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HISTORY OF HUMAN OCCUPATION AND ENVIRONMENTAL CHANGE IN WESTERN AND CENTRAL CARIBBEAN PANAMA

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ABSTRACT

Humans have altered terrestrial and marine coastal environments in Central America through land clearing and fishing for over 10,000 yrs. The intensity of human disturbance has been strongly influenced by local physiographic and climatic conditions that affect the productivity of the land and sea. The importance of these factors is readily apparent along the Caribbean coast of Panama. Environmental conditions have played an important role in the differing histories of population and environmental disturbance in Bocas del Toro along the western coast and Costa Arriba de Colón (Costa Arriba) along the central coast. Both regions suffered catastrophic mortality of indigenous peoples soon after European contact and did not return to pre-contact levels until at least the 19th century. During the Spanish colonial era, Bocas del Toro remained relatively sparsely populated until the early 20th century due to its isolation from the Pacific by high mountains, excessive rainfall, and relatively smaller area of alluvial flood plains for human habitation and agriculture. In contrast, the low-lying topography of Costa Arriba was conducive to early colonial occupation in the 16th century and rapid population growth and environmental disturbance since the mid-19th century. This earlier onset of intense human disturbance is likely responsible for the more degraded state of coral reefs in Costa Arriba compared to Bocas del Toro. The timeline of human interaction with the coastal environment of Caribbean Panama thus provides a deeper-time perspective from which to more accurately assess the causes of the recently observed collapse of Caribbean coral reefs.

Humans have had a profound and sustained influence on the natural environment of Central America since their arrival at least 11,000 yrs ago (Piperno et al. 1990, Cooke 1997, 2005). The terrestrial megafaunal extinction that occurred in Central America shortly after human arrival has been attributed in part to prehistoric Indian hunting (Janzen and Martin 1982, Alroy 2001), and the burning of vegetation for hunting and agriculture over the past millennia has produced the "anthropogenic forests" that characterize the region today (Denevan 1992). Human influence on marine environments in Central America over the past millennia has also been substantial, especially on Caribbean coral reefs (Jackson 1997, Jackson and D'Croz 1997, Pandolfi et al. 2003). Centuries to millennia of fishing and hunting have removed vast numbers of coral reef megafauna including monk seals, sea turtles, manatees, and large reef fishes. These animals began to decline in abundance several centuries ago, and are absent or rare on Caribbean coral reefs today (Jackson 1997, Wing and Wing 2001, Pandolfi et al. 2003, McClanachan et al. 2006, McClanachan and Cooper 2008).

Today, Caribbean coral reefs are in a state of crisis due to the widespread die-off of reef-building corals (Hughes 1994, Gardner et al. 2003, Pandolfi et al. 2003, Newman et al. 2006). The long history of human disturbance of terrestrial and coastal marine ecosystems in Central America points to an anthropogenic explanation for the

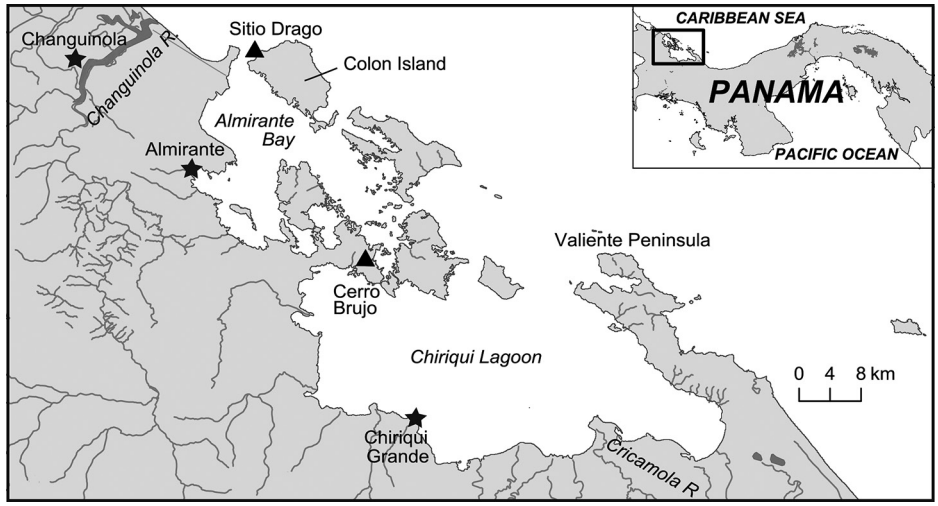

Figure 1. Bocas del Toro, Panama, and locations discussed in text. Stars are population centers, triangles are archaeological sites.

recent collapse of Caribbean coral communities. To understand the root causes of change on Caribbean reefs, it is important to know the complete history of human activities in the region.

Archaeological and historical data provide a deep-time perspective for understanding the dramatic changes witnessed on Caribbean reefs in the past decades. Here I discuss the human history of Caribbean Panama with special attention to the regions of Bocas del Toro and Costa Arriba. Bocas del Toro is located in the western coast of Caribbean Panama, defined here as the area bounded to the west by the Changuinola River, to the east by the Valiente Peninsula, and to the south by the continental divide that separates the Caribbean and Pacific slopes (Fig. 1). These boundaries coincided with those of the province of Bocas del Toro until the 1990s, after which the eastern part of this region was transferred to the Ngöbe-Buglé indigenous territory, or "comarca." Costa Arriba is located along the central Caribbean coast of Panama east of the Panama Canal and is defined here as the area bounded by the Chagres River to the west, the indigenous territory of Kuna Yala to the east, and a smaller mountain chain to the south (Fig. 2). This region constitutes the eastern portion of Colón province.

Setting

Panama

The Caribbean coast of Panama is geographically complex, composed of numerous islands, estuaries, and beaches. Fringing and patch reefs are located within a range of hydrodynamic conditions, from protected lagoonal environments to windward-facing offshore reefs exposed to considerable swell. Lagoonal and leeward coastlines are typically fringed with mangrove forests and contain small mangrove islands and extensive seagrass beds, while offshore and windward coastlines are typically bordered by sandy beaches or reef flats. In the western and eastern parts of Panama, mountain

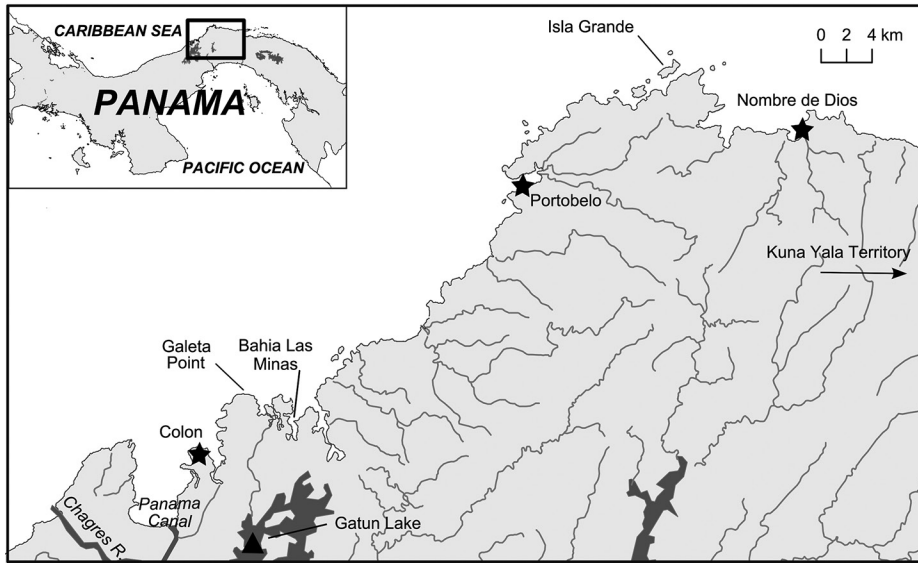

Figure 2. Costa Arriba, Panama, and locations discussed in text. Stars are population centers, triangles are archaeological sites.

ranges divide the northward-facing Caribbean and southward-facing Pacific sides of the isthmus into distinct drainage basins and microclimates.

Due to the orographic effect, the Caribbean slope has higher annual precipitation (330 cm annually in Bocas del Toro and 200–400 cm in Costa Arriba; Cubit et al. 1989, Kaufmann and Thompson 2005) than the Pacific slope (130 cm; Cooke et al. 1996) and lacks a pronounced dry season. The comparative aseasonality on the Caribbean slope has strongly influenced the differing histories of human land use on either side of the continental divide in Panama.

