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Historical change in coral reef communities in Caribbean Panama

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in

Oceanography

by

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The Dissertation of Katie Lynn Cramer is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

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DEDICATION

For my parents, Harry and Connie Cramer

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ABSTRACT OF THE DISSERTATION

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by

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Professor Jeremy Jackson, Chair

Scientists have witnessed a profound transformation in Caribbean coral reefs since the 1980s that includes a widespread mortality of corals and a shift in coral species composition. These changes have been widely attributed to modern disturbances such as coral disease and coral bleaching that have become prevalent in the most recent decades. However, the demise of corals in the Caribbean represents the most recent chapter in a long history of human alteration of Caribbean reef ecosystems. Centuries of human over-exploitation of turtles, manatees, monk seals, and predatory and large herbivorous fishes had virtually eliminated these organisms from reefs long before the 1980s. Historical deforestation of watersheds draining onto reef habitats had likely also substantially changed reef environments prior to this time. The timing and ultimate causes of change in Caribbean coral communities remains unresolved because of a lack of quantitative information about the state of these reefs from a time period preceding the 1980s.

My dissertation reconstructed coral and mollusk community composition from reefs in Caribbean Panama over approximately the past 150 years to extend the timeline of ecological change. This work showed that changes in coral and mollusk communities occurred at least 50 years ago and likely as far back as the mid 19th century, a period coinciding with rapid human population growth and deforestation in the regions of study. Data confirmed that major changes in coral and mollusk communities off the Central American coast predate the first appearance of coral disease and bleaching outbreaks and that the demise of Caribbean coral populations is likely rooted in older anthropogenic disturbances such as fishing and deforestation. This work provides a more accurate ecological baseline of Caribbean coral reefs that will provide a better frame of reference for future reef management actions.

CHAPTER 1: GEOGRAPHY, HUMAN OCCUPATION, AND ENVIRONMENTAL CHANGE IN WESTERN AND CENTRAL CARIBBEAN PANAMA

ABSTRACT

Humans have occupied Central America for more than ten thousand years, and have altered terrestrial and marine coastal environments through land clearing, agriculture, and fishing ever since they arrived. 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 in Panama, where human population density and intensity of land use were higher on the Pacific slope compared to the Caribbean slope since early pre-historic times. Nevertheless, substantial human alteration of forest and coral reef environments on the Caribbean coast extends back a thousand years or more. In both Bocas del Toro to the west and the Costa Arriba in central Panama, differences in environmental conditions appear to have played an important role in these regions' differing histories of population and environmental disturbance. 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 subsequent colonial era, Bocas del Toro remained sparsely populated until the early 20th century due to its isolation from the Pacific by high mountains, excessive rainfall, and small area of alluvial flood plains for human habitation and agriculture. In contrast, the low-lying topography of the Costa

Arriba was conducive to early colonial occupation in the 17th 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 along the 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 communities.

INTRODUCTION

Humans have had a profound and sustained influence on the natural environment of Central America since their arrival at least 11,000 years ago (Piperno et al. 1990, Cooke 1997). The terrestrial megafaunal extinction that occurred in Central America shortly after human arrival has been attributed in part to Paleo-Indian hunting (Janzen and Martin 1982, Alroy 2001, Koch and Barnosky 2006), 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 thousands of years of fishing has removed vast numbers of coral reef megafauna including monk seals, 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 loss 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 recent collapse of Caribbean coral communities. To understand the causes of change in Caribbean coral reef ecosystems, it is important to know the complete history of human activities in the region which may be responsible for ecosystem change.

Geological, archeological, and historical data provide a deep-time perspective for understanding of the recent changes that have been witnessed on Caribbean reefs in the past decades. Here I discuss the history of Caribbean Panama with special attention to the regions of Bocas del Toro and Costa Arriba (Figure 1.1). The Bocas del Toro region is located in the western coast of Caribbean Panama, defined here as the area bounded by the Sixaola and Changuinola Rivers to the west and the Calovébora River to the east and bounded to the south by the continental divide that separates the Caribbean from the Pacific slope (Figure 1.2). 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. The Costa Arriba region is located along the central Caribbean coast of Panama and is defined 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 (Figure 1.3). This region constitutes the eastern portion of Colón province.

GEOLOGICAL SETTING

The Caribbean Sea was isolated from the tropical eastern Pacific by the rise of the Isthmus of Panama and the final closure of the Central American seaway approximately 4 to 3 million years ago (Coates et al. 1992, Coates and Obando 1995, O'Dea et al. 2007). The separation of the oceans resulted in the reorganization of circulation patterns in the Caribbean and Gulf of Mexico, and led to reduced upwelling and a collapse in primary productivity in these regions (Allmon 1996, 2001; O'Dea et al. 2007). These changes in oceanographic conditions in turn resulted in major ecological changes to nearshore environments, including accelerated rates of origination and extinction of reef-building corals (Budd et al. 1996), mollusks (Vermeij and Petuch 1986, Jackson et al. 1993, Johnson et al. 2007, Smith and Jackson 2009), as well as an overall expansion of coral reef habitat (Johnson et al. 2007, 2009). The peak of this faunal turnover occurred approximately 2 million years ago during the early Pleistocene (Jackson and D'Croz 1997, O'Dea 2007) and resulted in the environments and communities that typify most coastal Caribbean ecosystems today: clear, warm, oligotrophic waters dominated by coral reef and seagrass habitats.

Since the Pleistocene Epoch, Caribbean reefs have maintained a typical coral zonation pattern according to depth and wave action. This zonation is characterized by three common species of scleractinian corals acting as the primary builders of reef framework (Goreau 1959, Glynn 1973, Kinzie 1973, Geister 1977), with thickly branching elkhorn coral *Acropora palmata* dominating at reef crest and shallowest depths of the fore reef (0-5m), more thinly branching staghorn coral *Acropora cervicornis* dominating at intermediate depths (5-25m) on exposed reefs and more shallow depths on protected reefs, and species from the *Montastraea annularis* species complex (Knowlton et al. 1992) dominating on a variety of reef habitats from less than 5m to greater than 30m. This zonation pattern has been found to be remarkably stable in the Pleistocene and Holocene fossil reef deposits throughout the region (Mesolella 1967, Jackson 1992, Pandolfi and Jackson 2001, 2006, 2007, Greer et al. 2009) despite large fluctuations in sea level and climate during this period.

The recent (Holocene) coral reefs of Caribbean Panama began to develop in their present locations approximately 7000 years ago with the formation of fringing reefs dominated by *A. palmata* in shallow zones (Macintyre and Glynn 1976). As this species continued to grow vertically to keep up with rising sea level during the Holocene marine transgression, lagoon environments developed shoreward of coral growth along exposed portions of the coast, and more delicately branching coral species such as *Porites furcata* and *A. cervicornis* appeared on the back reef and in lagoonal environments (Macintyre and Glynn 1976).

Present-day coral reefs in the Bocas del Toro archipelago formed about 7000 years ago by the flooding of lower topographic areas during Holocene transgression, resulting in the two large embayments that characterize this region (Anderson and Handley 2002). The various islands that constitute the archipelago sequentially separated from the mainland, starting with the creation of the Boca del Drago opening of Almirante Bay to the Caribbean Sea (Figure 1.2). In the subsequent few thousand years, other islands began to separate from each other and from the mainland, and the current configuration of the region was obtained about 1000 years ago (Anderson and Handley 2002).

During approximately the last 2000 years, the vertical development of reef growth at Galeta reef in the western part of Costa Arriba as well as at other reefs along exposed portions of Panama's Caribbean coast have been limited by the slowing rate of sea level rise and from sedimentation following the flooding of continental shelf environments (Macintyre and Glynn 1976). Because Panama is south of the Caribbean hurricane belt (Neumann et. al. l978), lower rates of reef destruction have allowed many reefs in Caribbean Panama to keep up with sea level rise and to reach the sea surface. As a result, at some Costa Arriba reefs, corals have reduced their active contribution of new reef framework during the past two millennia as sea level rise has slowed. This period has seen a decline in the importance of the quickly-growing *Acropora* coral species and a general decline in coral abundance as these exposed reefs have begun to fill in and become cemented pavements (Macintyre and Glynn 1976, Macintyre et al 2007). This successional pattern does not appear to apply to less exposed reef in Caribbean Panama, however.

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

The seasonal climate of Panama is determined by the interaction of the northeasterly trade winds with the seasonal movement of a low-pressure band termed the Intertropical Convergence Zone (ITCZ ; Jackson and D'Croz 1997). Panama lies within the path of the ITCZ from approximately May-December, and the flow of the tradewinds is interrupted and precipitation is variably intense throughout Panama during this time. During the rest of the year, the influence of the trade winds is stronger, and conditions are generally drier, particularly on the Pacific side. The Caribbean slope continues to receive substantial amounts of precipitation throughout the year from the condensation of moisture from the trade winds as they are deflected upward along the north side of the continental divide (Bennett 1968). By the time the trade winds reach the Pacific side of the divide, they are depleted of moisture and have a desiccating effect. As a result, the Caribbean slope has higher annual precipitation (330 cm annually in Bocas del Toro and 200-400 cm in Costa Arriba; Kaufman et al. 2005, Cubit et al. 1989) than does the Pacific slope (130 cm; Cooke et al. 1996) and lacks the Pacific side's 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 the 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 the Bocas del Toro region is generally less directly exposed than the Costa Arriba region to the northeasterly trade winds. As a result, Costa Arriba is more generally affected by wind-driven waves, tides, turbidity, and incident solar radiation during the dry season than Bocas del Toro, and reef tracts are more extensive in the latter region (Cubit 1989, Guzmán 2003).

Topographic differences between Bocas del Toro and Costa Arriba are also responsible for their varying environments. The highest portion of Panama's continental divide, 3475m 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 Basin, 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 (Figure 1.1). Because this area of low relief does not experience the orographic rainfall that occurs in the western and eastern regions of Panama, the Canal Basin has more of a distinct dry season than does the rest of Caribbean Panama. East of the Canal Basin, a lower mountain chain begins that has a maximum altitude of 1000m (Coates 1997) and that is interspersed with broad alluvial valleys created by large rivers that run parallel to the coast. This part of the Caribbean coastline lacks the rugged cliffs and short rivers and streams that characterize Bocas del Toro. As a result, Bocas del Toro possesses a relatively more extreme topography and smaller alluvial floodplain area, while Costa Arriba contains narrow alluvial strips and rolling coastal hills that are 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 (Figure 1.2). Outside and to the east of these lagoons, the coastline is generally more exposed to oceanic conditions, although barrier reefs protect some nearshore environments close to river mouths. 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 freshwater to the coastal zone year-round (IGNTG 1988, Guzmán et al 2005). The water from these rivers forms a freshwater lens that is approximately 0.5m 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. The northwest portion of Almirante Bay is directly influenced by creeks that drain a portion of the Changuinola Rover floodplain and is the site of extensive banana plantations (Figure 1.2). The lower water clarity within the lagoons has been attributed in part to the input of sediments and pollutants from agriculture, mining, and oil refining activities occurring nearby (Guzmán 2003, Guzmán and Jimenez 1992, Guzmán and Garcia 2002). A large river, the Cricamola, flows into Chiriquí lagoon and has created a large alluvial plain within the embayment.

The coral reefs of Bocas del Toro contain a diverse coral fauna, containing 87% of the known scleractinian coral species reported for Caribbean Panama (Guzmán 2003). The extent of reef development and diversity of corals is greater within Almirante Bay than within Chiriquí Lagoon, probably due to the better water quality of the former (Guzmán and Guevara 1998, D'Croz et al. 2005, Guzmán et al. 2005). Within the lagoonal environments, branching *Porites* spp corals (primarily *P. furcata*) are dominant at depths < 3m, with essentially monospecific *Porites furcata* "meadows" beginning at the boundary of the shallow seagrass zone (Greb et al. 1996, Guzmán and Guevara 1998). The shallow reef slope zone is dominated by the lettuce coral *Agaricia tenuifolia* at depths from 3-12m, transitioning to scattered massive corals *Colopophyllia natans*, *Montastea annularis* species complex, *Montastea cavernosa*, *Siderastrea siderea*, and *Stephanocoenia intercepta* (Guzmán 2003). Platy *Agaricia* corals characterize the deepest zones from 15-20m. The elkhorn and staghorn corals, *Acropora palmata* and *A. cervicornis*, are primarily restricted to offshore reefs and reefs far from centers of human population (Guzmán and Guevara 1998a, 1999, 2001, Vollmer and Kline 2008).

Costa Arriba

The Costa Arriba region contains relatively fewer cays, inlets, and islets to provide protection from the trade winds, resulting in reduced reef development compared to Bocas del Toro (Guzmán 2003). As in Bocas del Toro, more protected areas are fringed by mangrove forests, which grade into fringing reefs and seagrass beds. Two large lagoons that are somewhat protected from wind and wave action are Bahia Las Minas in the western portion of the region (located approximately 6km east of the entrance to the Panama Canal) and the bay of Portobelo in the eastern part of the region

(Figure 1.3). As in Bocas del Toro, exposed portions of the coast consist of either 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 and narrower coastal plain of Bocas del Toro.

The coral reefs of Costa Arriba contain just 77% of the coral diversity reported for Panama, less than that reported for Bocas (Guzmán 2003). Fringing reefs follow the mainland coastline with little vertical development, with reefs extending to approximately 15m maximum depth and most corals occurring shallower than 6m (Guzmán, Jackson, Weil 1991, Guzmán 2003). Coral communities are comprised mainly of *Diploria clivosa*, *Agaricia tenuifolia*, *Agaricia agaricities* spp, and *Millepora* spp in shallow zones ≥ 2m, with a short reef slope composed of *Diploria strigosa*, *Colpophyllia natans*, and *Siderastrea* spp. to about 15m. Compared to Bocas del Toro and the rest of the Caribbean, *Acropora* corals are conspicuously absent from most reefs in Costa Arriba. A reconstruction of reef development over the past 7000 years from cores collected by Macintyre and Glynn (1976) showed that, at least for Galeta Point reef in the western part of Costa Arriba, *A. palmata* and *A. cervicornis* were major components of the coral fauna during the phase of active framework-building that ceased approximately 2000 years ago when the reef "caught up" to sea level. 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, *personal communication*).

HUMAN HISTORY

The human history of Bocas del Toro and the Costa Arriba falls into three periods bounded by major changes in human subsistence, settlement patterns, and population: (1) pre-contact (~9000 BC – 1502 AD), (2) Spanish colonial (~1502-1800 AD), and (3) post-colonial (~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 years ago during the Late Pleistocene (Cooke 1997). During this time, the Central American climate was colder and drier than it is today, and the Panamanian landscape consisted of more open forest than the dense forests that characterize lowland regions today. This more open landscape allowed groups of hunting and gathering Paleo-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).

The Pacific slope of Panama has a longer history of continuous human settlement and land clearing than the Caribbean slope. Before Paleo-Indians even began practicing intensive agriculture and concentrating in sedentary villages, slash and burn activities had 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 (Figure 1.1) 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 in this area around 9200-7000 BC. People began to cut the forest and burn plots and cultivate maize around 2900-2050 BC and to intensify crop cultivation (including shortened fallow periods) around 1350 BC (Ranere and Cooke 1991). Located in the Canal Basin, 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 entered into a new phase of technological and social sophistication (Cooke 1997). The increased production efficiency of specialized crops such as maize and gourd/squash was followed by increased population growth and increased land use. During this time, settlements moved down from previously burned hill slopes to more concentrated villages in lowland alluvial zones along the Pacific coast, when 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-Colombian human settlement on the moist 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 (Cooke and Ranere 1992, Drolet 1980, 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 by maize-farming peoples 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). This expansion of settlements onto the moist and nutrient-depleted soils of the Caribbean slope may have been made possible by 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 cause comparatively little environmental impact because they did not employ slash-and-burn agriculture (Drolet 1980, Linares 1980a, Griggs 2005). The contrasting lifestyles of inhabitants on the Pacific and Caribbean slopes were likely related to their differing local environmental conditions. Lower seasonality on the Caribbean slope inhibited clearing of cut vegetation by fire and encouraged rapid reforestation of fallow fields, making intensive agriculture difficult (Bennett 1968, Gordon 1982). In addition, the narrow coastal plains in Bocas del Toro and eastern Costa Arriba do not contain the fertile 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

The earliest human settlement (600-700 AD) discovered on the Caribbean slope of Panama is 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, Linares 1980b). Inhabitants were 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," which is the opportunistic capture of species that forage in areas of disturbed vegetation (Linares 1980a, Linares 1976). Settlers did not rely heavily on marine resources, possibly because they were recent immigrants from the Volcan Baru region that were displaced after its eruption around 600 AD. (Linares 1980a).

