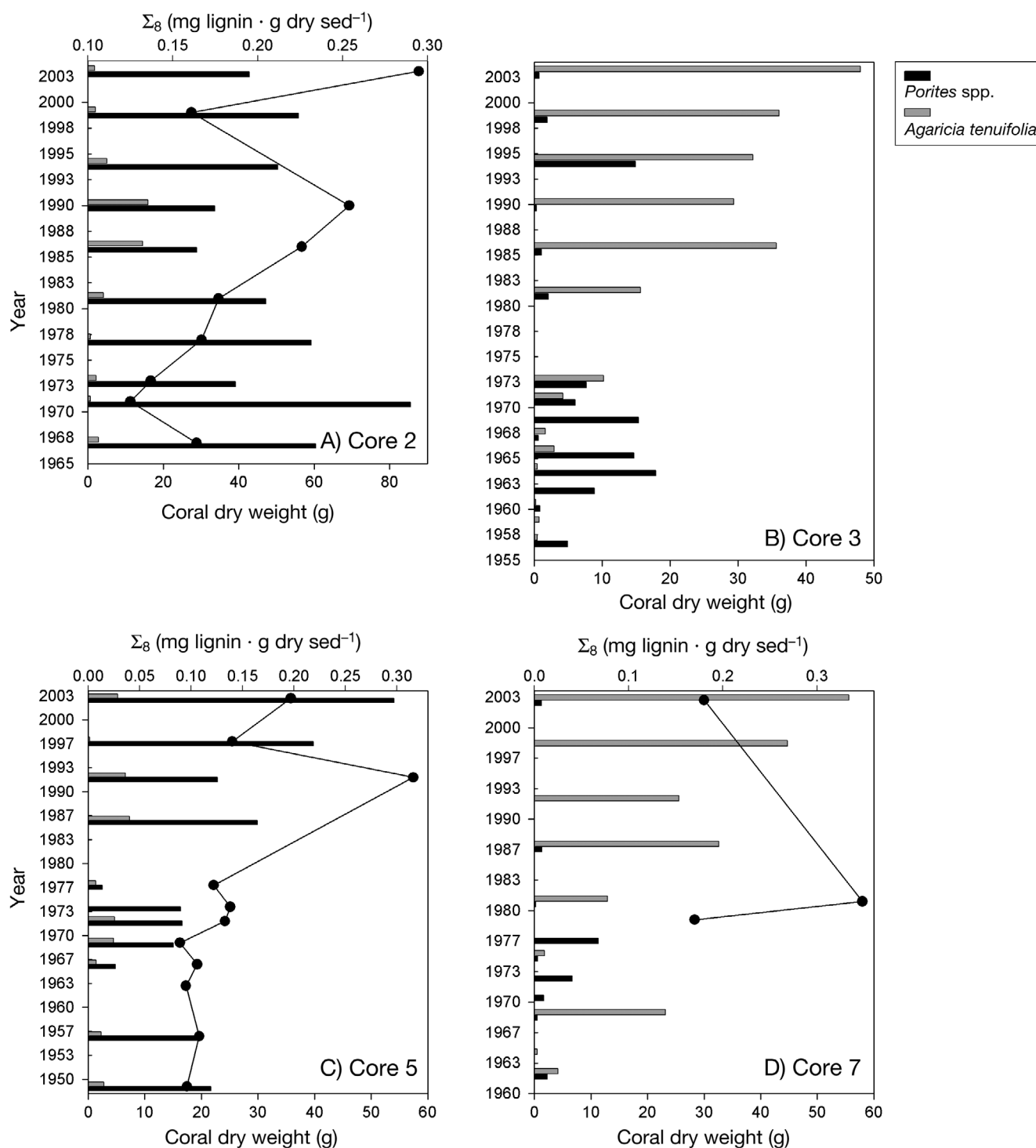


Fig. 2. Relationship between the turnover dynamics of coral assemblages (bar graphs) and the trajectories of Σ_8 (line graphs). (A) Core 2; (B) Core 3; (C) Core 5; (D) Core 7. The time-scales are aligned for Cores 2 and 3; note, however, that the y-axes are different for Cores 5 and 7. A Σ_8 -profile was not available for Core 3

extent of lignin degradation and provide information on the oxidation state of the lignin: the higher the value, the more degraded the lignin (Hedges et al. 1988b, Goñi et al. 1993, Bianchi et al. 2007). Spatial and temporal variations in these ratios (Fig. 3A,B),

combined with the sedimentary analyses, provide information on the separate and combined impacts of organic and inorganic inputs to the Bahía. Large down-core variations in the syringyl-to-vanillyl (S:V) and cinnamyl-to-vanillyl (C:V) ratios were observed