Both Bocas del Toro and Costa Arriba are characterized by typically wet "Caribbean" climates but experience varying environmental conditions due to differences in geography and topography. The curvature of the Caribbean coast of Panama is such that Bocas del Toro is less directly exposed to the northeasterly trade winds than Costa Arriba. The topography of Bocas del Toro is more extreme than Costa Arriba: the highest portion of Panama's continental divide, 3475 m Volcán Barú, is located just south of Bocas del Toro province and separates the Caribbean slope of Bocas del Toro from the Pacific slope of Chiriquí province. Smaller volcanic peaks are scattered along western Panama's central cordillera as far as the Panama Canal watershed, a roughly 30-km wide lowland with a maximum altitude of approximately 30 m that marks the eastern limit of tectonic activity that produced the Central American volcanic chain (Wallace 1997). This lowland area overlaps with the westernmost part of Costa Arriba, in Colón province (Fig. 2). Because this area of low relief does not experience the orographic rainfall that occurs in the western and eastern regions of Panama, the canal watershed has a more distinct dry season than the rest of Caribbean Panama. East of the canal watershed, a lower mountain chain begins that has a maximum altitude of 1000 m (Coates 1997) and is interspersed with broad alluvial valleys created by long rivers that run parallel to the coast. In general,

rolling coastal hills and seasonal precipitation make Costa Arriba more suitable for crop cultivation (Bennett 1968, Drolet 1980).

Bocas del Toro

The Bocas del Toro archipelago is divided into two large semi-enclosed lagoons: the Chiriquí Lagoon, which is influenced by freshwater discharge from several large rivers, and the smaller Almirante Bay, which is less affected by river runoff (Fig. 1). Outside and to the east of these lagoons, the coastline is generally more exposed to oceanic conditions. A steep coastal mountain chain extending up to 400 m in altitude runs approximately 1–3.5 km inland from the coast, resulting in short and fast-flowing rivers that produce a consistent flow of fresh water to the coastal zone year-round (Guzmán et al. 2005). The water from these rivers forms a freshwater lens that is approximately 0.5 m thick and rich in suspended organic material that flows into both lagoons (Guzmán et al. 2005).

Both Almirante Bay and Chiriquí Lagoon have a higher concentration of nutrients, chlorophyll, and zooplankton biomass compared to environments with more exposure to the Caribbean Sea and less exposure to river runoff (D'Croz et al. 2005). Water exchange with the Caribbean Sea is more restricted in Chiriquí Lagoon, and a large river, the Cricamola, feeds directly into the lagoon. The northwest portion of Almirante Bay is directly influenced by creeks that drain a portion of the Changuinola River floodplain, the site of extensive banana plantations (Fig. 1). The lower water clarity within the lagoons has been attributed in part to the input of sediments and pollutants from agriculture, mining, and oil transport and storage in coastal regions (Guzmán and Jimenez 1992, Guzmán and Garcia 2002, Guzmán 2003).

The coral reefs of Bocas del Toro contain 87% of the scleractinian coral species reported for Caribbean Panama (Guzmán 2003). The extent of reef development and diversity of corals is greater within Almirante Bay than Chiriquí Lagoon, due to better water quality in the former (Guzmán and Guevara 1998a, D'Croz et al. 2005, Guzmán et al. 2005). Within lagoonal environments, branching *Porites* corals—primarily *Porites furcata* (Lamarck, 1816)—are dominant at depths <3 m, with essentially monospecific *P. furcata* "meadows" beginning at the boundary of the shallow seagrass zone (Guzmán and Guevara 1998a). The shallow reef slope zone is dominated by the lettuce coral *Agaricia tenuifolia* (Dana, 1848) at depths from 3 to 12 m, transitioning to scattered massive corals *Colpophyllia natans* (Houttuyn, 1772), *Montastraea annularis* species complex (Ellis and Solander, 1786 sensu Weil and Knowlton 1994), *Montastraea cavernosa* Linnaeus, 1767, *Siderastrea siderea* (Ellis and Solander, 1786), and *Stephanocoenia intercepta* (Milne-Edwards and Haime, 1848) (Guzmán 2003). Platy *Agaricia* corals characterize the deepest zones from 15 to 20 m. The branching elkhorn and staghorn corals, *Acropora palmata* (Lamarck, 1816) and *Acropora cervicornis* (Lamarck, 1816), are primarily restricted to offshore reefs farther from human population centers (Guzmán and Guevara 1998a,b, 1999, 2001, Vollmer and Kline 2008).

Costa Arriba

Costa Arriba contains relatively fewer cays, inlets, and islets to provide protection from the trade winds, resulting in less reef development than Bocas del Toro (Guzmán 2003). As in Bocas del Toro, more protected areas are fringed by mangroves, which grade into fringing reefs and seagrass beds. Two large lagoons are

moderately protected from wind and wave action: Bahía Las Minas in the western portion of the region (about 6 km east of the entrance to the Panama Canal) and the bay of Portobelo 50 km eastward (Fig. 2). Exposed portions of the coast contain sandy beaches or reef flats. In addition to wind and wave energy, the shoaling reef flats present along the most exposed parts of the coast are subjected to periods of high solar radiation and periodic emersion from wind-enhanced tidal fluctuations (Cubit et al. 1989). The littoral zone of Costa Arriba is composed of a generally broader and flatter coastal plain, resulting in greater deposition of alluvial sediments near river mouths compared to the more topographically extreme coastal plain of Bocas del Toro.

The coral reefs of Costa Arriba contain 77% of the coral diversity reported for Panama, lower than that reported in Bocas del Toro (Guzmán 2003). Fringing reefs follow the mainland coastline with little vertical development, extending to approximately 15 m maximum depth with most corals occurring shallower than 6 m (Guzmán et al. 1991, Guzmán 2003). Coral communities are comprised mainly of *Diploria clivosa* (Ellis and Solander, 1786), *Agaricia* spp., and *Millepora* spp. in shallow zones ≥2 m, with a short reef slope composed of massive corals *Diploria strigosa* (Dana, 1846), *C. natans*, and *Siderastrea* spp. to about 15 m. Compared to Bocas del Toro and the rest of the Caribbean, *Acropora* spp. corals are conspicuously absent from most reefs in Costa Arriba. Analysis of Holocene reefs suggests that, at least for Galeta Point reef in the western part of Costa Arriba, *A. palmata* and *A. cervicornis* were major reef components during the phase of active framework-building that ceased approximately 2000 yrs ago when reef development "caught up" with sea level rise (Macintyre and Glynn 1976, Macintyre 2007). Today, small and isolated patches of *A. palmata* and *A. cervicornis* occur in the eastern portion of Costa Arriba, between Isla Grande and Portobelo (HM Guzmán, Smithsonian Institution, pers comm).

Human History

The human history of Bocas del Toro and Costa Arriba falls into three periods bounded by major changes in human subsistence, settlement patterns, and population: (1) pre-contact (about 9000 BC–1502 AD), (2) Spanish colonial (about 1502–1800 AD), and (3) post-colonial (about 1800–present).

Pre-Contact period

Abundant archaeological and paleobotanical data demonstrate that humans have been influential and continuous modifiers of tropical landscapes in Central America since at least 11,000 yrs ago during the Late Pleistocene (Cooke 1997, 2005). During this time, the Central American climate was colder and drier than today, and the Panamanian landscape consisted of more open forest than the dense modern forests. This more open landscape allowed groups of hunting and gathering Indians to traverse long distances in search of food resources, using fire to assist in land clearing for hunting and early crop cultivation (Cooke 1997).

Panama's Pacific slope has a longer history of continuous human settlement and land clearing than the Caribbean slope. Before Indians began practicing intensive agriculture and concentrating in sedentary villages, Archaic Period slash and burn activities had profound impacts on natural vegetation (Cooke et al. 1996). By 8500

BC, spearpoints and other artifacts appear in greater abundance along the Pacific slope, signaling an increase in population and residence time in a given location. This increase in sedentism was made possible by increased effort to collect and process plant foods (Cooke 1997). Data from a sediment core from Lake Yeguada in central Pacific Panama show evidence of anthropogenic land clearing by fire dating to approximately 9000 BC (Piperno et al. 1990). This core records a pattern of increased intensity of land alteration over time, with more frequent cutting and burning of vegetation around 5000–3000 BC, the appearance of maize between 3000–2000 BC, a peak in farming activities around 2000 BC, and finally a subsequent decline in alteration of vegetation. Early human habitation and landscape alteration also occurred on the Caribbean slope of Panama. Sediment cores from the Chagres River valley (now underneath man-made Lake Gatun in the Canal Zone) in central Caribbean Panama show that hunter-gatherers were present around 9200–7000 BC. People began to cut the forest and burn plots and cultivate maize by around 2900–2050 BC and to intensify crop cultivation (including shortened fallow periods) around 1350 BC (Ranere and Cooke 1991). Located in the canal watershed, one of the driest regions of Caribbean Panama, the Chagres site is the only prehistoric settlement on the Caribbean slope of the country that shows clear evidence of early land clearing by fire. The Lake Yeguada and Chagres River valley data demonstrate that exhaustion of soil resources via burning occurred thousands of years ago on both slopes of Panama.