Cerro Brujo was vacated for two to three centuries and then re-settled 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 Bocas del Toro region (Figure 1.4, Table 1.1). Middens reveal that bivalve, fish, turtle and manatee were the most important marine animals consumed. Gastropods were not an important source of food. Important bivalves included the mangrove oysters *Crassostrea rhizophorae* and *Isognomon alatus*, and epifaunal coral reef-associated *Arca zebra*, *Arca* *imbricata*, and *Chama macerophylla*, 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 pre-historic land use was based on the cultivation of root-crops and fruiting trees (Linares 1980a), resulting in the maintenance of a continuous 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 suggests 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 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 (Figure 1.2) suggests that pre-Columbian Bocas del Toro was more densely inhabited and more socially complex than suggested from the Cerro Brujo site. Sitio Drago, dated to 800-1200 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). The ceramic artifacts from Sitio Drago suggest that 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 multiple more 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 swidden 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). 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.

Ethnohistoric data from the time of European contact corroborates the notion of relatively low-impact land use by native peoples in Bocas del Toro, but suggests that this region was more heavily populated and economically sophisticated than does 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 and his men 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 Mesoamerican peoples (the Sigua) were established in the western part of the region between the Sixaola and Changuinola Rivers (Cooke 2003, Lothrop 1942b). Numerous indigenous groups speaking related languages inhabited the coastal zones, foothills, and river valleys (Gordon 1982). It appears that many of these groups were warring against one another, and that 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 attests to the fact 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 Mesoamerican “high” societies. The absence of foreign items imported from outside Panama in the Bocas del Toro region suggests 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 these resources were not as exploited as they were in more populous parts of Central America.

Ethnographic studies of the modern-day descendents from the cultural group that settled Cerro Brujo, the Ngöbe (formerly Guaymí) Indians, suggest 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 surviving indigenous inhabitants of Bocas del Toro. Today, those groups that live outside of developed areas (particularly in the Ngöbe-Bugle 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). The region is topographically much lower than Bocas del Toro but precipitation levels are in general just as high. As a result, the Costa Arriba region contains a greater number of intermittent river valleys and narrow alluvial floodplains than Bocas del Toro. 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 the contact period (Drolet 1980). Other artifacts show that 16th century settlements were organized into cheifdoms whose movements and territorial settlement patterns were related to increasing 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 also heavily exploited fish and other marine resources as evidenced by the presence of net weights for freshwater and marine fish as well as notched weights that indicate the harvest of turtles in more open sea areas (Drolet 1980). Middens contain an abundance of the nearshore gastropod *Cittarium pica*, 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 back from the coast within the Bayano River valley (Figure 1.3). 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 strong tradewinds characteristic of the Costa Arriba.

Ethnohistorical data confirms 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 1502-03, who described the settlement surrounding the embayment 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 relate 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 as on the Pacific slope. 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, although 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 years 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 were 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 1824).

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 century 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 manatee, turtle, and monk seal removed from Caribbean waters during this time (Dampier 1697, Wafer 1704, 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 tell if overall environmental impact to coastal ecosystems changed 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 that nested on the exposed beaches of the archipelago (Dampier 1697).

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).

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 aggression (Roberts 1824). 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 1824). The major change from pre-historic 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 1824). 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 1824). 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 turtle for trade after they had observed the success of the Ngöbe in this industry (Gordon 1982).

At the close of the 18th 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 turtle and other marine resources. Thus, even though the population of the region was small, the impact to coastal ecosystems from fishing must have been substantial (Pandolfi et al. 2003).

Costa Arriba

In contrast, the 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 (Jaen 1970, 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 during the latter half of the 16th century (Jaen 1970), and problems with erosion from land clearing (Hussey 1939), the Atlantic port was relocated in 1597 a couple of kilometers to the west at Portobelo, a site located at the mouth of a large natural embayment with deep waters protected from wind and wave exposure. 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 shipbuilding, 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 due to European avoidance of the area because of the prevalence of malaria and yellow fever and the general "unhealthiness" of the surrounding mangrove swamps (Ward 1990). This shortage 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 (from approximately 8-13 houses) of Portobelo from the late 16th century to the early 17th century (Ward 1990). During this time, the population swelled during the annual trading fairs to a maximum of several thousand people, mostly comprised of 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 years (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 decimation 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 appeared to have 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-year colonial period, the Spanish and mestizo (mixed Spanish, indigenous, and African) population grew slowly, with an approximate 100-year doubling time (Heckadon-Moreno 1997). It wasn't until Central America's demographic revolution during the 20th century that the human population of this region began to greatly exceed estimated pre-conquest levels (Figure 1.4). The population doubling time decreased to 25-30 years, 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 century with the construction of the transisthmian railroad and Panama Canal and the introduction of banana cultivation (LaBarge 1960, Heckadon-Moreno 1993, Heckadon-Moreno 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 experienced greatly heightened human disturbance since the 19th century.

Bocas del Toro

During most of the 19th century, Bocas del Toro continued to be a 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 19th 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 outwards from the coastal area of the lagoon onto the Aguacate peninsula and the main islands within Almirante Bay and Chiriquí Lagoon (Stephens 2008). 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. Around the turn of the 20th century, the independent banana interests were consolidated into the behemoth United Fruit Company, 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 westwards 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 the mouth of Almirante Bay, 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 in the western part of the province. Thousands of workers from the Antilles came to work the banana plantations and to settle in the coastal lowlands of Bocas del Toro. From 1910-1915, 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 further 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 unemployed laborers moved elsewhere (Figure 1.5), 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 of banana 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 levels, and that continues to the present (Figure 1.4). This increase has been fueled in part by a rapid increase in the Ngöbe population (Gordon 1969, Republic of Panama 2010; Figure 1.5) 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 ever 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 fifty times per year (Bourgois 1985, Stephens 2008). This method of dispersal inadvertently delivered chemicals directly to waterways that eventually drained to the ocean. Fertilizer used 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 affects on aquatic life including corals (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 accomplished by the banana industry in Bocas del Toro literally paved the way for a second phase of development and immigration in the 1980s (Figures 1.4, 1.5). 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 frequently visited 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 in Chiriquí Lagoon. 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 Caribbean 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 socio-economic 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 (Pandolfi et al. 2003, Guzmán 2003). Monitoring of coral reefs revealed declines in coral cover of up to a 10% decline during the late 1990s to early 2000s, although some reefs still have high living coral cover as high as 50-90% locally on some fringing reefs (Guzmán 2003). A suite of coring studies conducted in Almirante Bay found a recent and historically unprecedented replacement of the dominant coral species, from branching *Porites furcata* to *Agaricia tenuifolia*, attributed to deteriorating water quality due to land use changes (Aronson et al 2004, 2005, Hilbun 2009).

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 2003, Guzmán and Jimenez 1992, Guzmán and Garcia 2002). 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 new "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 fish 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 et al. 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, including green and hawksbill turtles, manatee, grouper, snapper, and the extinct Caribbean monk seal, that were important in pre-colonial and colonial times are rare or absent today (Mou Sue et al. 1990, Meylan 1999, Pandolfi et al. 2003).

Costa Arriba

The low-lying western portion of the Costa Arriba continued to be utilized as the principal transisthmian transportation route with the construction of the transisthmian 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). Populations began to grow during the railroad construction boom in the mid 1800s and towards the end of the 19th century during the building of the Panama Canal finished in 1915 (Bennett 1968, McCullough 1977, Heckadon-Moreno 1993). Development was concentrated in the city of Colón, situated on the eastern side of the opening of the canal (Figure 1.6). 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 American west (Abbot 1913). The population and area of Colón continued to grow durin4 the construction of the Panama Canal, and by the beginning of the 20th century, the population of western Costa Arriba reached 40,000, exceeding pre-contact levels (Heckadon-Moreno 1993, Figure 1.4). 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 transisthmian 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. During the construction of the Caribbean opening of the canal, vast amounts of reef coral were dredged in order to clear a path for ship traffic and to fill in mangrove swamps over which military bases, cities, and airports were later constructed (Guzmán 2003). Reefs were also repeatedly dredged to extract large quantities of corals for the construction of breakwaters at the entrance to the canal (Guzmán 2003). 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 (Guzmán 2003). 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.

Western Costa Arriba continued to suffer from various severe disturbances. Since the completion of the oil refinery in Bahia 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). Proximity to the canal also exposes the region to chronic pollution associated with port, industrial, and farming activities. A study of pollutants in corals found higher levels of mercury levels present near the port city of Colón and near Bahía Las Minas (Guzmán et al. 2002).

Post-colonial environmental disturbance in eastern Costa Arriba is less than that tto 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 descendents 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 unceasingly encroached upon forests (Republic of Panama 2001). The poor soils and high erosion rates due to 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 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 have increased significantly within the past 50 years (Guzmán and Jarvis 1996, Guzman and Garcia 2002, Guzman and Jimenez). Along the eastern coast, live coral cover greatly decreased at Portobelo and Isla Grande since 1985 (Guzmán 2003), probably due to declining water quality from land clearing. As in Bocas del Toro, turtles, and manatees, and large reef fish are rare or absent on nearshore reefs in the region (Meylan 1999, KL Cramer *pers. obs.*).

CONCLUSIONS

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 years. At the time of Spanish contact over 500 years ago, coastal population of Bocas del Toro and Costa Arriba were large enough to have noticeably altered the coastal landscape. 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.

Given their long history of human exploitation and disturbance, it seems unlikely that the ongoing recent decline of coral reefs and associated communities was restricted to the few decades that they have been observed by scientists. Paleontological analyses of reef communities from Bocas del Toro and the Costa Arriba described in the subsequent chapters strongly support this hypothesis.

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Table 1.1. Bocas del Toro population estimation methods

BOCAS DEL TORO

Year	Population	Calculation	Source
1500	31801	median estimate of density at Cerro Brujo archaeological site (3.5 people / km^2) x area of Bocas del Toro province (9086 km^2)	Linares 1980a, Republic of Panama 2000
~1550	3180	10% of pre-contact population	Cooke 1997
1832	3861	population of Panama x mean proportion of population from Bocas del Toro province since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1851	5422	population of Panama x mean proportion of population from Bocas del Toro province since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1864	9318	population of Panama x mean proportion of population from Bocas del Toro province since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1880	12940	population of Panama x mean proportion of population from Bocas del Toro province since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1900	13000	estimate of 13000 people "scattered about the islands"	Blaney 1900
1911	22732	population of Bocas del Toro province	Republic of Panama, 1941
1920	27239	population of Bocas del Toro province	Republic of Panama, 1941
1930	15851	population of Bocas del Toro province	Republic of Panama, 1941
1940	16523	population of Bocas del Toro province	Republic of Panama, 1941
1950	22392	population of Bocas del Toro province	Republic of Panama, 2000
1960	32600	population of Bocas del Toro province	Republic of Panama, 2000
1970	43531	population of Bocas del Toro province	Republic of Panama, 2000
1980	53487	population of Bocas del Toro province	Republic of Panama, 2000
1990	110364	population of Bocas del Toro province + .5 population of Ngobe-Bugle territory (because ~.5 of area of territory previously in Bocas del Toro province)	Republic of Panama, 2000
2000	144309	population of Bocas del Toro province + .5 population of Ngobe-Bugle territory (because ~.5 of area of territory previously in Bocas del Toro province)	Republic of Panama, 2000
2010	190358	population of Bocas del Toro province + .5 population of Ngobe-Bugle territory (because ~.5 of area of territory previously in Bocas del Toro province)	Republic of Panama, 2010

Table 1.2. Costa Arriba population estimation methods

COSTA ARRIBA

Year	Population	Calculation	Source
1500	21514	twice the median estimate of density at Cerro Brujo archaeological site (7 people/ km^2) x area of four administrative districts that make up Costa Arriba (3073 km^2)	Linares 1980a
~1550	2151	10% of pre-contact population	Cooke 1997
1832	7096	population of Panama x mean proportion of population from Costa Arrriba since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1851	9966	population of Panama x mean proportion of population from Costa Arrriba since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1864	17125	population of Panama x mean proportion of population from Costa Arrriba since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1880	23782	population of Panama x mean proportion of population from Costa Arrriba since 1911	Susto 1960 in Bennett 1968, Republic of Panama 2000
1911	25647	population of Colon province - mean proportion of Costa Arriba from Kuna Yala territory since 1911 - mean proportion of Costa Arriba from Donoso district since 1920	Republic of Panama 1941, 2000, 2010
1920	38931	population of Colon province - population of Kuna Yala territory - population of Donoso district	Republic of Panama 1941, 2000, 2010
1930	40232	population of Colon province - population of Kuna Yala territory - population of Donoso district	Republic of Panama 1941, 2000, 2010
1940	54845	population of Colon province - population of Kuna Yala territory - population of Donoso district	Republic of Panama 1941, 2000, 2010
1950	71981	population of Colon province - mean proportion of Costa Arriba population from Kuna Yala territory since 1911 - mean proportion of Costa Arriba population from Donoso district since 1920	Republic of Panama 1941, 2000, 2010
1960	81379	population of Colon province - population of Kuna Yala territory - mean proportion of Costa Arriba population from Donoso district since 1920	Republic of Panama 1941, 2000, 2010
1970	104724	population of Colon province - mean proportion of Costa Arriba population from Donoso district since 1920	Republic of Panama 1941, 2000, 2010
1980	127874	population of Colon province - mean proportion of Costa Arriba population from Donoso district since 1920	Republic of Panama 1941, 2000, 2010
1990	158712	population of Colon province - population of Donoso district	Republic of Panama 1941, 2000, 2010
2000	194537	population of Colon province - population of Donoso district	Republic of Panama 1941, 2000, 2010
2010	222631	population of Colon province - population of Donoso district	Republic of Panama 1941, 2000, 2010