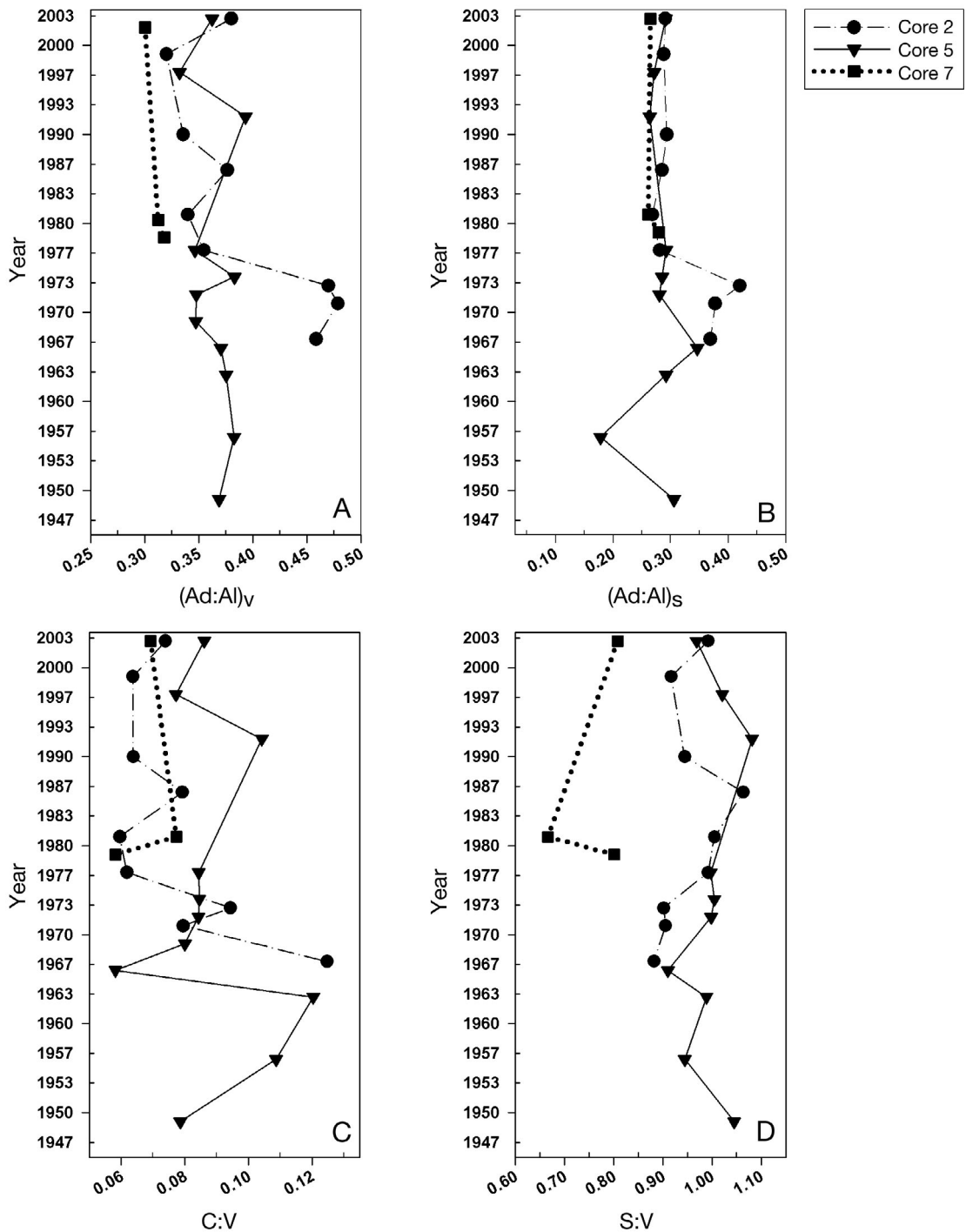


Fig. 3. Down-core profiles of lignin ratios in Cores 2, 5, and 7. (A) Vanillyl acid-to-aldehyde ratio; (B) syringyl acid-to-aldehyde ratio; (C) cinnamyl-to-vanillyl ratio; (D) syringyl-to-vanillyl ratio