After widespread maize agriculture appeared on the central Pacific slope sometime before 400 AD, pre-Columbian groups began a new phase of technological and social sophistication (Cooke 1997, 2005). The increased production efficiency of specialized crops such as maize and gourd/squash was followed by intensified population growth and land use. At this time, settlements moved down from previously burned hill slopes to more concentrated villages in lowland alluvial zones along the Pacific coast. These coastal settlements were used more often as seasonal camps for harvesting fish, crab, and mollusks from the littoral zone during the driest and least productive farming months (Drolet 1980, Cooke et. al. 1996)

The sparser and younger record of pre-Columbian human settlement on the Caribbean slope of Panama strongly suggests that the Pacific side was settled first and supported a larger human population until the Spanish conquest in the early 16th century (Drolet 1980, Cooke and Ranere 1992, Griggs 2005). Settlements greatly expanded in Costa Arriba and in the area between Bocas del Toro and Costa Arriba (present-day Veraguas province) during 800 BC–750 AD, possibly as maize-farming peoples immigrated from the Pacific. This expansion indicates an increase in population pressure on both slopes and a search for new areas to exploit (Drolet 1980, Griggs 2005). The establishment of settlements on moist and nutrient-depleted soils of the Caribbean slope may not have been possible without the development of maize cultivation (Grigg 2005).

Coastal habitation on the Caribbean slope also appears to have been less environmentally disruptive than that on the Pacific side. Archaeological sites represent small and itinerant settlements that employed subsistence activities that caused comparatively little environmental impact because they did not employ widespread slash-and-burn agriculture (Drolet 1980, Linares 1980a, Griggs 2005). The contrasting lifestyles of inhabitants on the Pacific and Caribbean slopes were related to differing local environmental conditions. Lower seasonality on the Caribbean slope inhibited

large-scale clearing of cut vegetation by fire and encouraged rapid reforestation of fallow fields, making intensive agriculture difficult (Bennett 1968, Gordon 1982). In addition, the coastal zone in Bocas del Toro and eastern Costa Arriba do not contain the extensive alluvial floodplains, mudflats, and upwelling zones characteristic of the Pacific side that are the most productive farming and fishing environments (Linares 1980a).

Bocas del Toro.—Until recently, the earliest human settlement (600–700 AD) discovered on the Caribbean slope of Panama was the Cerro Brujo archaeological site located on the Aguacate peninsula in Bocas del Toro (Linares 1980a). Situated 1 km from the coast in an area separating Almirante Bay from the Chiriquí Lagoon, this site was one of four small dispersed hamlets found in a 20 km^2 area (Linares 1977, 1980b). Inhabitants engaged in a relatively low-impact settlement pattern based on "forest-farming" (selection of desirable forest tree, shrub, and herb species via a slash-and-mulch system of agriculture) and "garden-hunting" (opportunistic capture of species that forage in disturbed vegetation; Linares 1976, 1980a). Settlers did not rely heavily on marine resources, possibly because they were recent immigrants from the inland Volcán Barú region that were displaced after its eruption around 600 AD (Linares 1980a). However, recent research has found no evidence that Volcán Barú erupted around that time (Holmberg 2009).

Cerro Brujo was vacated for two to three centuries and then resettled around 900 AD by a small (120 person maximum) group of people that relied more heavily on coastal marine resources, primarily from nearby seagrass, mangrove, and coral reef habitats (Linares 1980a). Extrapolation of density estimates from this site (3–4 people km^{-2}) gives a median population estimate of approximately 32,000 people in the entire Bocas del Toro region (Fig. 3, Table S1). Middens reveal that bivalves, fishes, turtles, and manatees were the most important marine animals consumed, while gastropods were not an important food source. Important bivalves included mangrove oysters *Crassostrea rhizophorae* (Guilding, 1828) and *Isognomon alatus* (Gmelin, 1791), and epifaunal coral reef-associated clams *Arca zebra* (Swainson, 1833), *Arca imbricata* (Bruguière, 1789), and *Chama macerophylla* (Gmelin, 1791), all species that could have been obtained by wading or swimming a short distance from the shoreline (Borgogno and Linares 1980). Green turtle and manatee from seagrass habitat and snapper and snook from mangrove channels and shallow coral reef habitats were also taken. Harvesting of marine animals occurred relatively close to the settlement site, indicating that nearshore marine resources were still plentiful. Plant remains indicate that prehistoric land use was based on the cultivation of root-crops and fruiting trees (Linares 1980a), resulting in the maintenance of plant cover over the soil and relatively low rates of soil erosion (Gordon 1982). The abundance of mammal species associated with disturbed or secondary growth habitat and the paucity of arboreal or closed-canopy forest animals suggest that the gardens surrounding settlements were substantial (Linares and White 1980, Cooke 1984).

Since its discovery in the 1970s, Cerro Brujo has served as the model for interpreting prehistoric human habitation of the western Caribbean slope of Panama. Under this model, groups of people from a similar cultural tradition migrated from the fertile highlands near Volcán Barú down along both sides of the continental divide during the 1st century AD, after which their social and subsistence

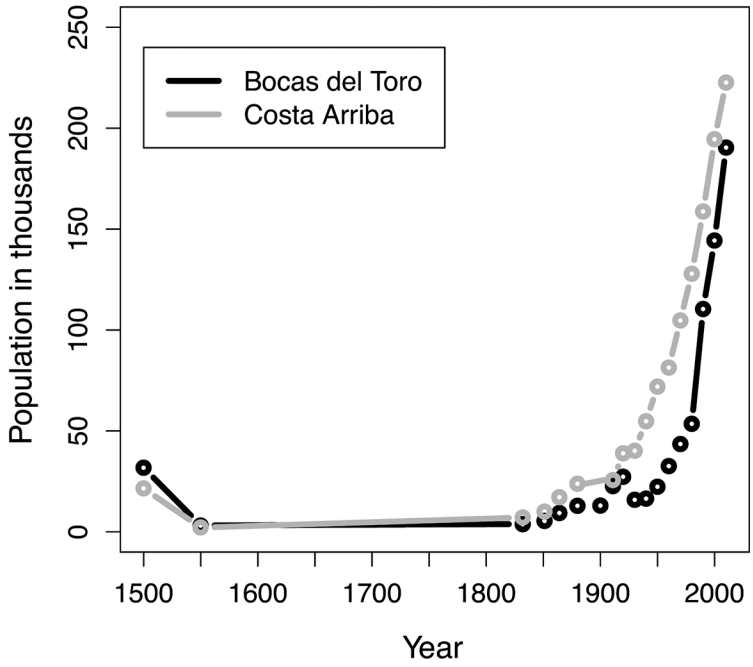

Figure 3. Population of Bocas del Toro and Costa Arriba, Panama, pre-contact period to today. See Tables S1 and S2 for population estimation methods.

systems began to diverge. Settlers on the Pacific slope discovered fertile farming grounds and concentrated on specialized agriculture based on maize and other seed crops, while settlers on the Caribbean slope concentrated on the diverse and abundant coastal marine resources and a less intensive form of agriculture based on root crops and fruiting trees (Linares 1977).

However, excavation in 2003 of a new site called Sitio Drago located on Colón Island in Almirante Bay (Fig. 1) reveals that pre-Columbian Bocas del Toro was more densely inhabited and socially complex. Sitio Drago, dated to 750–1450 AD, is contemporaneous with the second settlement phase of Cerro Brujo and with maize-oriented settlements on the Pacific coast of western Panama (Wake et al. 2004, Wake et al. in review). The presence of several seed processing milling stone fragments suggests that a mixed seed/root/tree cropping occurred at Sitio Drago, in contrast to the focus at Cerro Brujo on root crops exclusively (Wake 2006, Wake et al. 2012, Wake and Mendizábal in press). Ceramic artifacts suggest its inhabitants were involved in long-distance trade with numerous regions in Central America (Bond 2008). Ceramic types associated with northwestern Costa Rica as well as from the Pacific slope of western Panama indicate communication between Bocas del Toro and various other complex societies. The higher prevalence and greater diversity of non-local ceramic types found in Sitio Drago compared to Cerro Brujo suggest that more trading occurred in the former area (Bond 2008). The location of Sitio Drago at the intersection of the Caribbean Sea and Almirante Bay on Isla Colón would have made this site an ideal trading hub.