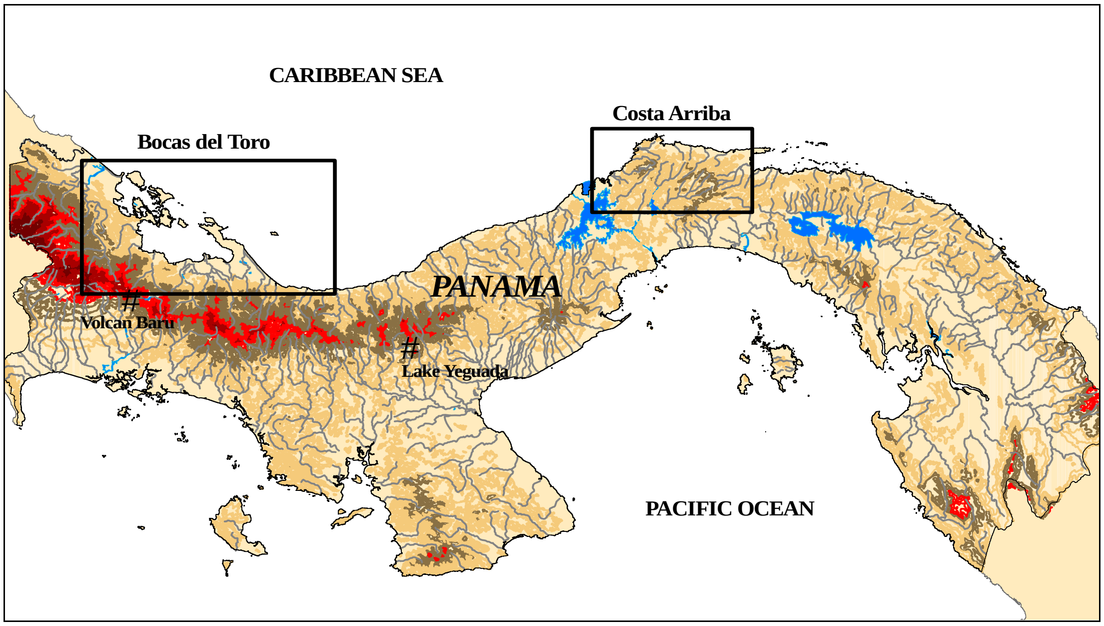

Figure 1.1. Study regions and the two prehistoric human settlements discussed in text outside of study regions

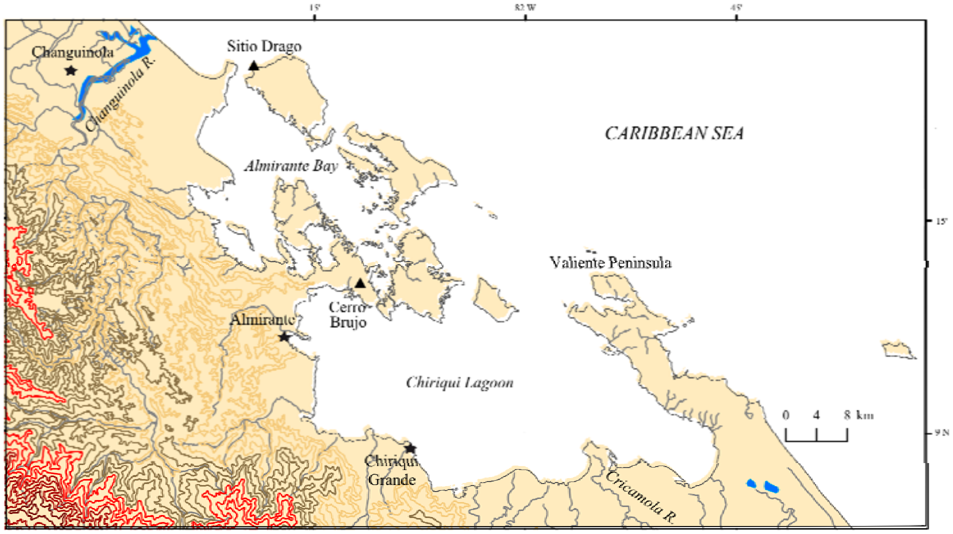

Figure 1.2. Map of Bocas del Toro with triangles indicating archaeological sites

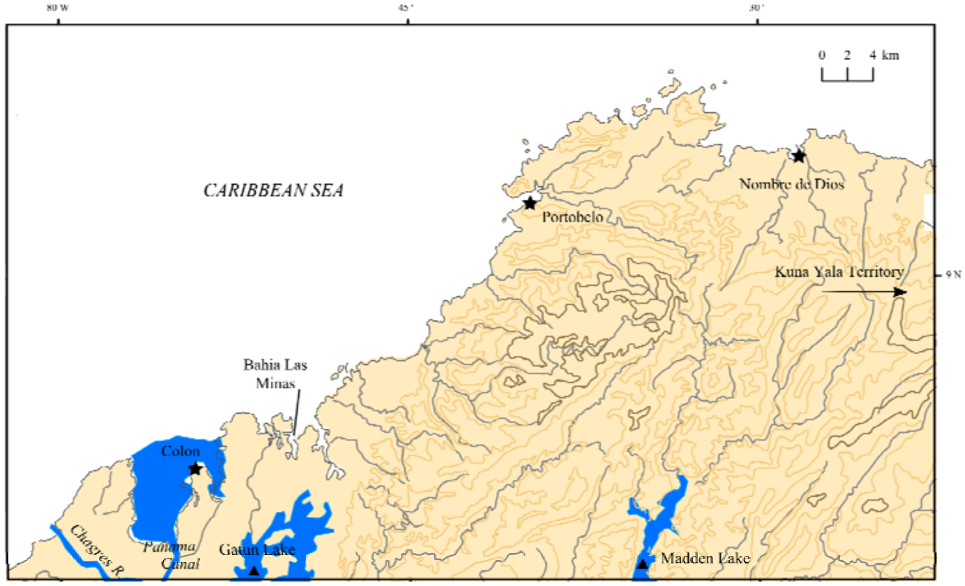

Figure 1.3. Map of Costa Arriba with triangles indicating archaeological sites

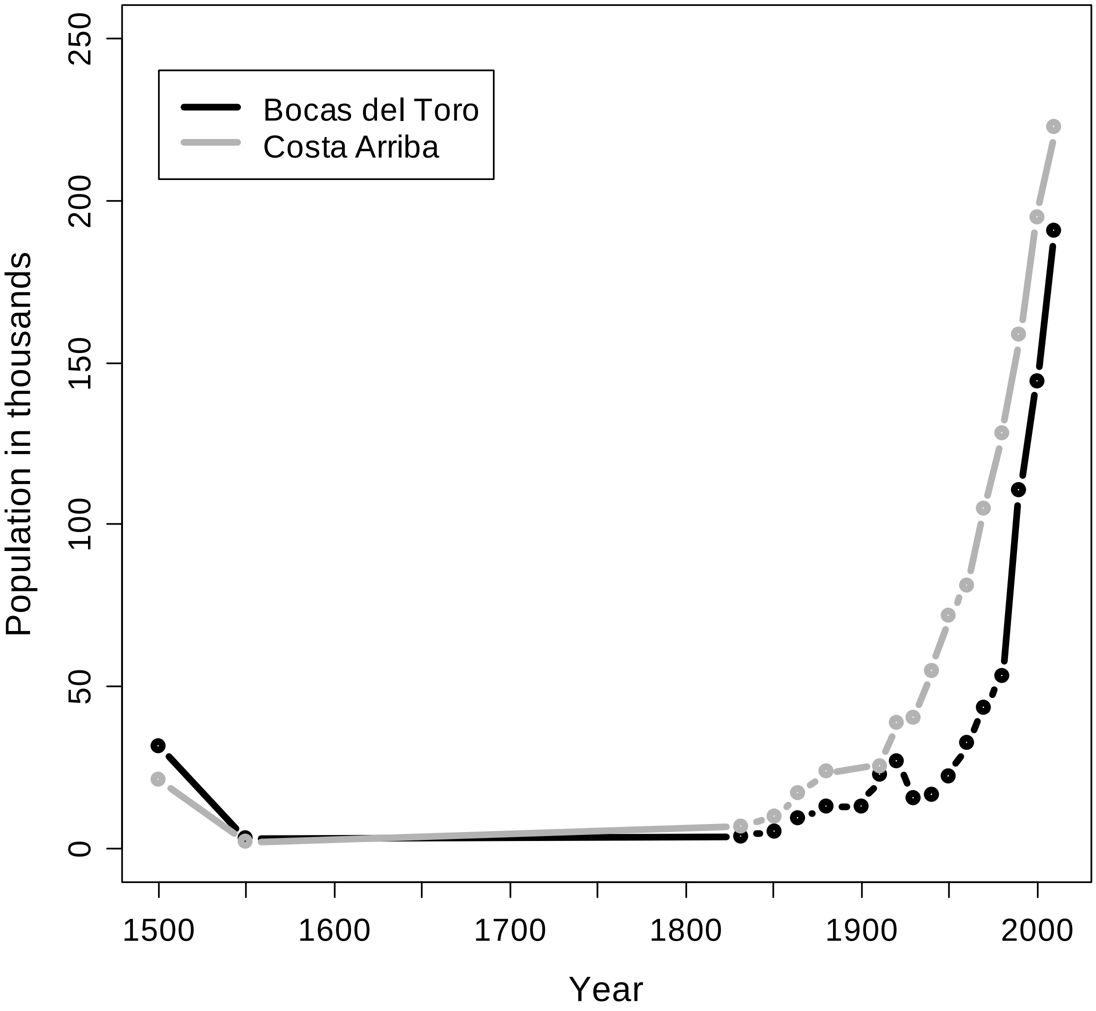

Figure 1.4. Population of Bocas del Toro and Costa Arriba, pre-contact period to present

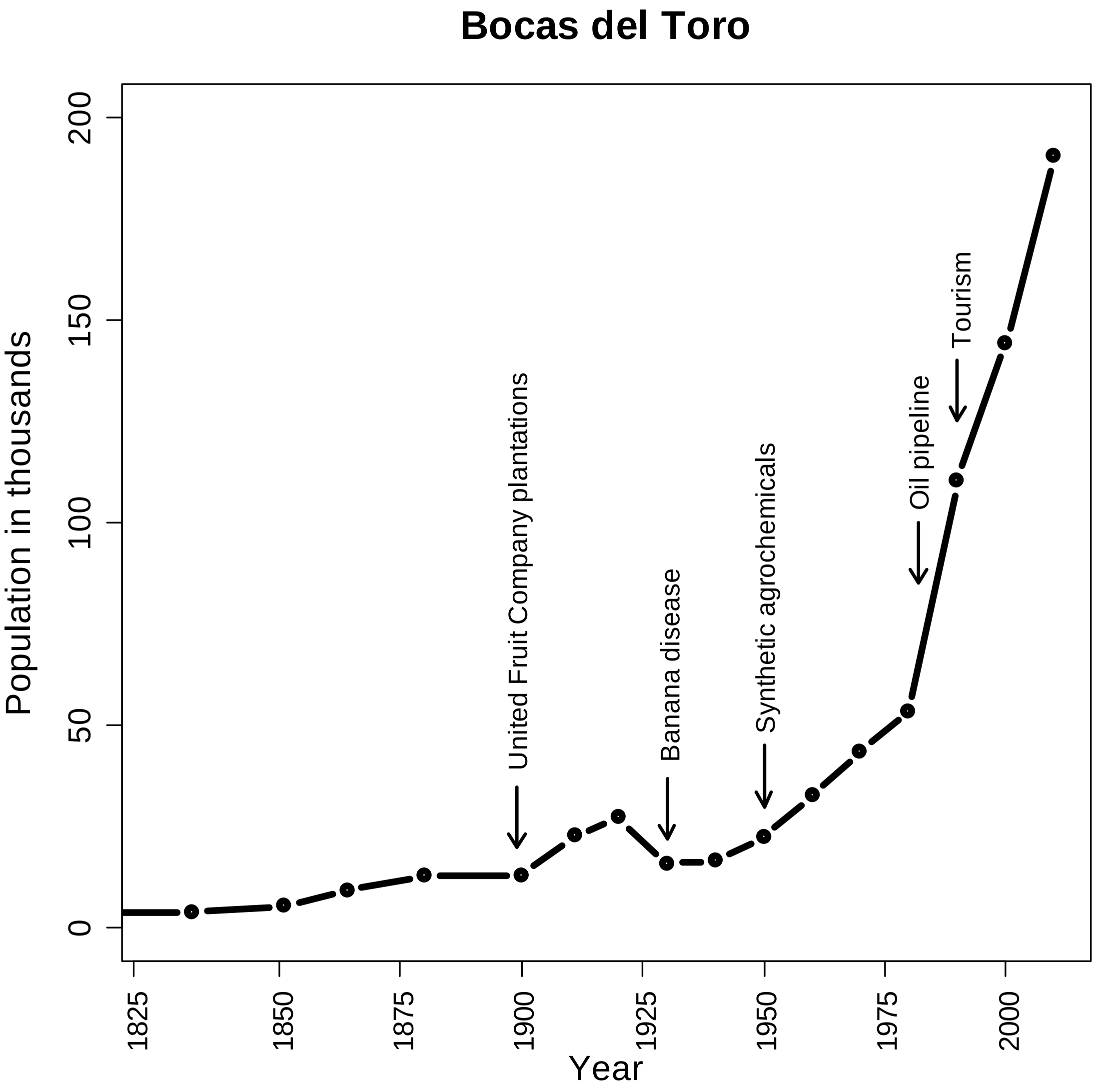

Figure 1.5. Human population of Bocas del Toro since 1832 and major events affecting the nearshore environment

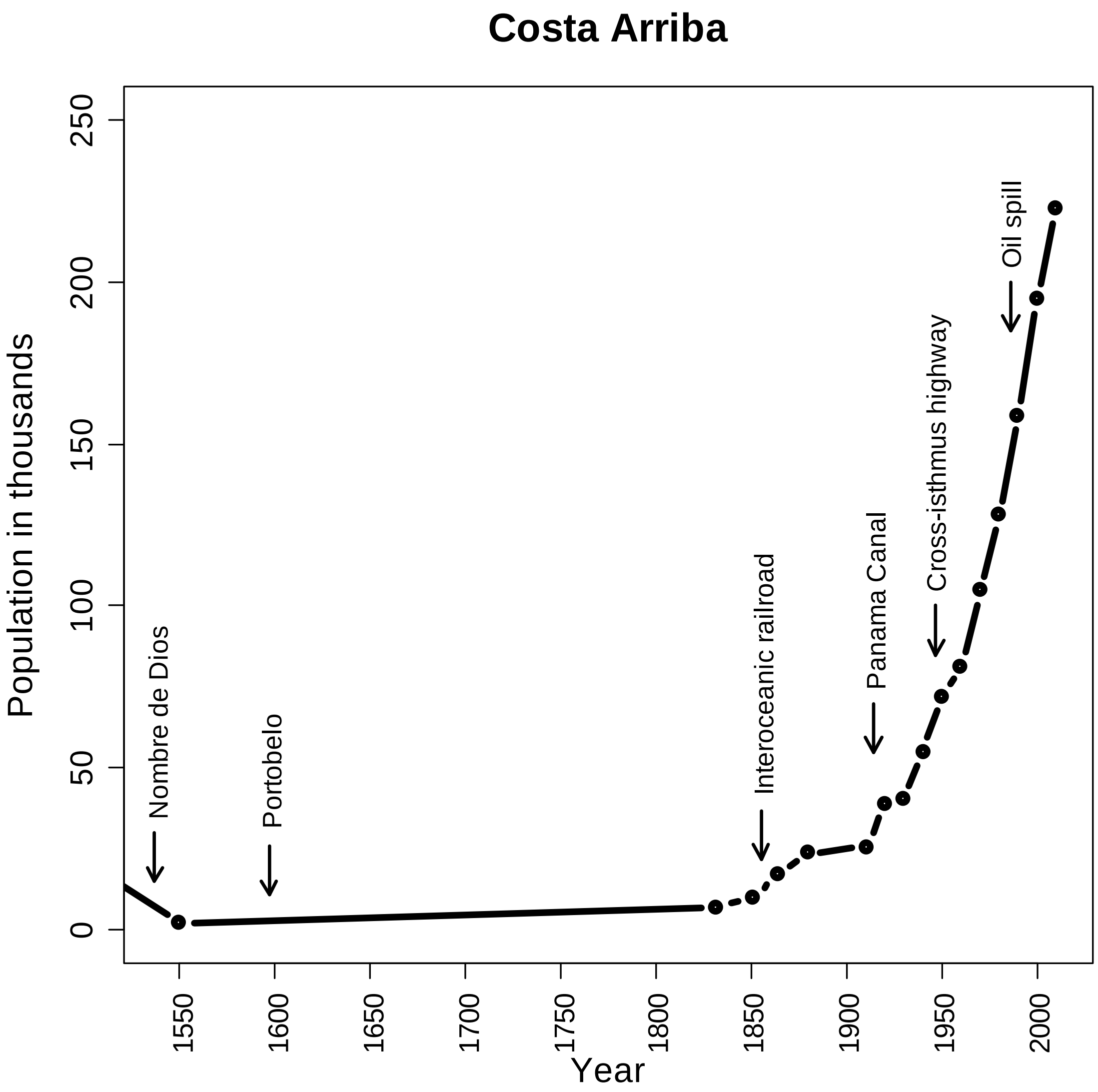

Figure 1.6. Human population of Costa Arriba since ~1550 and major events affecting the nearshore environment