in Cores 2, 5, and 7 (Fig. 3C,D). These variations most likely reflect changes in terrestrial plant assemblages due to the expansion of banana plantations, as well as enhanced inputs of this material during flooding events. Interpretation of the ratios in Fig. 3 will be elaborated in the Discussion.

DISCUSSION

Prior to agricultural development, Bahía Almirante was surrounded by primary vegetation in bog and swamp habitats (Phillips et al. 1997). The potential for introduction of allochthonous organic carbon to

the Bahía increased with conversion of the land to agricultural use. Aronson et al. (2004) provided evidence of a recent and unprecedented phase shift from dominance of *Porites* spp. to dominance of *Agaricia tenuifolia* in Bahía Almirante. They suggested that the degradation of water quality drove the transition to *Agaricia*, because agariciids in general and *A. tenuifolia* in particular are more tolerant of high nutrient concentrations and high sedimentation rates than other Caribbean corals (Shyka & Sebens 2003, Mallela et al. 2004). The extremely low frequency of hurricanes in Panamá presented an opportunity to examine chronological changes in terrigenous input in relation to local land use and flooding events. Although a causal connection has been postulated between changes in water quality and alterations to the coral assemblages of the Bahía (Aronson et al. 2004, Collin et al. 2009), this is the first study of which we are aware that directly links the 2 patterns there, or in any other reef system for that matter.

Land-use changes, flooding, and T_{err} OM input

Water quality in Bahía Almirante is strongly influenced by exposure to runoff, oceanic water entering and exiting through 2 channels, and sedimentary resuspension. The spatial gradient of increasing water quality from Sector A (poor) to B (intermediate) to C (the best of the 3 areas) reflects the interaction of mesoscale oceanography, rainfall, and land use. Water quality in turn influenced the historical dynamics of the coral assemblage along the gradient.

Site 5 (Sector C) exhibited a lower sedimentation rate than Sites 2 (Sector B) and 7 (Sector A), which were similar. The difference is not surprising, considering that Site 5 was located in the sector least exposed to runoff from the Changuinola flood plain. Core 5 contained a generally lower percentage of fine sediments than Core 7, again reflecting lower runoff. The high abundance of the seagrass *Thalassia testudinum* observed at Site 5 corroborates the inference that water quality was higher there than at the other 2 sites (see Carruthers et al. 2005), despite its proximity to the city of Almirante.

Increases in Σ_8 and S:V coincided with decreases in C:V values in 1971–1977, 1997, and 2003. The increases in S:V correlate in time with flooding events, documented as peaks of rainfall at Changuinola and Bocas del Toro, which introduced large quantities of T_{err} OM to the area. The changes in these ratios likely indicate inputs of mixed woody and non-woody angiosperm materials, some of which may have been

derived from banana plantations. Note, however, that we can only speculate about banana plantations as a specific source; S:V and C:V ratios must be used cautiously as indices of the sources of T_{err} OM due to the potential problem of selective leaching and differential decay of syringyl, cinnamyl, and vanillyl phenols (Hernes et al. 2007, Bianchi & Canuel 2011).

The decline in C:V ratios at Sites 2 and 5 after the early 1960s may reflect the inferred temporal increase in the input of woody organic matter (Goñi & Thomas 2000). The substantially lower S:V ratio at Site 7 than at Sites 2 and 5 highlights the importance of inputs from within the Changuinola flood plain, as opposed to mangroves along the shoreline of Bahía Almirante. Although the Bahía is surrounded by mangroves and all sites were bordered by mangroves, the C:V and S:V ratios are consistent with woody organics and inconsistent with mangrove peats, both in general (Dittmar et al. 2001) and in the Bahía (Hilbun 2009).