Although Sitio Drago was more densely populated and socially complex than Cerro Brujo, the subsistence pattern of root and tree cropping, garden hunting, and fishing was probably similar at both sites (Wake et al. 2004). Middens reveal that similar marine animals were harvested at both sites: all of the bivalve species important at Cerro Brujo were abundant in Sitio Drago middens, with the addition of another oyster (*Pteria* spp.) that lives on gorgonian sea fans (Wake et al. 2004, Wake et al. in review). Gastropods, including conchs (*Stombus* spp.) and predatory Muricids (*Murex* spp.) appear to have been more important sources of food or adornment items at Sitio Drago than at Cerro Brujo.

More recently, a site pre-dating Cerro Brujo (dated to approximately 0–400 AD) has been discovered in the north-central part of Colón Island that contains ceramics of the same type as the early component at Cerro Brujo (T Wake, University of California, Los Angeles, unpubl data). Further investigation of this site will surely extend the timeline of human settlement and magnitude of environmental impacts in the Bocas del Toro region.

Ethnohistoric data from the time of European contact corroborate the notion of relatively low-impact land use by native peoples in Bocas del Toro, but suggest that this region was more heavily populated and economically sophisticated than do the archaeological data. Notes from Columbus' visit to the coast of "Veragua" (an area extending from Nicaragua to the Belén River east of Bocas del Toro province) during his final voyage to the New World in 1502–1503 reported that a "numerous but dispersed population, living in small communities near streams and modest rivers, characterized the central Bocas del Toro area around Almirante Bay" (Sauer 1969 paraphrasing Colón 1959).

Columbus observed numerous indications that the inhabitants were engaged in active trading with outside peoples. Traders from northern Central America were spotted in canoes plying the offshore waters of Bocas del Toro, and a group of Meso-American peoples (the Sigua) were established in the western part of the region between the Sixaola and Changuinola Rivers (Lothrop 1942, Cooke et al. 2003). Numerous indigenous groups speaking related languages inhabited the coastal zones, foothills, and river valleys (Gordon 1982). Many of these groups were warring against one another, and an incursion of people from the northern regions of Central America may have been slowly underway at the time of European contact (Gordon 1982, Cooke 2005). Indians were spotted by the Spaniards wearing plates and badges of tribal leadership made of gold, a signal of complex and hierarchical social structure (Sauer 1969).

Along with the ethnohistoric records of Indians adorned with gold, the discovery of gold artifacts in western Caribbean Panama has led some researchers to conclude that this area was an important center for pre-Columbian isthmian gold production (Cooke et al. 2003). The presence of mines in the area between Bocas del Toro and Colón confirms that gold items found in the area were sourced locally (Cooke et al. 2003). The presence of gold artifacts in Mayan territories in the Yucatan with similarities to ornaments made in Veragua (Lothrop 1952) suggests a degree of interaction between western Caribbean Panama and sophisticated Meso-American "high" societies. There is an absence of foreign items imported from outside Panama in Bocas del Toro, suggesting the flow of goods was one way between the regions, possibly by coercion or force. The presence of the Sigua Indians in Bocas del Toro has been explained as an attempt by their leader

Moctezuma to obtain raw materials (including gold) for use in Mexico (Lothrop 1942). Distant Indian groups traveled to Bocas del Toro to obtain sarsaparilla, manatee skins, cacao, and turtle shell (Castillero Calvo 1995), suggesting that Bocas del Toro was naturally exceptionally rich in these resources or that they were not yet as heavily exploited as they were in more populous parts of Central America.

Ethnographic studies of the modern-day descendants of the cultural group that settled Cerro Brujo, the Ngöbe (formerly Guaymí) Indians, show that indigenous settlement and subsistence patterns have changed little over the past millennia in Bocas del Toro (Roberts 1827, Linares 1977, Young 1980, Gordon 1982). The Ngöbe are the largest group of surviving indigenous inhabitants of Bocas del Toro. Today, those groups that live outside of developed areas (particularly in the Ngöbe-Buglé territory in the eastern part of the region) are still organized into small, mobile dispersed hamlets practicing relatively low-impact long-fallow slash-and-mulch agriculture of root crops and other plants, and fishing in mangrove and coral reef environments (Roberts 1827, Young 1980, Gordon 1982).

Costa Arriba.—Archaeological and paleobotanical data show that the inland river valleys and coastal lowlands of Costa Arriba were well populated thousands of years ago. Stone tools used for processing maize (*manos* and *metates*) dating to around 1 AD attest to the antiquity of maize-oriented peoples (Drolet 1980). Because the region is topographically much lower than Bocas del Toro but precipitation levels are comparably high, Costa Arriba contains a greater number of intermittent river valleys and narrow alluvial floodplains. Early inhabitants here probably practiced a more intensive form of maize agriculture that included periodic burning on terraces, slope lands, and alluvial plains (Drolet 1980). Widespread distribution of *manos* and *metates* and tools for clearing forests suggests that most riverine zones were heavily occupied up to the contact period (Drolet 1980). The presence of other artifacts reveals that 16th century settlements were organized into cheifdoms whose movements and territorial settlement patterns were undertaken to increase access to good agricultural lands, indicating high population densities. Maize cultivation probably was initially focused on drier hillslopes and subsequently spread downward to lowland riverine coastal areas (Drolet 1980). This settlement pattern allowed for a shifting maize cultivation system like that still practiced by modern-day inhabitants in remote parts of Costa Arriba, where two annual maize harvests occur: one on the drier hillslopes during the wet season, and one on wetter floodplain during the drier season (Drolet 1980).

Lowland groups heavily exploited coastal aquatic resources as evidenced by the presence of net weights for freshwater and marine fishes and notched weights that may indicate the harvest of turtles in more open sea areas (Drolet 1980). Middens contain an abundance of the nearshore gastropod *Cittarium pica* (Linnaeus, 1758), indicating a reliance on coral reef habitats for food. Nevertheless, the higher concentration of artifacts in inland river valleys and the prevalence of maize-related items suggest that pre-Columbian inhabitants in eastern Costa Arriba were more agriculturalists than fishermen (Drolet 1980). Coastal settlements appear to have been frontier fishing villages that were used to contribute to the food production system of a larger polity headquartered more inland within the Bayano River valley (Fig. 2). Marine resources appear to have been more important during the wet

season, the easiest time of year for navigating nearshore marine environments due to the slackening of the strong trade winds characteristic of Costa Arriba.

Ethnohistorical data confirm that Costa Arriba was more densely populated and the terrestrial environment more visibly altered than Bocas del Toro. The earliest European account of Indian settlements in Costa Arriba was written by Ferdinand Colón in 1502–1503, who described the settlement surrounding the bay near Portobelo as "very large, beautiful, and populous, and has about it much cultivated land" and stated that "the region that lies around the port is not wild, but cultivated and full of houses, one distant from another by a stone's throw or a crossbow shot; it appears like a painted scene the most beautiful there is" (from Colón 1959 in Sauer 1969).

Other observations by Colón's party state that gold was prevalent in the vicinity of Nombre de Dios and Portobelo, where Indians wore gold leaves as nose ornaments (from Colón 1959 in Helms 1979). It was also noted that the entire coast from Bocas del Toro to Costa Arriba and eastern Caribbean Panama was an area of exchange of indigenous goods, and that "along the coast were five towns of active trade" (from Colón 1959 in Helms 1979). In the eastern part of Costa Arriba near present-day Isla Grande, it was noted that the land was covered by short grass and had few trees, an indication of extensive land clearing for cultivation of maize and other crops (from Colón 1959 in Drolet 1980). Other conquest-period accounts state that population centers were concentrated in fertile alluvial valleys nestled back from the coast that constituted the best agricultural lands in the area, and that neighboring settlements were often engaged in a state of warfare in competition for agricultural lands (Drolet 1980).

In summary, humans have been a continuous presence throughout Panama for thousands of years, with distinct settlement and subsistence patterns on either side of the continental divide. Land clearing activities were more pronounced on the seasonally dry Pacific slope due to the use of slash-and-burn agriculture for specialized seed crops such as maize. Although survey effort has been much lower on the more densely forested and humid Caribbean slope, it appears that human populations were smaller and did not intensively clear the large expanses of land using fire. Nevertheless, people did noticeably disturb the prehistoric Caribbean landscape using a slash-and-mulch system of forest gardening and crop cultivation resulting in a mosaic of fields, gardens, and secondary and primary forest (Gordon 1982). Costa Arriba was more heavily populated and deforested than Bocas del Toro, but both regions participated in an extensive trading network. Populations from both regions actively exploited coastal marine resources, but it is not known whether those exploitation levels were ecologically sustainable.