CHAPTER 2: HISTORICAL CHANGE IN CORAL COMMUNITIES IN CARIBBEAN PANAMA

ABSTRACT

Caribbean coral communities have undergone dramatic changes since the 1970s that include a catastrophic decline in coral abundance. However, because most studies of coral reef degradation are based on ecological surveys that began in the 1980s, the extent of earlier historical changes in coral reefs resulting from human activities is unknown. Paleontological data can be used to extend the time scale of ecological change on reefs. I used paleontological sampling techniques to construct a timeline of change in scleractinian coral communities that extends back a century or more. The composition of the coral community from four death horizons extracted from large pits dug under the living reef at 5m water depth was compared with that of the living coral community in the Bocas del Toro and Costa Arriba regions of western and central Caribbean Panama. Calibrated radiocarbon dates revealed that pits extended as far back as the mid-19th century at lagoonal sites and as far back as the mid- 20th century at offshore sites. Changes in coral communities were taxonomically and geographically complex. In Bocas del Toro, the most striking patterns were a decline in coral species richness since 1960 at offshore and lagoonal reefs and a decline in the relative abundance of the previously-dominant staghorn coral *Acropora cervicornis* before 1960 at lagoonal reefs. The change in *A. cervicornis* relative abundance began at the beginning of and was progressive throughout the time series, revealing a gradual pattern of change in the coral community

that was conclusively underway before the 1960s and that may have been underway at least 150 years ago. These results demonstrate that the decline in *A. cervicornis* began decades or more before the appearance of coral disease and bleaching epidemics in the 1980s that have resulted in massive coral die-offs over the past decades. Coral communities were more stable throughout the time period for Costa Arriba reefs, possibly due to lower sampling effort and/or the older history of human disturbance in this region. The degree of change in coral communities was greater in lagoonal environments at both regions, implicating land-based runoff as a driving factor of change.

INTRODUCTION

Ecological surveys have shown striking declines in coral abundance since the 1970s on coral reefs in the Caribbean (Connell 1997, Gardner et al. 2003) and in the Pacific (Bellwood 2004, Bruno and Selig 2007). This decline has been particularly pronounced on Caribbean reefs, which are classified as the most degraded reefs globally (Pandolfi et al. 2003). Shifts in coral community composition, or replacements of previously dominant coral species (primarily *Acropora*) by other corals (e.g. *Agaricia* spp. and *Porites astreoides*), have accompanied the overall decline in coral abundance (Hughes 1994, Aronson and Precht 1998, Aronson et al. 2004, 2005, Green et al. 2008). Analyses of Pleistocene reef deposits showed that *Acropora* species maintained their dominance at shallow and intermediate depths on Caribbean reefs over intervals of 10,000s-100,000s of years despite large fluctuations in sea level and climate (Jackson 1992, Pandolfi and Jackson 2001, 2006, 2007, Greer et al. 2009). Aside from localized declines in dominance from terrigenous sedimentation and/or wave exposure associated with sea level change (Mesolella 1967, Macintyre and Glynn 1976, Macintyre et al. 1977, Macintyre 2007), *Acropora* species dominance in the Caribbean continued during the Holocene (Lighty et al. 1982, Geister 1980, Aronson and Precht 1997, Aronson et al. 2002). Given this continuity in Caribbean coral communities through geological time, it appears that recent coral community shifts are a response to novel human-caused disturbances.

The recent community shifts have been attributed to coral mortality events in the 1980s and 1990s that were mediated by coral bleaching (Aronson et al. 2000, 2002) and by disease epidemics within reef invertebrate populations (Aronson et al. 1998, Harvell et al. 1999, Knowlton 2001). The ultimate causes of bleaching and disease include local disturbances such as overfishing (Jackson et al. 2001) and land-based pollution (Keller and Jackson 1993, Fabricius 2005) as well as regional/global disturbances such as climate change (Hughes et al. 2003). Fishing and pollution began well before the initiation of systematic reef monitoring studies in the 1970s, and the ecological deterioration of Caribbean reefs via fishing began centuries ago (Jackson 1997, Pandolfi et al. 2003, McClenachan et al. 2006, McClenachan and Cooper 2008). Clearly, if we wish to understand the full impact of these disturbances on coral reef communities, an older and more accurate ecological baseline is needed.

The durability of scleractinian coral skeletons provides a ready basis for the assessment of coral species composition and diversity from reefs of the past. Coral skeletons have been used to characterize the community composition of Pleistocene reefs (Pandolfi and Jackson 2001, 2006) and to assess taphonomic patterns (Pandolfi and Greenstein 1997a, 1997b, Greenstein and Pandolfi 2003) and trends in species dominance

(Aronson and Precht 1997, Aronson et al. 1998, Aronson 2004, 2005) of fossil Holocene reefs in the Caribbean. The latter suite of studies focused on changes in the dominant coral species collected as fragments from cores. These studies found that the branching corals *Acropora cervicornis* in Belize and *Porites furcata* in Panama were replaced by the lettuce coral *Agaricia tenuifolia* within the past few decades, and that these events were unprecedented over the past several millennia. Because *A. tenuifolia* is more tolerant of high turbidity and high nutrient conditions than *Acropora* spp. (Adey et al. 1977, Rogers 1979, Shyka and Sebens 2000), this transition was attributed at least in part to increasing eutrophication of reefs from land clearing (Aronson 2004, 2005). However, the coring studies were focused on identifying switches in species dominance and did not assess changes in abundance in the remainder of the scleractinian coral community.

In order to provide a more detailed description of historical coral community change, I assessed relative abundance changes for all scleractinian corals over the past centuries. I did this by excavating coral skeletons in discrete layers from large-diameter pits on modern reefs in western and central Caribbean Panama. I also surveyed the living coral communities at each site to compare modern reefs with past reefs. The approximate timing of change in coral community composition was determined by radiocarbon dating coral samples from each layer of each pit. This study produced a time series of coral community composition that I utilized to: (a) obtain a more accurate ecological baseline of the “natural” state of Caribbean reefs, (b) determine whether community changes varied over a gradient of reef environmental conditions, and (c) determine whether coral community change preceded the observed coral mortality events of the 1980s and 1990s.

METHODS

STUDY SITES

Coral life and death assemblages were sampled in the Bocas del Toro region along the western coast of Caribbean Panama and in the Costa Arriba region along the central coast of Caribbean Panama (Figure 2.1a). These regions have an extensive history of human exploitation and disturbance of coastal environments extending back at least 1000 years (Drolet 1980, Linares 1980, Gordon 1982, Pandolfi et al. 2003, Guzman 2003, Bond 2008). Reefs from both regions have been exposed to increasing amounts of land-based pollution over the past century, beginning with construction of the Panama Canal at the end of the 19th century near Costa Arriba (Guzman 2003) and with large-scale banana agriculture at the beginning of the 20th century in Bocas del Toro (LaBarge 1960, Stephens 2008). Pollution has further intensified over the past decades from land clearing for agriculture, cattle ranching and urban development (Gordon 1982, Heckadon-Moreno 1993, Guzman 2003, KL Cramer *pers. obs.*)

Samples were collected from a total of nine reef sites, six from Bocas del Toro and three from Costa Arriba. Reef sites were selected to represent a range of environmental conditions, from lagoonal environments influenced by moderate to substantial amounts of river runoff to offshore environments more influenced by oceanic conditions including seasonally strong wind and wave action. Both of these regions lie well south of the Atlantic hurricane belt (Neumann et. al. l978). Reefs exposed to strong wave action were inappropriate for this study because their cemented reef framework could not be excavated by hand. The six reef sites sampled in Bocas del Toro span a distance of approximately 60 km, with three sites located within lagoonal environments

(STRIPT, PTDTO, and PTLRL), and three sites located in semi-exposed offshore reef environments (BAST, NPOPA, and TOB). The three reef sites surveyed in the Costa Arriba span a distance of approximately 45 km, with one site (BVTRA) located in a semi-protected lagoonal environment in the lee of a small island, and two reef sites in semi-exposed offshore environments (ISLNAR and MAME). The ISLNAR site was located approximately 4 km east of Bahia Las Minas, the site of numerous oil spills, including a major spill in 1986 (Jackson et al. 1989). Reef sites were classified as offshore reefs if they were located on the windward sides of islands or on exposed parts of the mainland coast and were classified as lagoonal reefs if they were located on the leeward side of islands or within a lagoon. Although reef sites were separated into two distinct "offshore/lagoonal" categories, these sites actually span a range of exposure to wind and wave action, with Costa Arriba offshore sites experiencing the greatest amount of exposure and Bocas del Toro lagoonal sites experiencing the least amount of exposure.

SAMPLING

The living coral community (*life horizon*) was measured as the percent live coral cover from point-intercept line transects, while the fossil coral community was measured as percent weight of coral rubble from four distinct layers within pits (*death horizons*). Sampling was conducted at 5m water depth using SCUBA. The Smithsonian Tropical Research Institute's Bocas del Toro Research Station and Galeta Marine Laboratory were used as bases of operation at each of the sampling regions.

Coral death assemblages were collected by excavating four approximately 20cm-thick layers from a 60cm-diameter circular pit (Figure 2.1b). Pits were excavated from patches with little or no living coral and were immediately adjacent to modern reef areas with living coral cover. Excavations were aided by the support of a circular metal frame which was inserted into the sediment/coral rubble matrix to prevent collapse of the walls of the pit during excavations. Before excavation began, a metal rebar pole was manually pushed 1m into the reef framework at four evenly-spaced points along the circumference of the frame to detect massive coral colonies that were either >60cm in diameter or that were located on the edge of the frame and would prohibit its penetration into the matrix. If these large coral colonies were detected, the location of the frame was moved <1 m from the original site until all four poles could penetrate 1 m deep into the reef framework. This method did not prevent the frequent sampling of massive coral colonies <60cm in diameter in the pit excavations. As excavation progressed, the 40cm-deep metal frame was hammered into the reef framework. When the excavation reached 40cm below the sediment surface, another 40cm-deep metal frame 55cm in diameter was placed inside the larger metal frame and the excavation of the bottom two layers proceeded in the same manner as for the top two layers. Coral rubble and sediments were extracted with small gardening shovels and ice scoopers and placed into bottomless buckets lined with a mesh netting that retained all material > 7mm, including mollusk shells. Material was extracted from four distinct layers extending down to 80cm below the reef surface: 0-20 cm, 20-40 cm, 40-60 cm, and 60-80 cm. Material from each pit layer was considered a separate death horizon.

The coral life horizon was sampled via a 40m point-intercept transect survey that sampled the coral community at 5cm increments. Each line transect survey therefore provided a total of 800 data points. The 5cm sampling increment was selected because it captured over 95% of the richness recorded in continuous transects of the same length on average, and 40m-length transects were selected to maximize sampling of more rare or patchily distributed species in the living assemblage. Corals that were not positively identified to genus or species in the field were photographed and later identified with the use of standard references. Each transect line was placed 1-2 m away from its corresponding pit. Transect lines were generally spaced 20-50 m apart, depending on the total extent of reef area available for survey. Therefore, pits and transect lines covered a large area of each reef site and could be subject to differing amounts of water motion, particularly for offshore reefs. As a supplement to the point-intercept surveys, 2m-wide belt transect surveys (1m on either side of transect line) were conducted to detect rare species.

This sampling scheme allowed for comparison of spatial and temporal variation in coral community composition. The spatial component of sampling was represented by three nested levels: regions, reef sites, and pits/transects (Figure 2.1). The temporal component of sampling was represented by four death horizons within each pit plus the living horizon from a transect. Thus, this sampling scheme produced 27 total *replicates*, three from each of the nine reef sites sampled (six from Bocas del Toro plus three from Costa Arriba). Each of the 27 replicates contained five time horizons, resulting in 135 separate coral assemblages. These assemblages were the fundamental sampling unit, hereafter *samples*.

TAXA

A total of 35 taxonomic groupings were identified (20 species and 15 complexes of congeneric species that could not be readily distinguished), hereafter *species*. For some death horizon samples, the identification of a coral fragment was narrowed down to two species but could not be positively identified to a single species. The apportionment of the weight of these fragments was carried out using the following procedure. If both of the candidate species were present in the sample, the fragment weight was prorated according to the relative weights of those species categories. If neither candidate species was present in the sample, the relative weights from the nearest horizons in the same pit or other pits at the same reef site were used to prorate the weight of the coral fragment. If neither possible species was present in any other death horizon at that site, the species was assigned to the "unknown" category and excluded from analysis. Samples that could not be identified to one or two categories were also placed in the "unknown" category. This category represented an average of 3% of the death horizon and 0% of the life horizon. Small scleractinian cup corals from the families Rhizangiidae and Dendrophyllidae and the hydrozoan coral *Stylaster* spp. were not included in the analyses because they were very minor components of the coral community. The hydrozoan coral *Millepora* was included in the analyses because it is a major component of coral communities in shallow reef zones of Bocas del Toro and Costa Arriba.

STATISTICAL ANALYSIS

Due to non-normality and heteroskedasticity of data, a combination of non-parametric statistics was used to investigate trends in species richness and individual species proportions over time and among reef environments. For all analyses, the sampling unit was a single time horizon within a single replicate, resulting in 6 sites x 3 pits x 5 time horizons = 90 samples total for Bocas del Toro, and 3 sites x 3 pits x 5 time horizons = 45 samples total for Costa Arriba. Species proportion trends were assessed statistically for all species comprising ≥ 10% of the community at any one pit at any one time horizon. The analysis of trends in species proportions over the entire time series (all five time horizons) was conducted via two different approaches. The first approach did not consider the replicate from which an individual sample belonged (i.e. assumed independence among samples) using the Kruskal-Wallis one-way ANOVA of ranked means with time horizon as treatment factor. The second approach considered the replicate from which a sample belonged using the Friedman test, a non-parametric repeated-measures ANOVA. Because results from the Kruskal-Wallis and Friedman tests were identical for all comparisons, the Kruskal-Wallis results were presented for simplicity.

For species proportions that showed significant trends over the entire time series, post-hoc comparisons between individual horizons were conducted utilizing a bootstrapping procedure. This procedure sampled each time horizon with replacement to generate a bootstrapped distribution for species proportion, computed a mean value for each horizon, and computed differences between mean values for each pair of horizons. The procedure was repeated 1,000 times, and 95% confidence intervals were computed from 95th quantiles of the distribution of differences between mean values. For each pair of time horizons, measures were significantly different if the 95% confidence intervals for the difference between mean values did not include zero (= two-tailed test; Efron and Tibshirani 1986).