Σ_8 profiles were similar in Cores 2, 5, and 7 (Fig. 2), yet sedimentation rate was greater at Site 7, where the transition to *Agaricia* occurred, than at Site 5, where it did not. In absolute terms, therefore, more lignin was deposited at Site 7 and/or there was less post-depositional degradation of lignins at that site. The slightly lower $(Ad:Al)_v$ profile in Core 7 (Fig. 3A) and the proximity of Site 7 to the flood plain suggest both less degradation and a greater organic input at that site. Intensive agriculture on the flood plain produced more plant detritus and mobilized more inorganic sediment—especially fine-grained material—compared to Site 5. We suggest that lignins were associated with fine sediments to a greater degree at Site 7 than at the other sites (cf. Goñi et al. 1998), and that those fine sediments provided greater protection from degradation.

Terrigenous input and coral assemblages

We detected the phase shift at Site 7 in Sector A, where it was correlated with the earliest observed peak in lignin-phenols (Fig. 2). Sites 2 and 3 in Sector B, which are considered in aggregate here, showed the phase shift (Site 3) or at least an increase in *Agaricia* (Site 2) after 1970 that was correlated with a large increase in lignin-phenols. Site 5 in Sector C, which did not undergo the phase shift, showed minor increases in *Agaricia* that corresponded to increases in lignin-phenols. Those increases in lignin-phenols occurred despite the physiographic protection of Sector C. Thus, although the hydrographic gradient

of exposure to runoff from the Changuinola flood plain explains the extent of the shift in coral dominance in the 3 sectors, the lignin profiles per se do not fully explain the extent of that phase shift.

The transition to *Agaricia* did not occur at intermediate depths on reefs in Sector C and occurred partially in Sector B because physiography ameliorated the degree of terrigenous input to both of those sectors. *Porites* also retained its dominance at shallow depths throughout the Bahía, regardless of what happened at intermediate depths (Aronson et al. 2005). These observations strongly suggest that light attenuation was an important proximal influence on the phase shift to *Agaricia* where it occurred (van Woessik et al. 1995). Higher light levels in Sectors B and C during years of heavy rainfall (Fig. 2 in Collin et al. 2009) might have prevented, or partially prevented, the phase shift at intermediate depths in those 2 sectors. It is likely that variations in $T_{err}OM$ inputs, light, sedimentation rates, and sedimentary composition interacted to drive the trajectories of the coral assemblages.

Cramer et al. (2012) likewise observed spatial variability in the historical dynamics of coral assemblages in Bahía Almirante. Their age models, however, are at variance with the geochronologies presented here. The departure of their age models from ours is a result of the different dating techniques used in the 2 studies. Cramer et al. (2012) used radiocarbon dating by absorption mass spectrometry (AMS), which is far less accurate at young ages than the ^{210}Pb analysis employed in this study (Cronin et al. 2000, McKee et al. 2005, and many others). Recalibration of their radiocarbon-based age models using our more-accurate ^{210}Pb chronologies supports our scenario that a graded transition from *Porites* to *Agaricia* was the predominant ecological signal in the Bahía in recent decades.

In conclusion, the recent shift in dominance from *Porites* to *Agaricia* in Bahía Almirante, which was unprecedented on a millennial scale (Aronson et al. 2004), can now be confidently attributed to decreased water quality as a result of altered patterns of land use. Peaks in lignin-phenols, which did not occur simultaneously in the 3 sectors but were generally associated with heavy rainfall, were accompanied by increases in *Agaricia* of varying magnitudes at our 4 sites. Light levels, rates of sedimentation, and sedimentary composition covaried and determined the extent to which pulses of terrigenous input accelerated the phase shift from *Porites* to *Agaricia*. Spatial heterogeneity in the extent of the phase shift is thus explicable in terms of physiographic and hydro-

graphic variability, strengthening the link between terrigenous input and changes in the composition of coral assemblages in Bahía Almirante.

Whether or not terrigenous input is a major cause of ecological change on coral reefs in general, it certainly was an important driver of the phase shift in Bahía Almirante. The complexity of causation, even on the small spatial scale of the Bahía, highlights the challenge of fully explaining coral reef degradation.

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