Colonial Period

The Spanish conquest of Central America resulted in the extermination of up to 99% of the indigenous population within a period of 40–50 yrs after first Spanish contact at the turn of the 16th century (Cooke 1997). Much of the indigenous population that was not killed by introduced diseases, war, or internal conflicts was transported to North or South America as slaves. Thus, much of Central America, including Panama, became virtually depopulated within the first half of the 16th century (Bennett 1968, Denevan 1992). Indigenous populations in Panama declined from an estimated several million to a few hundred thousand during this period

(Cooke 1997), and many of the survivors retreated into forested mountainous regions (Dampier 1697, Roberts 1827).

Along the Caribbean slope of Panama, the loss of the indigenous population was not compensated for by an increase in European or other immigrants. Although strategically and economically important as a center of transit, the Caribbean slope was not a major population center of the Spanish empire (Ward 1990). Aside from modest mining operations and grazing operations for newly-introduced livestock, the Spanish did not use Panama as a source of raw natural resources for export (Behrendt 1943). Thus, the conquest resulted in a dramatic decrease in human population and exploitation of the terrestrial environment. During this time, much of the Caribbean forest that had been altered by the cumulative effects of millennia of indigenous agriculture began to regenerate (Abbot 1913, Bennett 1968).

Although human pressure on terrestrial resources was certainly reduced after the Spanish conquest, pressure on marine resources may actually have increased. There was an explosion of ocean-based commerce along Panama's Caribbean coast during the 16th and 17th centuries due to Panama's central location between North and South America. Written accounts by Caribbean explorers and traders reveal the staggering quantity of marine megafauna such as manatees, turtles, and monk seal removed from Caribbean waters during this time (Dampier 1697, Wafer 1704, Exquemelin 1969, Jackson 1997, McClenachan et al. 2006, McClenachan and Cooper 2008). Some of these accounts note the abundance of marine food sources and the frequent exploitation of these animal populations by coastal indigenous groups (Dampier 1697, Wafer 1704), noting that net fishing near rivermouths and intertidal zones was more common than fishing on coral reefs. However, data on pre-Columbian exploitation of coastal resources in Caribbean Panama are too sparse to directly compare overall environmental impact to coastal ecosystems between the pre- and post-contact periods.

Bocas del Toro.—Historical records show that the coastal area of Bocas del Toro was much less densely inhabited during the colonial period than it was before European contact. The region was peripheral to Spanish society and economy, and no major Spanish settlements were established here during the colonial period (Castillero Calvo 1995). Possibly due to limited interaction with the Spanish, a small but continuous indigenous presence was maintained in the region during this time. The indigenous inhabitants of Bocas del Toro also had a reputation for fiercely defending themselves against Spanish aggression (Dampier 1697, Roberts 1827). Nevertheless, the region was visited frequently by English and other pirates, privateers, and profiteers who took advantage of the protected waters inside Almirante Bay and Chiriquí Lagoon to repair their ships and hunt the abundant turtles and manatees that nested on the exposed beaches of the archipelago (Dampier 1697, Exquemelin 1969).

During the 16th century, indigenous groups were still raising tapirs and peccaries as domesticated animals for food and trade (Gordon 1982). The presence of tapirs, a forest-dwelling animal, suggests that relatively undisturbed forest was still prevalent. Until the 17th century, Bocas del Toro was still described as an important and populous maize-producing country where explorers were always met by numerous Indians wherever they visited the shore (Gordon 1982). This was true

even of the islands inside Almirante Bay, which were easily approached by sea and frequently visited by European traders (Gordon 1982).

Throughout the 18th century, Miskito Indians from Nicaragua carried out raids on Ngöbe Indian villages along the Bocas del Toro coast, focused particularly on villages in the Chiriquí Lagoon (Cockburn 1735). During these raids, villagers were captured to be sold as slaves to British colonists in Jamaica. In 1722, Spanish authorities complained that the Miskito had captured over 2000 Indians within the Caribbean coast of Costa Rica and Bocas del Toro combined (summarized in Conzemius 1932). Miskito "slave-hunting" raids in the Talamanca region of Costa Rica near the border of Panama are thought to be a major contributor to the depopulation of this region (Conzemius 1932). These raids likely also diminished the indigenous population in coastal Bocas del Toro during the 18th century, although to a lesser extent.

By the early 19th century, coastal indigenous settlements appear to have diminished from disease (Gordon 1982), and, possibly, as Indians retreated from the coast to avoid European (Roberts 1827) and Miskito (Heckadon Moreno 2011) aggression. One British trader from Jamaica spent several months in a Ngöbe settlement located in the upper Cricamola River valley approximately 12 km inland from the Chiriquí Lagoon. His description of the settlement during this time closely mirrors the settlement and subsistence patterns described for the inhabitants of the Cerro Brujo archaeological site in Bocas del Toro from 900 AD: numerous dispersed hamlets without a central village that were engaged in slash-and-mulch agriculture, garden hunting, and fishing (Roberts 1827). The major change from prehistoric agricultural practices was the focus on maize and banana cultivation, with large areas along the shore of the river cleared for plantations of these crops (Roberts 1827). Bocas del Toro was reported to be a remote and sparsely inhabited region during this time: "the banks of many of the rivers falling into these lagoons, are now totally destitute of inhabitants; although, at one period, the country contained a numerous population consisting of various tribes, some of them, from the apparent remains of their ancient settlements, of considerable antiquity" (Roberts 1827). Although no major Indian settlements were located on the shore, smaller groups of upland peoples such as the Teribe traveled to or seasonally inhabited coastal areas to hunt turtles for trade after they had observed the success of the Ngöbe in this industry (Gordon 1982).

At the beginning of the 20th century, Bocas del Toro was a backwater province in the newly independent Republic of Panama, a forested hinterland that was cut off from the rest of Panama by a formidable mountain range and with no overland route to any cities. Commerce was mainly in sea turtles and other marine resources (Heckadon Moreno 2011). Thus, although the population of the region was relatively small, the impact to coastal ecosystems from fishing must have been substantial (Pandolfi et al. 2003).

Costa Arriba.—In contrast, Costa Arriba was an economically and politically strategic region throughout the colonial period, with two major ports and a transisthmian road, which carried 60% of all precious metals that entered Spain from the New World (Heckadon Moreno 1997). The western portion of Costa Arriba is located in the lowest portion of the isthmus, the Chagres River valley, and was utilized by the Spanish as an overland route for the transport of goods between

oceans during the 16th–18th centuries (Hussey 1939). At the eastern portion of Costa Arriba, the towns of Nombre de Dios and Portobelo were the principal Caribbean trading and transportation hubs of the Spanish empire. The western and eastern regions of Costa Arriba were integrated through a system of roads and waterways and constituted a vital conduit for the transportation of natural resources and people across the isthmus.

Nombre de Dios was founded in 1537 as the site of the annual commercial fairs for the trading of riches acquired in Mexico and Peru (Jaén Suárez 1979, Ward 1990). In 1587, Nombre de Dios was a city of approximately thirty households and inhabited by foreigners and transients that did not make the area their permanent home (Ward 1990). After numerous attacks on the port by English buccaneers in the latter half of the 16th century—often assisted by escaped African slaves living in settlements scattered throughout Costa Arriba—and problems with erosion from land clearing (Hussey 1939), the Atlantic port was relocated about 2 km to the west at Portobelo in 1597, a site located at the mouth of a large natural embayment with deep waters protected from wind and wave exposure (Hussey 1939, Jaén Suárez 1979, Pike 2007). According to the engineer tasked with the construction of defensive forts and other infrastructure, Portobelo had all the components necessary for building a new city: solid ground, a good climate for growing maize, a large number of trees for ship-building, fresh water from numerous small rivers that emptied out into the bay, and a large swamp that could be drained for grazing cattle (Ward 1990).

Portobelo experienced a severe labor shortage at the end of the 16th century because of European avoidance of the area due to the prevalence of malaria and yellow fever, and the general "unhealthiness" of the surrounding mangrove swamps (Ward 1990). This suggests that indigenous inhabitants were entirely extirpated from this area by the end of the 16th century. Historical records confirm the continued small permanent population (approximately 8–13 houses) of Portobelo from the late 16th to early 17th century (Ward 1990). During this time, the population swelled during the annual trading fairs to a maximum of several thousand people, comprised of merchants, travelers, and sailors from all over Latin America, as well as Spanish soldiers sent to guard against the activities of English privateers (Ward 1990). By the end of the 17th century, Portobelo's importance as a mercantile port waned as the Spanish began transporting treasures between Spain and its North and South American colonies by traveling around Cape Horn to avoid incessant pirate attacks (Behrendt 1943, Ward 1990). By the beginning of the 18th century, Nombre de Dios and Portobelo were reported to have been virtually abandoned, overtaken with vegetation and in a state of ruin (Dampier 1697, Wafer 1704). Costa Arriba probably underwent a more dramatic indigenous population loss during the colonial period than Bocas del Toro because of the higher rates of interaction with the Spanish (Abbot 1913, Drolet 1980).