This bootstrapping procedure was also utilized to assess differences between two samples for other measures of interest, including coral species richness, total weight of coral rubble analyzed, and coral community dissimilarity. Coral richness of the life horizon was computed with and without the rare species surveys to determine whether any species that were "lost" between the death and life assemblages were still in fact present in the near vicinity at 5m water depth. Community dissimilarity was measured with the Bray-Curtis dissimilarity, a measure which takes into account rare species (Bray & Curtis 1957, Clarke 1993). The Analysis of Similarity (ANOSIM; Clarke 1993) procedure was used to test for coral community difference between sampling regions and between reef environments by comparing the within-group versus between-group Bray-Curtis dissimilarities. A test statistic R was computed by ANOSIM, which scales from -1 (samples within a group are less similar to each other than are than samples between groups) to +1 (samples within a group are more similar to each other than are samples between groups). A significance value for R (at $p = 0.05$ level) was computed by randomly assigning replicates to either group to determine whether the observed R value was significantly different from that expected by chance. This permutation was performed 1000 times. For all analyses, statistical significance was determined at the $p = 0.05$ level. All analyses were conducted using the R software package (R Development Core Team 2008).

RADIOCARBON DATING

One or two coral rubble fragments from each death horizon within each pit (i.e. sample) were radiocarbon dated to obtain estimates of age ranges providing a total of 139 radiocarbon dates. Fragments from the finger coral *Porites furcata* were selected for dating because it was the most widely distributed species among all pits and death horizons. The lettuce coral *Agaricia tenuifolia* was used in three samples that did not contain *P. furcata*. The tip of each rubble fragment was selected so that the most recent growth was dated. Only samples that were free of visible calcareous overgrowth and internal boring were selected for analysis. The samples were prepared and analyzed for radiocarbon at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory (Davis et al. 1990).

The results of the radiocarbon analyses are reported as the "fraction modern" as defined in Reimer et al. (2004) and as calendar years AD from the calibration of radiocarbon ages. Conversions to calendar years were conducted using one of two reference datasets. Fraction modern values less than 0.927 (corresponding to ages older than approximately 1750 AD) were converted to calendar years using the Calib 6.0 program (Stuiver and Reimer 1986) and the IntCal/MarCal calibration dataset based on tree-ring data (Hughen et al. 2004, Reimer et al. 2004). Radiocarbon ages greater than 0.927 were converted to calendar years using the Calibomb program (Reimer et al. 2004) and a surface water $\Delta^{14}C$ reconstruction for the Caribbean from a *Montastrea faveolata* coral core from Puerto Rico (Kilbourne et al. 2007). The calibration procedure included conservative estimates of measurement uncertainty for all parameters, and provided calendar age ranges that included one standard deviation. Due to a large number of fluctuations in ocean surface water $\Delta^{14}C$ values during the 19th and 20th centuries, fraction modern values often corresponded to more than one possible calendar age range. When possible, some age ranges were eliminated by assuming stratigraphic order of ages among horizons within a pit. The calibrated age for each coral fragment was estimated by including all remaining possible age ranges and computing the midpoint of the range. Due to the dramatic increase in bomb-produced ^{14}C concentrations in surface ocean waters that began in the late-1950s and peaked in the mid-1970s, coral fragments with very high $\Delta^{14}C$ values could be readily assigned "post-bomb" (i.e. post-1960) calendar ages, often with very high precision (± 5 years or less).

The calibrated age ranges were used to determine whether samples within a given region, reef environment, and death horizon were coeval and could therefore be combined for statistical analysis. Samples were pooled only if their calendar age ranges overlapped, reducing the sample size for most death horizons. This method allowed the determination of the pre- and post-bomb boundary for data by region and reef environment. For each region, horizon, and environment, the calibrated age range was simply the minimum and maximum possible age of the pooled radiocarbon dates. This method assumed that layers within a pit represented a chronological sequence.

POTENTIAL TAPHONOMIC BIASES

The paleontological data used in this study may contain biases resulting from processes that occurred in the period spanning the death and sampling of corals. These processes have the potential to alter death assemblages to the point that they no longer represent the living assemblages from which they originated. Therefore, straightforward comparisons of community structure among life and death horizons are valid only if three assumptions are met: (1) the horizons represent a chronological sequence, (2) each horizon represents a similar span of time, and (3) each horizon contains all of its original community components. These assumptions can be violated by two processes: the amalgamation and physical alteration of coral skeletal material (Scoffin 1992).

The amalgamation of coral skeletal material within or between death horizons can occur via bioturbation or wave action. Decapod crustaceans are common in back-reef sediments and have the capability of transporting coral rubble pieces vertically and horizontally within their extensive burrow networks (Suchanek et al. 1986, Dworschak and Ott 1993, Felder et al. 2009). Similarly, storm waves can transport rubble pieces located on or near the sediment surface away from their original place of deposition (Scoffin 1992).

Another potential bias arises from different degrees of time averaging (amalgamation of corals of different ages) between death horizons and between the death and life horizons. The 20 cm-thick death horizons sampled in this study represent a time-averaged assemblage, but there is no reason to expect that the degree of time averaging would vary among horizons within a pit in a systematic way. More problematic is the degree of time averaging between the life and death horizons. Although the transect surveys of the living community also represent time-averaged samples because they include coral colonies that differ in age by decades to centuries, it is difficult to assess whether the life assemblage is more or less time averaged relative to the death assemblages.

A final bias arises from rates of coral skeleton deterioration that vary by growth form, potentially resulting in an under-representation of more quickly eroding forms in the death assemblages. Although more robust colony forms with denser skeletons (i.e. massive and sub-massive colonies) can better resist mechanical dissolution and abrasion, these forms can also be subject to a greater degree of bioerosion from boring and encrusting organisms (Scoffin 1992, Pandolfi and Greenstein 1997b). This pattern may not apply to all coral reefs, however: a study of taphonomic alteration of corals in the Florida Keys found no difference in preservational state among growth forms (Greenstein and Pandolfi 2003). The problem of preservational biases is probably not serious for the data presented here because it is unlikely that rubble pieces could have been completely destroyed within the historical time period sampled.

RESULTS

CORAL DATA

Most of the rubble pieces extracted from the pits were found in life position as part of a densely-packed coral matrix. Thicket-forming species such as *Aagaricia tenuifolia*, *Porites furcata*, and *Madracis mirabilis* were generally found as intact colonies that were often fragmented during the excavation process. The average minimum diameter of rubble pieces measured was 21.7 mm (n = 354, 95% CIs: 4.6 - 88.1 mm). Branching, plating, and foliose growth forms were mostly well preserved with few incidences of internal bioerosion. However, mollusk and polychaete boreholes were common in the more robust massive and sub-massive growth forms. For all growth forms, rubble from offshore reef sites was often covered with crustose coralline algae, although this normally did not prevent positive identification to a species category.

The pits yielded a substantial amount of coral skeletal material: a total of 1088 kg of scleractinian plus *Millepora* corals were positively identified and analyzed from the six reef sites in Bocas del Toro and 445 kg from the three reef sites in Costa Arriba. Although the total amount of coral material collected was not uniform across holes and time horizons, the mass of coral material analyzed did not vary significantly among horizons for either Bocas del Toro or Costa Arriba. However, the total mass of coral material analyzed within a sample (i.e. time horizon within a pit) was significantly greater at lagoonal than offshore sites in both the Bocas del Toro (lagoonal/offshore mean weights = 17.2/12.7 kg; bootstrap test: $p < 0.05$) and Costa Arriba regions (lagoonal/offshore mean weights = 16.6/12.3 kg; bootstrap test: $p < 0.05$; Figure 2.2). For both regions, the variation in coral community composition was slightly greater between reef environments (i.e. offshore v lagoonal) than within reef environments (Bocas del Toro: ANOSIM $R = 0.15$, $p < 0.001$; Costa Arriba: ANOSIM $R = 0.41$, $p < 0.001$).

BOCAS DEL TORO

Radiocarbon dates

A total of 93 coral fragments from Bocas del Toro were radiocarbon dated and represented calendar ages that ranged from 1290 AD ± 25 to 2003 AD ± 3 (Table 2.1). The comparison of uncalibrated radiocarbon ages among death horizons revealed that pits from lagoonal sites extended further back in time than pits from offshore sites (Table 2.1). While post-bomb (approximately post-1960 and Fraction modern ages >1) ages were located in all four death horizons at offshore sites, post-bomb dates were restricted to the 0-20 cm horizon at lagoonal sites. Therefore, in lagoonal sites three deepest horizons (60-80cm, 40-60cm, 20-40cm) definitively represented the time period before 1960. In contrast, in offshore sites many of the pits had deeper horizons that represented the time period after 1960, signifying that many offshore pits did not extend back before 1960. The shorter time span represented by the offshore pits is likely due to the higher sediment production rates from the erosion of the calcareous algae (*Halimeda*) that are abundant in this reef environment. For both environments, the general stratigraphic order of post- and pre-bomb dates suggested minimal mixing between horizons.

The calibration of radiocarbon ages allowed for a more detailed assessment of the time periods represented by each death horizon within each pit. In general, calendar ages of coral fragments within a pit were in stratigraphic order, and many adjacent horizons within a pit overlapped in age (Table 2.1). The range of possible ages represented by the oldest (60-80cm) horizon was 1911-1996 AD for offshore sites and 1255-1959 AD for lagoonal sites, confirming the longer time span encompassed in the lagoonal pits and the need to analyze coral communities separately by environment. Combining coeval samples within a horizon and environment resulted in the removal of 16 out of 36 samples from offshore sites and 10 out of 36 samples from lagoonal sites.

Coral community composition

The pit excavations confirmed the high level of diversity and spatial variation in coral communities reported in recent ecological surveys of Bocas del Toro reefs (Guzman and Guevara 1998a,b, 1999, 2001). A total of 31 species categories were sampled in either the death or life assemblages, comprising 89% of the species reported for this area (Table 2.5). Species which were not sampled in this study were observed on reef zones above or below 5m water depth. Coral community composition varied more over space (among replicates within a single horizon) than over time (among horizons within a single replicate) at both reef environments (bootstrap test: $p < 0.05$). This pattern is illustrated in the lack of clustering of samples by time horizon in the ordination biplots (Figure 2.3).

A significant decline in coral species richness occurred over the time series at offshore sites (Kruskal-Wallis $X^2 = 12.6$, $p < 0.05$) and lagoonal sites (Kruskal-Wallis $X^2 = 21$, $p < 0.001$). These overall trends were driven by the lower richness of the living horizon compared to some or all of the death horizons (Figure 2.4). Richness was significantly lower between the living horizon and the 20-40, 40-60, and 60-80 cm horizons at offshore sites, and significantly lower between the life horizon and all death horizons at lagoonal sites (bootstrap test: $p < 0.05$). Adding rare species recorded in the belt-transect surveys to the point-intercept transect surveys significantly increased the total diversity for the living horizon at offshore and at lagoonal sites (bootstrap test: $p < 0.05$). While the richness of the life horizon including rare species was still significantly lower than all death horizons at lagoonal sites, it was not significantly different from any of the death horizons at offshore sites. No significant trend in richness was detected among the death horizons for either reef environment.

The group of species that was “lost” between the death and life assemblages was not dominated by any single family or colony growth form. Species lost included *Diploria clivosa/strigosa*, *D. labyrithiformis*, *Eusmilia fastigiata*, *Madracis mirabilis*, *Meandrina* spp, *Millepora* spp, and *Mussa angulosa* (Table 2.5). Three of these species categories were not common in any of the death horizons, suggesting that naturally rare species have become even more so over time or that these species were undersampled in the transect surveys of the life horizon. These species did not disappear completely from Bocas del Toro reefs, however. The majority of lost species were recorded in the rare species surveys, but were so uncommon and/or patchily distributed that they were not recorded in the line-transect surveys. The *Diploria* and *Millepora* species categories were observed as components of the living reef at depths <5 m, which suggest that they have been extirpated from the deeper portion of their vertical range during the time period sampled.

Three species – *Acropora cervicornis*, *Agaricia tenuifolia*, and *Porites furcata* - were the most abundant in Bocas del Toro, each comprising ≥ 20% of the coral community on average in at least one time horizon at both reef environments. Combined, these species comprised 65% of the coral community averaged over all samples. The most striking temporal trend observed among these three species was the large decline in the relative abundance of *A. cervicornis*, which occurred progressively through the time series in both offshore and lagoonal reef environments but was only significant in the latter. The decline in *A. cervicornis* was accompanied by an initial increase and subsequent decrease in the relative abundance of *P. furcata*. A progressive increase occurred in *A tenuifolia* relative abundance throughout the time series (Figures 2.5, 2.6). Temporal trends in species proportions were statistically significant for *A. cervicornis* and *P. furcata* for lagoonal sites only, driven mainly by significant declines between the death and life horizons (Table 2.6). However, *A. cervicornis* declined significantly between the 20-40 and 0-20cm horizons. The decline in *A. cervicornis* was more consistent among replicates within lagoonal sites, with the mean species proportion declining from 14% - 0% between the 60-80cm and living horizons. Once an important component of reefs located in the Chiriquí and Almirante lagoons, this species is now virtually locally extinct within these areas, and is presently restricted to isolated small stands on a few patch reefs (Guzman 1998a, Vollmer and Kline 2008). Although the overall proportional decline in *A. cervicornis* was greater at offshore sites (from 39%-6% of community between 60-80cm and life horizons) than lagoonal sites (from 19%-0% of community between 60-80cm and life horizons) , decline was more variable among replicates at offshore sites. The progressive nature of the decline in *A cervicornis* indicates that the loss of this species occurred gradually rather than abruptly throughout the time series, and extends back to the deepest (=oldest) horizons sampled.

At the level of individual pit, changes in proportions of these three species followed one of three general trajectories. The majority of pits underwent a two-stage successional sequence, with a decline in *A. cervicornis* / increase in *P. furcata* followed by a decline in *P. furcata* / increase in *A. tenuifolia*. The remainder of pits did not contain *A. cervicornis* in abundance at any horizon, and either displayed no change in species proportions (e.g. pits from offshore site TOB) or a decline in *P. furcata* and increase in *A. tenuifolia* (e.g. pits from lagoonal site STRIPT; Table 2.1).

Signicifant overall declines occurred for two subdominant species ($\geq$ 10% of community at a time horizon) at offshore and lagoonal sites, both driven by changes between the death and life horizon. For offshore sites, the relative abundance of *Millepora* spp. was significantly higher in the living horizon compared to the death horizons (K-W $X^2 = 16.2$, $p < 0.05$; bootstrap test: $p < 0.05$), representing a post-1960 increase in this species (Figure 2.5a). For lagoonal sites, *M. mirabilis* was significantly lower in the life compared to death horizons (K-W $X^2 = 20.2$, $p < 0.001$; bootstrap test: $p < 0.005$), representing a post-1960 decline in this species (Figure 2.5b). The decline in *M. mirabilis* was driven by one lagoonal site (PTDTO) which was once dominated by *Colpophyllia natans*, *A. cervicornis,* and *M. mirabilis* before it lost both branching species. Today, PTDTO is a high-turbidity reef with low percent living coral cover for Bocas del Toro (18%) and dominated by massive corals *Montastrea annularis*, *C. natans*, *P. astreoides*, and *Siderastrea* spp. The small number of replicates (three) within this single site limits the statistical confidence that can be placed in these results, however. The statistical and ecological significance of trends in subdominant species is similarly difficult to assess because their relative abundances varied greatly among replicates and did not change progressively over time.

The delineation of pre- and post-bomb radiocarbon ages provided a minimum age estimate of 1959 AD for the bottom (oldest) time horizon for both reef environments. Estimates of maximum sediment and rubble accumulation rates from lagoonal sites in Bocas del Toro (Hilbun 2009) and Belize (Aronson et al. 2004) provided a conservative estimate of maximum bottom age of 80-140 years. Thus, the significant changes in the proportion of branching *A. cervicornis* and *P. furcata* at lagoonal sites likely occurred during the mid 18th century or early 19th century, well before the onset of the white band-disease (WBD) epidemic that swept across the Caribbean beginning in the 1980s. The more dramatic decline in *A. cervicornis* at lagoonal sites reflects the greater extent of change in this environment and/or the longer time span represented in pits from this environment.