Although the coastal population of Costa Arriba was relatively low during the colonial period, the impact of the construction of the fortresses of Nombre de Dios, Portobelo, and San Lorenzo on nearby coral reef ecosystems must have been enormous. The fortresses and other buildings were constructed from the skeletons of slow-growing massive coral colonies (Ward 1990), dredged from reefs over 200 yrs (Guzmán 2003). It is estimated that at least 70,000 m^3 of coral was mined during these operations (Guzmán 2003). The affected coral reef ecosystems probably required centuries to recover from this disturbance, if they were able to recover at all.

In summary, during the Spanish colonial period the human and natural environment of Caribbean Panama underwent significant changes due to the decline of the native population and the concentration of Europeans in coastal settlements and in ships traveling along the coast. During this period of human population decline in Caribbean Panama, resource exploitation shifted from the cultivation and hunting of terrestrial resources to the intensive extraction of marine resources, particularly turtles and manatees (Dampier 1697, McClenachan et al. 2006).

Post-Colonial Period

The post-colonial period was a time of great transformation in the economy, population, and environment of Central America. The era began with a period of political and economic turmoil in the 19th century that culminated with the emergence of independent republics each focused on carving out their own economic niche. During the century after independence from Spain, Central America remained a fairly sparsely populated and undeveloped region (Behrendt 1943). During the 300-yr colonial period, the Spanish and mestizo (more generally, mixed Spanish, indigenous, and African) population grew slowly, with an approximate 100-yr doubling time (Heckadon Moreno 1997). It was not until the demographic revolution in Central America during the 20th century that the human population began to greatly exceed estimated pre-conquest levels (Fig. 3). The population doubling time decreased to 25–30 yrs, and the population increased from about 3 million at the beginning of the century to over 30 million by 1990. The most rapid rate of population growth occurred in the second half of the 20th century, when it more than tripled. During this time, the area of Central America covered by forest declined from about 75% to 30% (Heckadon Moreno 1997). With this population boom came increased colonization and exploitation of previously remote and wild areas of Central America, particularly on the wet and forested Caribbean slope.

In Caribbean Panama, the most influential impacts on post-colonial population and economic growth occurred during the 19th and 20th centuries with the construction of the transisthmian railroad and Panama Canal and the introduction of banana cultivation (LaBarge 1960, Heckadon Moreno 1993, 1997, Stephens 2008). Whereas the canal has been the primary catalyst of environmental change along the western part of Costa Arriba, the banana industry has been the catalyst in Bocas del Toro. Both the canal and the banana industry required major investment in transportation and energy infrastructure within Panama, increasing access and movement of peoples from the more densely populated Pacific slope to the Caribbean. Tens of thousands of principally West Indian foreign laborers were employed to construct the Canal and plant and harvest the banana plantations. More recently, the Panamanian government has implemented development strategies for transforming Caribbean forests into economically productive lands. All of these factors have made the Caribbean slope of Panama a new "colonization frontier" (Heckadon Moreno 1997). As a result, terrestrial and marine coastal ecosystems in Bocas del Toro and Costa Arriba have been subject to heightened human disturbance since the 19th century.

Bocas del Toro.—During most of the 19th century, Bocas del Toro continued to be a relative backwater inhabited by dispersed indigenous groups concentrated in upland sections of river valleys and occasionally visited by seafaring traders and fortune seekers. In the first half of the century, British traders began to explore the area for sea turtles and turtle shell, coconuts, cacao, sarsaparilla, and vanilla.

Some of these traders settled permanently on the larger islands within Almirante Bay (Stephens 2008).

In the latter half of the 19th century, localized patches of coastal lowland rainforest in Bocas del Toro were planted with banana for export to North America. A small portion of land was cleared in Chiriquí Lagoon in the 1880s, and banana plantations began to radiate outward from the coastal area of the lagoon onto the Aguacate Peninsula and the main islands within Almirante Bay and Chiriquí Lagoon (Stephens 2008; Fig. 1). Other banana interests arrived, leading to the eventual expansion of plantations into the northwest part of the province within the Changuinola and Sixaola River floodplains. The independent banana interests were consolidated into the behemoth United Fruit Company in 1905, which oversaw the continued expansion of operations from an office in the town of Bocas del Toro on Colón Island in Almirante Bay.

The 20th century was the beginning of an economic boom for Bocas del Toro that radically transformed its natural environment and human population. As banana production expanded westward to the lowland plains surrounding Almirante Bay, the production and transportation of the fruit shifted away from Chiriquí Lagoon. The town of Bocas del Toro underwent a rapid expansion in population and geographic extent that required the draining and filling of the mangrove swamp over which it was originally founded. In 1903, a canal was dug from the Changuinola River to the northwestern part of Almirante Bay to facilitate the transport of bananas from the extensive plantations in Changuinola to a location where they could be loaded onto large open ocean vessels. Banana production continued to increase as additional coastal forest and swampland were cleared for plantations. A new port town, Almirante, was built in 1909 in the back section of Almirante Bay, and the Changuinola canal was abandoned (Stephens 2008).

The first decades of the 20th century saw the height of banana production and associated development within Bocas del Toro. New bridges, railroads, buildings, and associated infrastructure were built, concentrated in the towns of Almirante, Changuinola, and Bocas del Toro town (on Colón Island) in the western part of the province (Fig. 1). Thousands of West Indian laborers came to work the banana plantations and to settle in the coastal lowlands of Bocas del Toro. West Indian and Creole settlements spread and dispersed among the islands and mainland lagoons of the archipelago throughout the 1900s. Deforestation likely increased as these settlers engaged in small-scale agriculture. Marine ecosystems were likely also affected by the settlers' extensive reliance on sea turtles (particularly the hawksbill turtle) and fishes for subsistence and commercial purposes (Heckadon Moreno 2011).

From 1910 to 1915, the United Fruit Company had approximately 6500 employees (Stephens 2008). This expansion declined in the 1920s due to fungal and bacterial diseases that increasingly and continually plagued the banana plants (LaBarge 1960). Various measures were attempted to combat the diseases but proved ineffective, and old plantation areas were abandoned for newer areas with uninfected soils. This resulted in the movement of plantations farther west and inland, and the clearing of additional mainland forest surrounding Almirante Bay.

During the 1930s and 1940s, banana diseases had destroyed the majority of plantations and many fields were abandoned or converted to cacao or abacá (manila hemp) plantations. The decline in banana production resulted in a population decline as

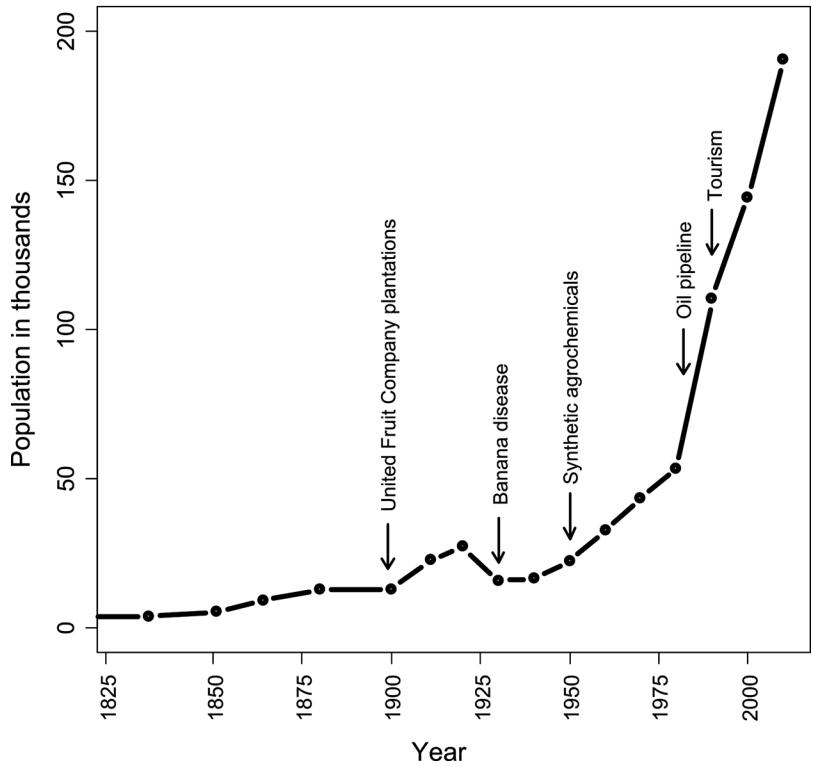

Figure 4. Human population of Bocas del Toro, Panama, since 1832 and major events that have affected the nearshore environment. See Table S1 for population estimation methods.

unemployed laborers moved elsewhere (Fig. 4), and some abandoned banana fields reverted back to forest.

The banana industry picked up again in the 1950s with the introduction of a more disease-resistant variety and the utilization of synthetic agrochemicals. The second half of the 20th century was the beginning of a marked increase in population to levels exceeding pre-contact numbers, a trend which continues to the present (Fig. 3). This increase has been fueled in part by the rapid growth of the Ngöbe population (Gordon 1969, Republic of Panama 2010; Fig. 4) that began to return to the coastal regions of the Bocas del Toro lagoons after retreating to upland river valleys in the beginning of the century (Bourgois 1985).

Starting in the 1950s, plantations were sprayed with the pesticides DDT, dieldrin, and chlorpyrifos in increasing quantities. This resulted in an explosion of new pests and the subsequent introduction of new agrochemicals (Henriques et al. 1997, Stephens 2008). By the 1980s, pest levels had become problematic enough that fungicides were sprayed aerially over plantations by five separate planes, with fields sprayed up to 50 times per year (Bourgois 1985, Stephens 2008). This method of dispersal inadvertently delivered chemicals directly to waterways that eventually drained to the ocean. Fertilizer use also increased during this period in the form of potassium and nitrogen compounds applied to soils (Stephens 2008). The effect of increased agrochemical usage to the coastal marine environment was probably substantial, as these chemicals have demonstrably negative effects on aquatic life including corals

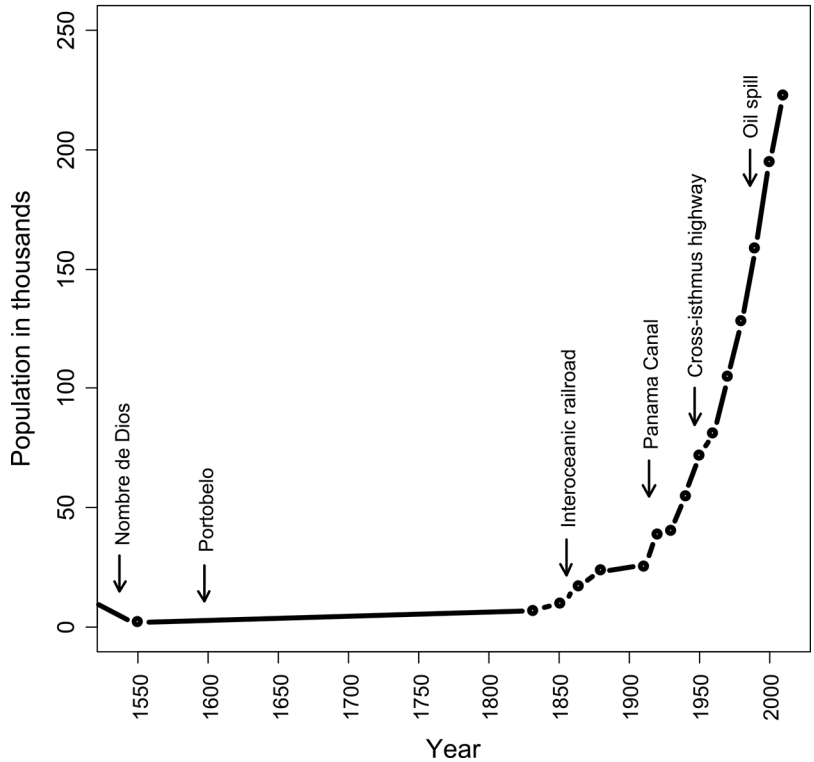

Figure 5. Human population of Costa Arriba, Panama, since about 1550 and major events that have affected the nearshore environment. See Table S2 for population estimation methods.

(Hawker and Connell 1991). Many of these chemicals have been directly released to the ocean via irrigation canals, groundwater runoff, and aerial spraying by planes (Stephens 2008). The main transport pathways of these chemicals to coral reef and mangrove environments are the Cricamola River in Chiriquí Lagoon, Changuinola canal in Almirante Lagoon, and the handful of smaller creeks that drain into either of the lagoons.

The "taming" of the lowland swamps and forest by the banana industry literally paved the way for a second phase of development and immigration in the 1980s (Figs. 4, 5). In 1982, a pipeline was completed to transport Alaskan crude oil across the Isthmus to the town of Chiriquí Grande in Chiriquí Lagoon, the site of an oil terminal visited frequently by large oil tankers and plagued by frequent oil spills (Suman 1987). The construction of the pipeline facilitated completion in 1984 of the first paved road over the continental divide connecting the Pacific slope to Bocas through Chiriquí Grande. With this new road came thousands of settlers from the Pacific slope in search of pasture and agricultural land (Suman 1987, Stephens 2008). The completion of paved sections of road along the narrow coastal plain in the 1980s and 1990s resulted in an unbroken connection from Costa Rica to the towns of Changuinola, Almirante, and Chiriquí Grande in Bocas del Toro, and brought increased settlement to the mainland area surrounding Almirante Bay and Chiriquí Lagoon (Stephens 2008).

Since the 1990s, Bocas del Toro has experienced an increase in development and environmental alteration fueled by tourism and land speculation. Clearing and development of coastal areas, particularly offshore islands, have greatly increased and land has been parceled up into small plots with little concern for negative environmental or socioeconomic impacts (Stephens 2008). During this period, an indigenous territory for the Ngöbe and Buglé Indians was established that extends from the east of the Valiente Peninsula to the Calovébora River in the west up to the central cordillera in the south. Development in this region is relatively minimal, although deforestation from subsistence farming and cattle ranching is increasing.

The coastal ecosystems of Bocas del Toro today show clear signs of severe ecological degradation (Guzmán 2003, Pandolfi et al. 2003). Monitoring of several coral reefs revealed as much as a 10% decline in coral cover during the late 1990s to early 2000s, although some fringing reefs still have living coral cover as high as 50%–90% (Guzmán 2003). Coral skeletons and mollusk shells excavated at 5 m water depth from large pits dug underneath modern reefs throughout the province revealed that dramatic changes in coral and molluscan reef communities occurred before 1960 in coastal lagoons and continued from 1960 to the present at offshore reefs (Cramer et al. 2012). Changes included the demise of the previously dominant staghorn coral *A. cervicornis* and the oyster *Dendostrea frons* (Linnaeus, 1758) that lives attached to gorgonian and staghorn corals, as well as reductions in bivalve size and simplification of gastropod trophic structure, indicating increasing environmental stress on reefs. Shallow coral communities underwent a two-phase successional sequence, from dominance by *A. cervicornis* to branching *P. furcata* and then foliose *A. tenufolia*. On lagoonal reefs, these changes were underway at least decades prior to the outbreaks of coral disease and bleaching in the 1980s, which are widely cited as the cause of coral demise across the Caribbean. The earlier timing of change in reef coral and molluscan communities in Bocas del Toro indicates that historical local disturbances such as land clearing and fishing are factors in the recent collapse of reefs in this region. In contrast, a suite of coring studies conducted in Almirante Bay found a recent (post-1960) and unprecedented replacement of the dominant coral species in shallow reef zones, from *P. furcata* to foliose *A. tenuifolia*, attributed to deteriorating water quality due to land use changes (Aronson et al. 2004, 2005, Hilbun 2009). The discrepancy in study results is possibly due to the greater variety of reef environments and quantity of material sampled in the large diameter pits relative to the narrow diameter cores.

Increased amounts of sediments and pollutants detected in these lagoons are attributed to banana plantations, ship traffic, and the oil terminal that are located within the Chiriquí Lagoon and Almirante Bay watersheds (Guzmán and Jimenez 1992, Guzmán and Garcia 2002, Guzmán 2003). Although much of the coastal strip of land fringing the lagoons is still covered by mangrove and evergreen forest, deforestation is encroaching on the coastal area as migrants from the Pacific slope advance along Panama's "agriculture colonization frontier" (Heckadon Moreno 1997).

The reef ecosystems of Bocas del Toro appear exhausted by subsistence fishing. Several species of conch (*Strombus* spp.) have been historically exploited to critical levels (Tewfik and Guzmán 2003), and sea cucumbers were severely depleted within a few months of harvesting during 1997 alone (Guzmán and Guevara 2002, Guzmán 2003). Large fishes such as jacks, barracudas, and snook were commonly

fished in the 1950s within Bahia Almirante and Chiriquí Lagoon (Gordon 1982), but are extremely rare in the lagoons today (Guzmán 2003, Dominici-Arosemena and Wolff 2005, KL Cramer pers obs). Spiny lobsters are also overfished on Bocas del Toro reefs, with individual body sizes and population densities smaller there than in other regions of the Caribbean (Guzmán and Tewfik 2004).