COSTA ARRIBA

Radiocarbon dates

A total of 46 coral fragments from Costa Arriba were radiocarbon dated and represented calendar ages that ranged from 977 AD ± 4 9 to 1983 AD ± 17 (Table 2.2). A comparison of uncalibrated radiocarbon ages among death horizons revealed that pits from lagoonal sites generally extended further back in time than pits from offshore sites. As with Bocas del Toro, post-bomb (i.e. post-1960, fraction modern > 1) ages were located in all four death horizons at offshore sites, while post-bomb ages were restricted to the 0-20cm horizon at the single lagoonal site (Table 2.2). Therefore, the three deepest horizons at pits from lagoonal sites represent the time period before 1960. In contrast to

Bocas del Toro, the majority of pits from offshore sites had pre-bomb ages in the 60-80 and 40-60 cm horizons, indicating that offshore pits from Costa Arriba extended further back in time/and or were subject to less mixing among layers than offshore pits from Bocas del Toro (Tables 2.1-2.4).

Although post-bomb dates were found deeper in the offshore compared to lagoonal pits, the oldest radiocarbon ages reported from either region were located in a pit from the offshore site ISLNAR. Thus, the overall difference in maximum age between pits from the two reef environments was diminished in Costa Arriba compared to that in Bocas del Toro. With the exception of the "old" pit from ISLNAR, post-bomb and pre-bomb dates were generally in stratigraphic order, suggesting minimal mixing between horizons.

The calibration of radiocarbon ages allowed for a more detailed assessment of the time periods represented by each death horizon within each pit. Aside from pit A from the reef site ISLNAR, calendar ages of coral fragments within a pit were in stratigraphic order or overlapped in age (Table 2.2). Calibrated dates from the 60-80cm horizon of this pit differ by approximately 900 years, indicating the vertical mixing of layers. Mixing may be the result of dredging operations that took place this area for the construction and maintenance of the Panama Canal (Guzman 2003). The range of possible ages represented by the oldest (60-80cm) horizon was 1841-1959 AD for offshore sites and 1843-1957 AD for lagoonal sites (Table 2.4). Including only coeval samples within a horizon and environment resulted in the removal of 7 out of 24 samples for offshore sites and 2 out of 12 samples for offshore sites.

Coral community composition

Coral communities from Costa Arriba showed different spatial and temporal trends compared to Bocas del Toro. A lower proportion of the total richness recorded for this region was sampled in any time horizon (77%), likely due to the smaller number of reef sites sampled in Costa Arriba. The majority of species categories not sampled in this study are not major components of Caribbean reefs in Panama (Guzman 2003, KL Cramer pers. obs). However, the genus *Diploria* was not recorded in any of the transects or pit excavations even though it was reported to be a major component of Costa Arriba coral communities from surveys conducted in the 1980s and 1990s (Guzman et al. 1991, 1994, Guzman 2003). As at Bocas del Toro, coral community composition varied more over space (among replicates within a single horizon) than over time (among horizons within a single replicate) at both reef environments (bootstrap test: $p < 0.05$), as illustrated by the lack of clustering of samples by horizon in the ordination biplots (Figure 2.7).

In contrast to Bocas del Toro, no overall significant temporal trend in richness occurred in Costa Arriba coral communities. Richness in the life horizon was markedly lower than that for the death horizons in the single lagoonal site (Figure 2.8), with a variety of naturally rare species “lost” between the death and life assemblages (Table 2.5). However, the small sample size for the single lagoonal site reduced the statistical power to detect significant trends. For both reef environments, the addition of rare species recorded in the belt transects to the life horizon significantly increased the life horizon richness (bootstrap test: $p < 0.05$) and reduced the richness differences between the death and life horizons.

The lettuce coral *A. tenuifolia* was the dominant coral species on Costa Arriba reefs, comprising 68% of the coral community averaged over all samples. The branching coral *P. furcata* was the second most abundant species, and together these two species comprised 78% of the coral community on average. *A. tenuifolia* was the dominant species at all horizons at offshore sites and at all death assemblage horizons at lagoonal sites (Figures 2.9 and 2.10). Other common but subdominant species included the platy and foliose *A. agaricites* and *Undaria* spp. at offshore sites and branching *M. mirabilis* at lagoonal sites. *A. cervicornis* was essentially absent from every pit in Costa Arriba, comprising < 1% of the coral community at any time horizon (Tables 2.2 and 2.5). Ecological surveys from the late 1980s showed that *A. cervicornis* was restricted in distribution but locally common on at least one less exposed reef site in this region (Guzman et al. 1991). Therefore, it is possible that this study did not record *A cervicornis* in Costa Arriba because of the lower spatial coverage of sampling conducted there. Another explanation for the absence of *A. cervicornis* in pits from Costa Arriba is that this species had already disappeared before the early 20th century, the median age of the 60-80cm horizon in both environments (Table 2.4). However, *A. cervicornis* was absent even from the pit in ISLNAR that extended back to the 10th century.

No significant overall trends were found in species proportions for any of the abundant species at either reef environment. AT the lagoonal site *P. furcata* and *A.tenufolia* displayed an increase during the older horizons and a decrease during the younger horizons, with a peak in relative abundance at 0-20cm for *P. furcata* and 40-60cm for *A. tenuifolia* (Figure 2.10). However, the small sample size precluded assessment of statistical significance of these trends. Because all horizons from this site were older than 1960, these patterns occurred prior to this year.

COMPARISON OF REGIONS

The within- and between-region variation in community composition was essentially equal (ANOSIM: $R = 0.08$, $p < 0.05$). The most conspicuous differences in community composition between regions were the high abundance of *A. cervicornis* in older time horizons in Bocas del Toro versus the near absence of this species in all time horizons in Costa Arriba and the overwhelming dominance of *A. tenuifolia* in all time horizons in Costa Arriba versus the relatively recent dominance of this species in Bocas del Toro. The ordination of samples from both regions together revealed that the majority of variation in coral community composition (51%) was explained by the first principal component (PC1) and that samples grouped by region and reef environment closely tracked PC1 (Figure 2.11). Differences in species composition among these four groups appeared to follow a gradient of exposure to oceanic conditions, with Bocas del Toro lagoonal sites on one end of the community spectrum and Costa Arriba offshore sites at the other end, driven primarily by the relative abundance of *A. tenuifolia*, *A .cervicornis*, *P. furcata*, and *M. mirabilis* (Figure 2.11). It is possible that these patterns were also driven by the differing time periods represented by each of these four groups, although neither the age ranges nor median of the age ranges of the oldest time horizon (60-80 cm) from these groups were ordered sequentially along PC1 (Tables 2.3 and 2.4).

DISCUSSION

COMMUNITY CHANGE

The paleontological data analyzed in this study revealed that reefs in Bocas de Toro have undergone a major reorganization in coral community structure that likely were occurring during the mid 18th century- early 19th century and were definitively well underway by 1960. This reorganization included a dramatic decline in the relative abundance of the staghorn coral *Acropora cervicornis* to < 1% of the living coral community. This species was historically dominant on reefs throughout the archipelago (KL Cramer, *unpublished data*) – even in semi-enclosed lagoons now characterized by very high turbidity levels – where it is now rare or absent. These results confirm that Bocas del Toro has suffered the same catastrophic loss of *A. cervicornis* as other regions in the Caribbean (Hughes 1994, Aronson and Precht 2001, Greenstein et al. 1998).

This study found a disproportionate loss in branching species and an increase in the importance of the sediment and nutrient-tolerant lettuce coral *Agaricia tenuifolia* at Bocas del Toro that is consistent with the *A. cervicornis* to *A. tenuifolia* transition witnessed on coral reefs in Belize during the 1980s-1990s (Aronson et al. 1998). Three branching species declined significantly in relative abundance between the death and life assemblage horizons: *A.cervicornis*, *P. furcata*, and *M. mirabilis*. The densely branching colony morphology of all three of these species does not allow for efficient removal of sediments, particularly in low water flow (lagoonal) environments (Bak & Elgershuizen 1976). *P. furcata* and *M. mirabilis* are moderately resistant to sedimentation and pollution (Tomascik and Sander 1987), while *A. cervicornis* is particularly susceptible to these stressors (Guzman et al. 1991, Bak and Criens 1981, Rogers 1979). Although differing from each other in other aspects of life history, all three of these species have high rates of asexual propagation via fragmentation of branches. Asexual recruits from these species have been shown to have much lower survivorship rates than newly settled sexually-produced larvae (Bak and Criens 1981, Hughes 1985), perhaps making these species more vulnerable to reef environmental change.

The shifts in composition seen on reefs at Bocas del Toro were accompanied by a significant loss in coral diversity. This loss is consistent with declines in coral abundance observed across the Caribbean since the 1970s (Hughes 1994, Gardner et al. 2003). The widespread loss of corals has diminished the abundance of naturally rare species to the degree that they became ecologically insignificant. While these losses do not constitute local species extinctions because rare individuals still exist on some reefs in the region (KL Cramer, *unpublished data*), they represent a clear *ecological extinction* (sensu Jackson et al. 2001) because they were not found in 720m of line transect surveys. The loss of coral diversity was delayed with respect to the timing of changes in the proportions of dominant species, indicating that major coral community changes preceded ecological extinctions.

In contrast to Bocas del Toro, coral communities in Costa Arriba appear to have remained relatively stable over the past century. Because the number of reef sites sampled in this region was half that sampled in Bocas del Toro, however, it is more difficult to extrapolate these results to the entire Costa Arriba region. The lagoonal site from this region (BVTRA) appears to have undergone a unique transition in species composition not seen on any other reefs sampled in this study, from dominance by the lettuce coral *A. tenuifolia* to the branching coral *M. mirabilis*. This reef presently is subject to high turbidity levels from sediment-laden rivers that drain an increasingly deforested watershed (Guzman 2003, KL Cramer *pers obs*). Because both coral species are characterized as being relatively tolerant of turbid and nutrient-elevated waters (Tomascik and Sander 1987, Shyka and Sebens 2000), the species transition cannot be attributed to the effects of land-based pollution alone. It is possible that this species transition was mediated by a bleaching event, as *A. tenuifolia* is particularly susceptible to bleaching (Lasker et al. 1984, Shulman and Robertson 1996, Aronson et al. 2000).

COMMUNITY CHANGE AND HUMAN DISTURBANCE

The spatial patterns of change in coral communities suggest a connection to declining water quality from land clearing. The nutrients, sediments, and pollution resulting from land clearing and that are transported to reefs are deleterious to coral survival, growth, and reproduction (Rogers 1990, Fabricius 2005). Due to their closer proximity to rivers and streams and lower rates of water circulation, lagoonal reef environments are more influenced by runoff than are offshore reefs. In both regions, lagoonal reefs experienced more pronounced changes in species proportions and greater declines in species richness. The overall degree of community change varied along a gradient of exposure to open ocean conditions: the reef environments located in the most enclosed lagoonal environments - Bocas del Toro lagoons - experienced the greatest temporal changes in coral community composition, and the reef environments located in the most exposed environments - Costa Arriba offshore reefs - changed the least. In both regions, lagoonal reefs experienced greater changes in the relative abundance of dominant species as well as more pronounced declines in coral richness between the death and life assemblage horizons. In Bocas del Toro, changes were driven in part by the large decline *A. cervicornis*, which has been locally extirpated from other Caribbean reefs in the recent geological past by the influx of high-sediment and nutrient waters from flooding events during the Holocene marine transgression (Macintyre 1972, Lighty et al. 1978, Macintyre 2007). A reconstruction of historical runoff patterns on reefs in Bocas del Toro lagoonal environments supports a direct link between coral community change and water quality: in coral death assemblages collected from cores, the abundance of *A. tenuifolia* was positively correlated with concentrations of terrestrially-derived organic matter from river runoff during high precipitation years and the abundance of *P. furcata* was negatively correlated with this measure (Hilbun 2009).

Coral community change in Bocas del Toro occurred gradually over approximately the past 80-140 years, revealing a trajectory of change that began well before the shifts witnessed on Caribbean reefs since the 1980s. The decline in the relative abundance of *A. cervicornis* prior to 1960 clearly demonstrates that this species' demise predates the appearance in the 1980s of the *Acropora*-specific pathogen responsible for white-band disease (Rowher 2010). WBD went on to kill approximately 95% of *A. cervicornis* across the Caribbean in the 1980s and 1990s, and was undoubtedly a major factor in the ecological extinction of this species. However, the paleontological data presented here reveal that what researchers perceived as the sudden loss of this species beginning in the 1980s may actually have been the culmination of more gradual changes that had been occurring at least decades to a century before.

The land and sea of Caribbean Panama have been altered by its human inhabitants for centuries to millennia. Parts of this coastline were reportedly extensively deforested for arboriculture and maize agriculture at the time of European contact (Gordon 1982), and ash from early slash-and-burn agriculture from approximately 900 A.D. (Linares 1980) attests to the long history of land clearing practices here. Thus, eutrophication and sedimentation of Caribbean reefs are not necessarily modern phenomena, although they have certainly intensified over the past century as this region moves towards greater economic development (Heckadon-Moreno 1993, 1997). Historical and archaeological records show that the decline of major ecological guilds of Caribbean reef organisms from fishing began at least centuries ago (Pandolfi et al. 2003, Wing and Wing 2001). In light of this long record of human disturbance along the Caribbean coastal zone, it would be surprising if Caribbean reefs did *not* contain a correspondingly long record of ecological alteration.

COMPARISON WITH PREVIOUS STUDIES

The trajectory of change observed on Bocas del Toro reefs in this study was more complex than the region-wide *P. furcata* - *A.tenuifolia* replacement reported in prior coring studies (Aronson et al. 2004, 2005, Hilbun 2009). Although a significant decline in the relative abundance of *P. furcata* occurred at lagoonal sites, this decline was less extreme and less consistent on a regional scale compared to the decline in *A. cervicornis*. The excavations showed that *A. tenuifolia* was an important component of these reefs throughout the time series. The discrepancy between this study and the coring studies is likely due to the larger surface area and greater variety of reef environmental conditions sampled in the current study. In addition, the coring study focused on trends in dominant species only while this study considered the relative abundance of all species, including subdominant but major components of the coral community.

POTENTIAL TAPHONOMIC BIASES

The consistent trends in species proportions and coral diversity coupled with the overall stratigraphic ordering of radiocarbon dates among death horizons indicate that the effects of vertical mixing in pits was minimal. The close packing and orientation in life position of the coral rubble sampled in this study and from the coring study in Bocas del Toro lagoonal environments (Aronson et al. 2004, 2005) confirms that large-scale mixing was not prevalent. In addition, ^{210}Pb geochronology of sediment cores from Bocas del Toro lagoonal environments show little or no mixing of sediment layers (Hilbun 2009).

CONCLUSIONS

This study revealed that complex changes occurred within coral communities extending back 50 years or more on reefs in Caribbean Panama. These changes were characterized by dramatic declines in the branching corals *Acropora cervicornis* and *Porites furcata* and a subsequent rise in dominance of the lettuce coral *Agaricia tenuifolia*. The shifts in coral species dominance were followed by a delayed loss of coral diversity. The magnitude of community change varied along gradients of exposure to land-based runoff, strongly suggesting that land clearing practices have contributed to the demise of Caribbean coral reefs. Results from this study conclusively show that coral community change was underway at least 20 years before the observation of coral disease and bleaching epidemics in the 1980s. The paleontological data analyzed here therefore support the view that the recent dramatic shift seen on Caribbean reefs are a culmination of human disturbances that have been affecting these ecosystems over historical time. The novel paleontological sampling technique utilized in this study provided the most detailed ecological baseline of Caribbean coral community structure to date. This baseline enabled a more accurate description of the timing, nature, and magnitude of recent ecological change on Caribbean reefs.