Ethnographic data suggest that coral reef ecosystems of Bocas del Toro were over-exploited by the 1950s or earlier. Even in regions inhabited by the Ngöbe that were not developed by the banana industry, spiny lobsters were increasingly rare in the 1950s and 1960s, and green and hawksbill turtles were heavily exploited for their meat, eggs, and shells, both for local consumption and export (Gordon 1982). Large marine animals that were important in pre-colonial and colonial times, such as green and hawksbill turtles, manatees, groupers, snappers, and the extinct Caribbean monk seal, are rare or absent today (Mou Sue et al. 1990, Meylan 1999, Pandolfi et al. 2003).

Costa Arriba.—The low-lying western portion of Costa Arriba continued to be utilized as the principal trans-isthmian transportation route with the construction of the Panama Railroad in the mid-19th century and the Panama Canal during the latter half of the 19th century. Prior to around 1850, western Costa Arriba was sparsely inhabited by families practicing subsistence agriculture (Abbot 1913, Heckadon Moreno 1993). From the colonial period to the start of the railroad in 1850, the population of the Canal Basin was probably no more than 1500 people (Heckadon Moreno 1993). Population levels increased in three waves: in the mid-1800s during the railroad construction boom, in the 1880s–1980s during the French attempt to dig a sea level canal, and in 1904–1914 during the completion of the Panama Canal by the United States (Bennett 1968, McCullough 1977, Heckadon Moreno 1993). Most immigrants were West Indian laborers that settled in the increasingly urbanized city of Colón, situated on the eastern side of the opening of the canal (Fig. 5). Prior to its transformation into Panama's Atlantic port around 1850, this part of the coast was described as a vast expanse of "unhealthy" mangrove swamps and mangrove islands inhabited primarily by crocodiles, mosquitoes, and sandflies (Abbot 1913).

The coastal environment was dramatically transformed after 1850 with the clearing, filling, and draining of mangrove swamps to create solid ground upon which to build Colón, and the city continued to grow during the gold rush era of the North American West (Abbot 1913). The population and area of Colón continued to grow during the construction of the Panama Canal: by the beginning of the 20th century, the population of western Costa Arriba reached 40,000, exceeding pre-contact levels (Heckadon Moreno 1993; Fig. 3). Today the majority of the population in Costa Arriba is concentrated in the heavily urbanized city of Colón, which now exceeds 200,000 people (Republic of Panama 2010).

Since WWII, Colón has been the focus of intensive immigration and industrial development associated with its status as the Caribbean terminus of the Panama Canal. After the completion of the trans-isthmian highway that parallels the canal, peasant farmers flocked to the canal area to exploit its forests and aquatic resources (Heckadon Moreno 1993). This influx marked the beginning of a rapid decline in forest cover within the Canal Zone that has been underway since the mid-20th century, and has also affected coastal Costa Arriba (Heckadon Moreno 1993, Guzmán 2003).

The overall effect of canal-related activities on the coastal environments of Costa Arriba has been enormous (summarized in Guzmán 2003). During the construction of the Caribbean opening of the canal, vast amounts of reef coral were dredged to clear a path for ship traffic and to fill in mangrove swamps over which military bases, cities, and airports were later constructed. Reefs were also repeatedly dredged to extract large quantities of corals for the construction of breakwaters at the entrance to the canal. Dredging of surrounding reefs extended westward to the Chagres River and Bahía Las Minas to the east, and continued until the 1970s for landfill used for additional US military bases as well as the oil refinery in Bahía Las Minas. The end result of this vast engineering project is a severely altered coastal zone with large tracts of mangroves, seagrasses, and coral reefs completely destroyed.

Coastal ecosystems in western Costa Arriba have continued to experience severe environmental disturbances in recent decades. Since the completion of the oil refinery in Bahía Las Minas in the 1960s, chronic oil spills (most notably in 1968 and 1986) have affected and destroyed coastal ecosystems in the region (Jackson et. al. 1989, Guzmán et. al. 1991, 1994, Keller and Jackson 1991). Proximity to the Panama Canal also exposes the region to chronic pollution associated with port, industrial, and farming activities. A study of pollutants in corals found elevated levels of mercury near the port city of Colón and near Bahía Las Minas (Guzmán and Garcia 2002).

Post-colonial environmental disturbance in eastern Costa Arriba is less than that to the west. After abandonment of the area by the Spanish in the early 1700s, this more rugged area of the coast reverted to a relatively remote and sparsely-populated area inhabited by indigenous peoples and descendants of escaped African slaves (Drolet 1980). From the colonial period up until middle of the 20th century, human impact on the environment was probably not much changed from pre-contact times, with subsistence activities dominated by swidden maize and root crop agriculture and by fishing (Drolet 1980). Environmental disturbance increased beginning in the 1950s as a result of tourism, urban development, and cattle ranching (Guzmán 2003).

During the last half of the 20th century, pasturelands have continuously encroached upon forests (Republic of Panama 2001). The poor soils and high erosion rates from heavy rainfall in the region do not support long-term grazing operations, and ranchers are continually on the move for new lands to clear. Other sources of coastal erosion include development of property for expatriates and dive tourism (Guzmán 2003).

The longer history of human alteration of the coastal environment has resulted in more severely degraded reefs in Costa Arriba compared to Bocas del Toro. Percent cover of living coral is lower than in other regions of Caribbean Panama, and Bahía Las Minas has the lowest living coral cover along the entire Caribbean coast (Guzmán 2003). Low abundance of coral is a direct result of the 1986 oil spill (Jackson et al. 1989, Guzmán et al. 1991). Corals show exposure to chronic oil, heavy metal, and mercury pollution that has increased significantly within the past 50 yrs (Guzmán and Jimenez 1992, Guzmán and Jarvis 1996, Guzmán and Garcia 2002). Along the eastern coast, live coral cover has decreased greatly at Portobelo and Isla Grande since 1985 (Guzmán 2003), probably due to declining water quality from land clearing. As in Bocas del Toro, turtles, manatees, and large reef fishes are rare or absent on nearshore reefs in the region (Meylan 1999, KL Cramer pers obs). In contrast to Bocas del Toro, the analysis of coral and molluscan material excavated from large pits dug on modern reefs in Costa Arriba

did not detect notable changes in coral or molluscan communities from the 19th century to present (Cramer 2011). This study also revealed that *A. cervicornis* was virtually absent from Costa Arriba reefs during this time period, signifying a natural paucity and/or an earlier demise of this species in Costa Arriba compared to Bocas del Toro.

Discussion

The terrestrial and coastal marine ecosystems of Caribbean Panama have a long history of human disturbance extending back thousands of years. Environmental conditions on the Caribbean slope are less amenable to intensive agriculture to support large populations than on the Pacific slope. Nevertheless, humans made their mark on Caribbean slope environments by land clearing and fishing over the past 1500 yrs. At the time of Spanish contact over 500 yrs ago, coastal populations of Bocas del Toro and Costa Arriba were large enough to have noticeably altered coastal environments. Archaeological data suggest that Caribbean coral reefs, seagrass meadows, and mangroves had already been depleted of the largest animals by this time, highlighting the antiquity of human impacts to coastal environments as well as terrestrial environments (Wing and Wing 2001, Pandolfi et al. 2003).

Despite these early depredations, the greatest impacts on coastal environments, including overfishing, undoubtedly occurred during the past two centuries when populations rapidly increased to pre-contact levels. The more degraded state of coral reefs in Costa Arriba reflects the longer history of intense human environmental alteration. Costa Arriba has probably always supported a higher density of people due to its less extreme topography and higher seasonality. This pattern was consistent through the colonial period and continues to today. While human population growth and development of land and shore increased dramatically in the 19th century, this did not occur until the turn of the 20th century in Bocas del Toro. However, both of these regions are currently experiencing even more rapid increases in population as people migrate from the Pacific to the Caribbean slope of Panama in search of land.

In summary, the long history of human exploitation and disturbance of Caribbean environments provides context for the historical degradation of coral reefs in these regions. Recent paleontological analyses of reef communities from Bocas del Toro and Costa Arriba strongly support the hypothesis that historical fishing and land clearing contributed to reef decline in these regions before outbreaks of coral disease and bleaching began in the 1980s. The timing of reef degradation in Bocas del Toro and Costa Arriba was influenced by the differing geographies and climate of these regions that in turn affected the relative intensities of historical marine and terrestrial resource use.

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