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Table 2.1 (facing page). Bocas del Toro. Radiocarbon results and proportion of common coral species. Ages of coral samples reported as conventional radiocarbon years before 1950 and as calibrated calendar years AD, both with one standard deviation.

Offshore sites

			Radiocarbon results		Species proportions		
Site	Pit	Horizon	14Cyr	Calendar age	*A.cerv*	*A.tenu*	*P.furc*
BAST	A	Living	-	2007	0.18	0.18	0.07
		0-20	> Modern	1992 ± 4	0.72	0.05	0.02
		20-40	> Modern, > Modern	1968 ± 1, 1968 ± 1	0.46	0.20	0.03
		40-60	> Modern	1974 ± 3	0.19	0.27	0.02
		60-80	> Modern, > Modern	1975 ± 1, 1975 ± 6	0.26	0.08	0.16
	B	Living	-	2007	0.00	0.29	0.10
		0-20	> Modern	1981 ± 15	0.03	0.67	0.16
		20-40	> Modern, > Modern	1975 ± 2, 1975 ± 2	0.08	0.37	0.12
		40-60	440 ± 35, 435 ± 30	1921 ± 28, 1925 ± 31	0.33	0.14	0.21
		60-80	380 ± 30	1935 ± 24	0.60	0.21	0.10
	C	Living	-	2007	0.23	0.23	0.09
		0-20	> Modern	1974 ± 6	0.05	0.00	0.95
		20-40	> Modern	1975 ± 1	0.09	0.07	0.79
		40-60	330 ± 30, 325 ± 30	1958 ± 1, 1958 ± 1	0.28	0.09	0.51
		60-80	330 ± 30, > Modern	1958 ± 1, 1975 ± 1	0.61	0.22	0.07
NPOPA	A	Living	-	2007	0.01	0.69	0.09
		0-20	> Modern	1978 ± 10	0.02	0.00	0.98
		20-40	420 ± 30	1954 ± 4	0.08	0.01	0.89
		40-60	> Modern	1978 ± 8	0.05	0.01	0.71
		60-80	390 ± 30, > Modern	1935 ± 25, 1962 ± 1	0.28	0.01	0.67
	B	Living	-	2007	0.08	0.50	0.02
		0-20	> Modern	2000 ± 3	0.11	0.26	0.35
		20-40	> Modern	1974 ± 6	0.58	0.08	0.25
		40-60	> Modern	1977 ± 9	0.39	0.14	0.40
		60-80	465 ± 30	1900 ± 55	0.57	0.10	0.10
	C	Living	-	2007	0.03	0.42	0.20
		0-20	> Modern	1981 ± 15	0.36	0.30	0.15
		20-40	> Modern	1981 ± 15	0.62	0.12	0.10
		40-60	> Modern	1981 ± 15	0.60	0.08	0.08
		60-80	> Modern	1981 ± 15	0.85	0.02	0.05
TOB	A	Living	-	2007	0.00	0.69	0.08
		0-20	> Modern	1999 ± 2	0.00	0.68	0.26
		20-40	> Modern	1981 ± 4	0.00	0.57	0.14
		40-60	> Modern	1975 ± 1	0.01	0.56	0.03
		60-80	> Modern, > Modern	1968 ± 0, 1978 ± 10	0.01	0.55	0.02
	B	Living	-	2007	0.00	0.68	0.05
		0-20	> Modern	1983 ± 5	0.00	0.64	0.00
		20-40	> Modern	1975 ± 1	0.00	0.66	0.21
		40-60	> Modern	1963 ± 0	0.01	0.72	0.20
		60-80	360 ± 30	1936 ± 23	0.01	0.67	0.27
	C	Living	-	2007	0.00	0.62	0.14
		0-20	> Modern	1975 ± 5	0.04	0.65	0.17
		20-40	> Modern	1969 ± 2	0.01	0.76	0.17
		40-60	410 ± 35	1930 ± 28	0.05	0.72	0.15
		60-80	220 ± 30, > Modern	1958 ± 1, 1974 ± 3	0.04	0.73	0.17

Lagoonal sites

			Radiocarbon results		Species proportions		
Site	Pit	Horizon	14Cyr	Calendar age	*A.cerv*	*A.tenu*	*P.furc*
PTDTO	A	Living	-	2007	0.00	0.00	0.00
		0-20	430 ± 30	1900 ± 56	0.00	0.38	0.13
		20-40	375 ± 30	1935 ± 24	0.13	0.11	0.06
		40-60	510 ± 30	1866 ± 27	0.20	0.03	0.03
		60-80	565 ± 30, 375 ± 35	1829 ± 61, 1935 ± 24	0.06	0.05	0.04
	B	Living	-	2007	0.00	0.00	0.00
		0-20	460 ± 30	1907 ± 48	0.00	0.02	0.00
		20-40	465 ± 30	1899 ± 56	0.05	0.02	0.01
		40-60	535 ± 35	1885 ± 70	0.26	0.07	0.00
		60-80	540 ± 30	1885 ± 70	0.16	0.02	0.04
	C	Living	-	2007	0.00	0.00	0.00
		0-20	450 ± 30	1925 ± 32	0.00	0.00	0.02
		20-40	435 ± 30	1926 ± 31	0.02	0.01	0.22
		40-60	520 ± 30	1853 ± 39	0.08	0.02	0.13
		60-80	500 ± 30, 440 ± 30	1832 ± 59, 1839 ± 62	0.01	0.01	0.02
PTLRL	A	Living	-	2007	0.00	0.51	0.24
		0-20	> Modern	1975 ± 1	0.01	0.05	0.68
		20-40	395 ± 30, 355 ± 30	1934 ± 25, 1936 ± 23	0.03	0.02	0.56
		40-60	415 ± 35	1930 ± 28	0.19	0.02	0.43
		60-80	425 ± 30, 335 ± 40	1926 ± 31, 1958 ± 1	0.45	0.02	0.18
	B	Living	-	2007	0.00	0.33	0.10
		0-20	420 ± 30	1930 ± 28	0.03	0.11	0.38
		20-40	670 ± 30, 395 ± 30	1609 ± 50, 1935 ± 25	0.02	0.07	0.40
		40-60	490 ± 30, 415 ± 35	1898 ± 57, 1930 ± 28	0.02	0.06	0.22
		60-80	535 ± 35, 480 ± 35	1822 ± 60, 1895 ± 52	0.04	0.02	0.13
	C	Living	-	2007	0.00	0.26	0.07
		0-20	> Modern	1985 ± 19	0.14	0.30	0.38
		20-40	440 ± 30	1926 ± 33	0.06	0.06	0.48
		40-60	385 ± 30	1935 ± 24	0.13	0.05	0.27
		60-80	465 ± 30	1900 ± 54	0.63	0.01	0.22
STRIPT	A	Living	-	2007	0.00	0.96	0.00
		0-20	> Modern	1964 ± 0	0.00	0.73	0.06
		20-40	660 ± 30, 600 ± 30	1618 ± 50, 1618 ± 50	0.00	0.29	0.25
		40-60	650 ± 30	1626 ± 50	0.00	0.06	0.85
		60-80	710 ± 30	1577 ± 52	0.00	0.05	0.91
	B	Living	-	2007	0.00	0.96	0.00
		0-20	425 ± 30	1930 ± 27	0.00	0.36	0.20
		20-40	455 ± 30, 400 ± 30	1904 ± 45, 1908 ± 48	0.00	0.31	0.13
		40-60	730 ± 30, 720 ± 30	1549 ± 49, 1569 ± 53	0.00	0.37	0.58
		60-80	1075 ± 30, 825 ± 30	1290 ± 35, 1470 ± 31	0.00	0.39	0.56
	C	Living	-	2007	0.00	0.89	0.00
		0-20	460 ± 35	1901 ± 56	0.00	0.89	0.07
		20-40	420 ± 30	1914 ± 9	0.00	0.83	0.10
		40-60	435 ± 30, 425 ± 30	1925 ± 31, 1926 ± 31	0.00	0.70	0.13
		60-80	430 ± 30	1925 ± 32	0.00	0.43	0.30

Table 2.2. Costa Arriba. Radiocarbon results and proportion of common coral species. Ages of coral samples reported as conventional radiocarbon years before 1950 and as calibrated calendar years AD, both with one standard deviation

Offshore sites

			Radiocarbon results		Species proportions			
Site	Pit	Horizon	14Cyr	Calendar age	*A.cerv*	*A.tenu*	*M.mira*	*P.furc*
ISLNAR	A	Living	-	2007	0.00	0.99	0.00	0.00
		0-20	>Modern	1983 ± 17	0.00	0.95	0.00	0.00
		20-40	1405 ± 30	977 ± 49	0.00	0.93	0.00	0.01
		40-60	1340 ± 30	1038 ± 51	0.00	0.94	0.00	0.02
		60-80	1295 ± 30, 420 ± 30	1086 ± 51, 1914 ± 9	0.00	0.80	0.00	0.05
	B	Living	-	2007	0.00	0.92	0.00	0.03
		0-20	>Modern	1981 ± 15	0.00	0.88	0.00	0.00
		20-40	>Modern	1979 ± 12	0.00	0.78	0.00	0.00
		40-60	420 ± 30	1930 ± 28	0.00	0.82	0.00	0.00
		60-80	385 ± 30, 305 ± 30	1958 ± 1, 1958 ± 2	0.00	0.81	0.00	0.02
	C	Living	-	2007	0.00	0.94	0.00	0.01
		0-20	>Modern, > Modern	1983 ± 17, 1981 ± 16	0.00	0.87	0.00	0.00
		20-40	>Modern	1975 ± 1, 1975 ± 1	0.00	0.69	0.00	0.01
		40-60	415 ± 30	1930 ± 28	0.00	0.75	0.00	0.02
		60-80	495 ± 30	1899 ± 58	0.00	0.80	0.00	0.03
MAME	A	Living	-	2007	0.00	0.86	0.01	0.07
		0-20	>Modern	1964 ± 1	0.00	0.86	0.00	0.10
		20-40	>Modern, > Modern	1975 ± 1	0.00	0.68	0.00	0.23
		40-60	>Modern	1974 ± 3	0.00	0.70	0.06	0.19
		60-80	>Modern	1975 ± 6	0.00	0.65	0.18	0.11
	B	Living	-	2007	0.00	0.68	0.01	0.15
		0-20	>Modern	1977 ± 6	0.00	0.97	0.00	0.00
		20-40	>Modern	1975 ± 6	0.00	0.92	0.00	0.00
		40-60	260 ± 35	1959 ± 1	0.00	0.95	0.00	0.01
		60-80	330 ± 30, > Modern	1958 ± 1, 1975 ± 6	0.00	0.91	0.00	0.04
	C	Living	-	2007	0.00	0.52	0.00	0.00
		0-20	> Modern	1975 ± 1	0.00	0.55	0.00	0.20
		20-40	> Modern	1968 ± 0	0.00	0.52	0.00	0.38
		40-60	415 ± 30	1931 ± 28	0.00	0.65	0.00	0.29
		60-80	435 ± 30, 400 ± 30	1926 ± 31, 1933 ± 26	0.00	0.56	0.00	0.35

Lagoonal sites

			Radiocarbon results		Species proportions			
Site	Pit	Horizon	14Cyr	Calendar age	*A.cerv*	*A.tenu*	*M.mira*	*P.furc*
BVTRA	A	Living	-	2007	0.00	0.19	0.00	0.04
		0-20	> Modern, > Modern	1963 ± 0, 1967 ± 0	0.00	0.81	0.02	0.13
		20-40	420 ± 30	1930 ± 28	0.00	0.94	0.00	0.02
		40-60	370 ± 30	1936 ± 23	0.00	0.86	0.00	0.05
		60-80	485 ± 30, 430 ± 30	1900 ± 57, 1927 ± 30	0.00	0.86	0.00	0.02
	B	Living	-	2007	0.00	0.02	0.78	0.00
		0-20	415 ± 30	1931 ± 28	0.00	0.23	0.06	0.45
		20-40	405 ± 30	1932 ± 27	0.00	0.33	0.07	0.37
		40-60	425 ± 30	1931 ± 26	0.00	0.40	0.10	0.12
		60-80	450 ± 30	1908 ± 49	0.00	0.20	0.05	0.06
	C	Living	-	2007	0.00	0.14	0.43	0.00
		0-20	>Modern	1975 ± 1	0.00	0.13	0.32	0.30
		20-40	420 ± 35, 415 ± 30	1927 ± 32, 1930 ± 28	0.01	0.25	0.47	0.13
		40-60	455 ± 35	1908 ± 49	0.00	0.78	0.09	0.09
		60-80	445 ± 30, 440 ± 30	1925 ± 32, 1927 ± 30	0.00	0.72	0.04	0.12

Table 2.3. Bocas del Toro. Calendar dates AD by horizon and reef environment from calibration of radiocarbon ages.

Offshore sites

Horizon	Number fragments dated	Number coeval samples	Age range (AD) of coeval samples
0-20	9	6	1966 - 1996
20-40	11	6	1966 - 1996
40-60	11	5	1966 - 1996
60-80	14	3	1911 - 1959

Lagoonal sites

Horizon	Number fragments dated	Number coeval samples	Age range (AD) of coeval samples
0-20	9	6	1844 - 1957
20-40	13	8	1905 - 1960
40-60	12	5	1814 - 1957
60-80	14	7	1762 - 1959

Table 2.4. Costa Arriba. Calendar dates AD by horizon and reef environment from calibration of radiocarbon ages.

Offshore sites

Horizon	Number fragments dated	Number coeval samples	Age range (AD) of coeval samples
0-20	7	5	1966 - 2000
20-40	7	5	1967 - 1991
40-60	6	4	1902 - 1959
60-80	10	3	1841 - 1959

Lagoonal sites

Horizon	Number fragments dated	Number coeval samples	Age range (AD) of coeval samples
0-20	4	1	1903 - 1959
20-40	4	3	1902 - 1959
40-60	3	3	1859 - 1957
60-80	5	3	1843 - 1958

Table 2.5. Coral species categories recorded in each time horizon, for taxa reported in Bocas del Toro (Guzman and Guevara) or Costa Arriba (Cubit and Williams 1983, Guzman 2003). * = species previously recorded in Bocas del Toro only, † = species previously recorded in Costa Arriba only.

	Bocas del Toro					Costa Arriba				
Species	Living	0-20	20-40	40-60	60-80	Living	0-20	20-40	40-60	60-80
Acropora cervicornis	+	+	+	+	+		+	+	+	+
Acropora palmata							+			+
Acropora prolifera *										
Agarica agaricites spp	+	+	+	+	+	+	+	+	+	+
Agaricia fragilis										
Agaricia humilis	+	+	+	+			+	+		
Agaricia lamarcki	+									
Agaricia tenufolia	+	+	+	+	+	+	+	+	+	+
Colpophyllia natans	+	+	+	+	+	+	+	+	+	+
Dichocoenia stokesi					+	+				
Diploria clivosa/strigosa		+	+	+	+					
Diploria labyrinthiformis		+	+	+	+					
Eusmilia fastigiata		+	+	+	+	+	+	+	+	+
Favia fragum	+	+	+	+	+		+	+	+	+
Helioceris cucullata	+	+	+	+	+	+	+	+	+	+
Isophyllastrea rigidia / Isophyllia sinuosa	+		+	+	+					
Madracis decactis	+	+	+	+	+	+	+	+		+
Madracis mirabilis	+	+	+	+	+	+	+	+	+	+
Madracis other	+	+	+		+	+				
Manicina spp	+	+	+	+	+		+	+	+	+
Meandrina spp	+	+		+		+	+	+		
Millepora spp	+	+	+	+	+	+	+	+	+	+
Montastrea annularis spp	+	+	+	+	+	+	+	+	+	+
Montastrea cavernosa	+	+	+	+	+	+				
Mussa angulosa		+	+	+	+					
Mycetophyllia spp	+	+	+	+	+			+	+	+
Oculina spp	+	+	+	+	+	+	+	+	+	+
Porites astreoides	+	+	+	+	+	+	+	+	+	+
Porites branneri †										
Porites colonensis		+		+			+	+	+	+
Porites furcata/divaricata/porites	+	+	+	+	+	+	+	+	+	+
Scolymia spp	+	+	+	+	+		+	+	+	+
Siderastrea spp	+	+	+	+	+	+	+	+	+	+
Solenastrea spp										
Stephanocoenia intercepta	+	+	+	+	+	+	+	+	+	+
Undaria spp / juvenile *Agaricia*	+	+	+	+	+	+	+	+	+	+
Total	25	28	27	28	27	19	23	23	20	22
Median/pit	8	13.5	15.5	16	15.5	10	9	12	10	12
Mean/pit	7.9	13.9	15.5	15.7	15.6	8.4	11.6	12.4	11.3	12.9

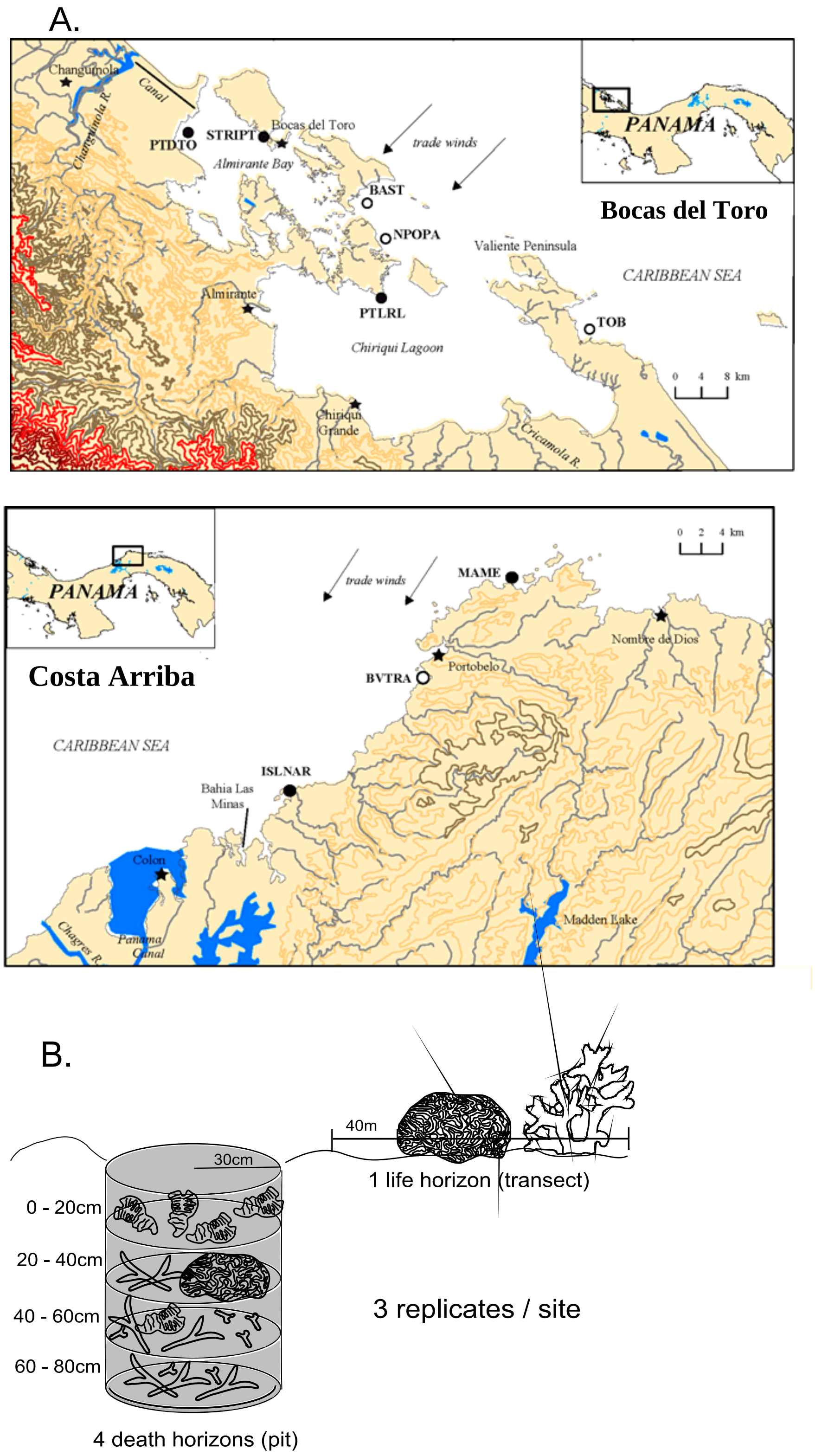


Figure 2.1. Sampling design. (A) regions and reef sites, (B) pits and transects. Open circles represent offshore reef sites and closed circles represent lagoonal reef sites.

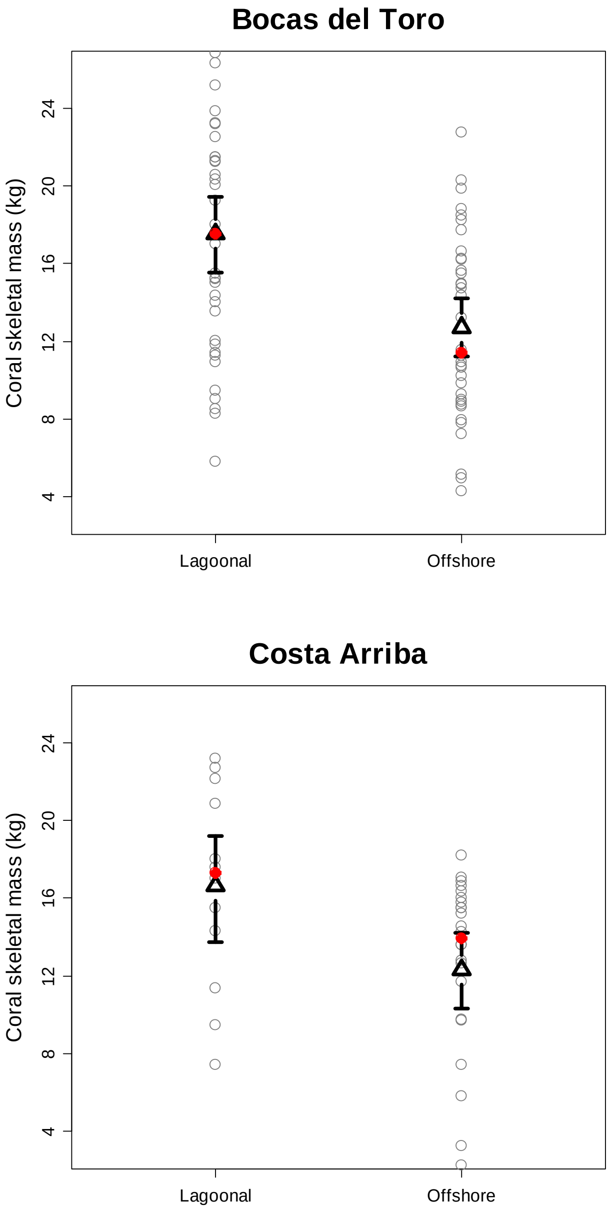


Figure 2.2. Total mass of coral rubble analyzed for offshore and lagoonal sites. Open circle = individual pit, triangle = mean, closed circle = median, black bars = 95% bootstrapped confidence intervals.

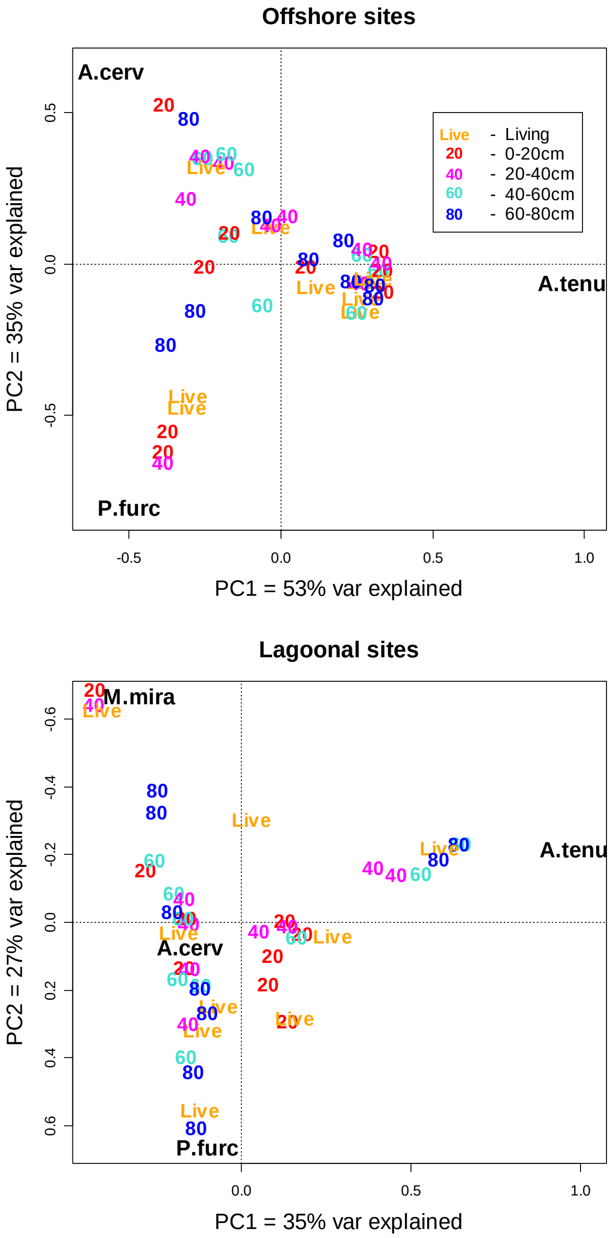


Figure 2.3. Bocas del Toro. Principal Components Analysis of species proportions, offshore and lagoonal sites. Data points represent an individual horizon from an individual pit.

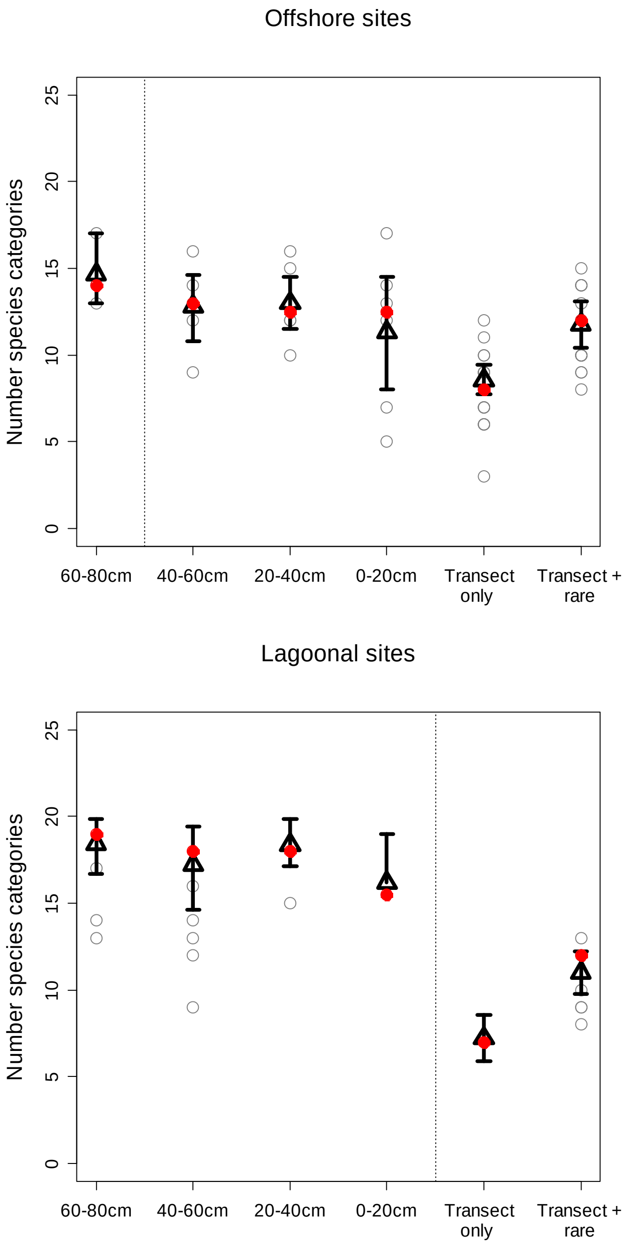


Figure 2.4. Bocas del Toro. Species richness by time horizon. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Richness for living assemblage represented by point-intercept transect survey only and by point-intercept transect survey combined with additional survey for rare species. Horizons to left of dotted line are pre-1960.

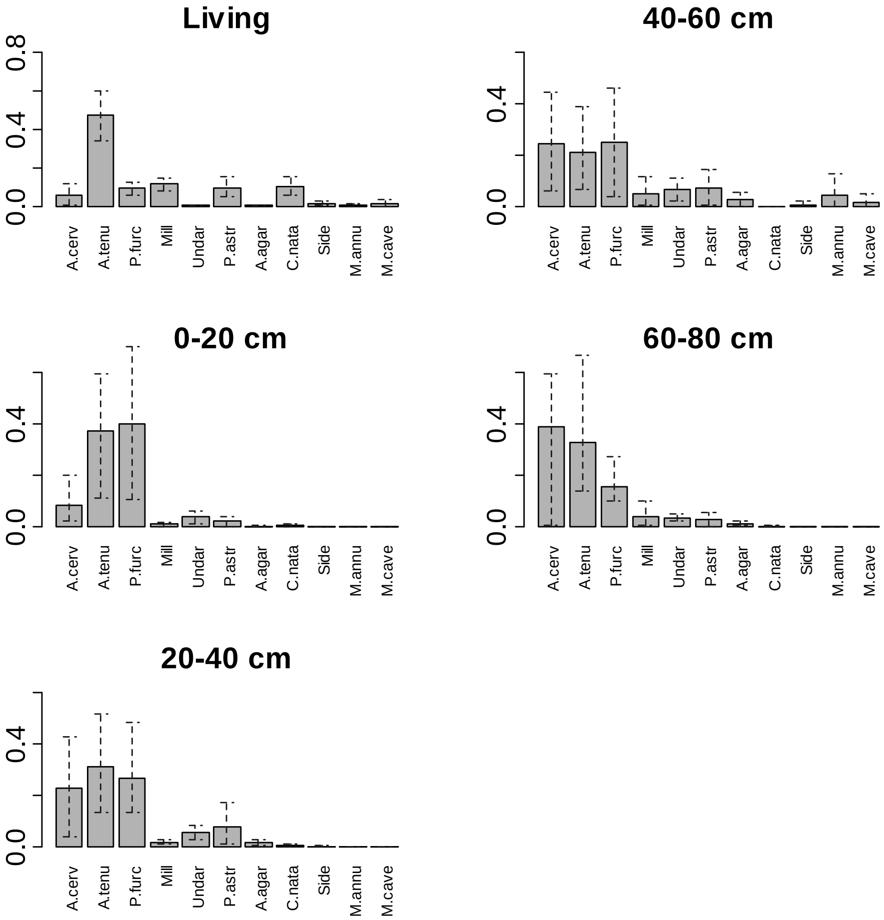


Figure 2.5. Offshore sites, Bocas del Toro. Mean relative abundance (proportion total weight) of species comprising at least 1% of community at any one time horizon. Dashed bars are 95% bootstrapped confidence intervals. Years for death horizons are median calibrated radiocarbon dates with bootstrapped 95% confidence interval for the median.

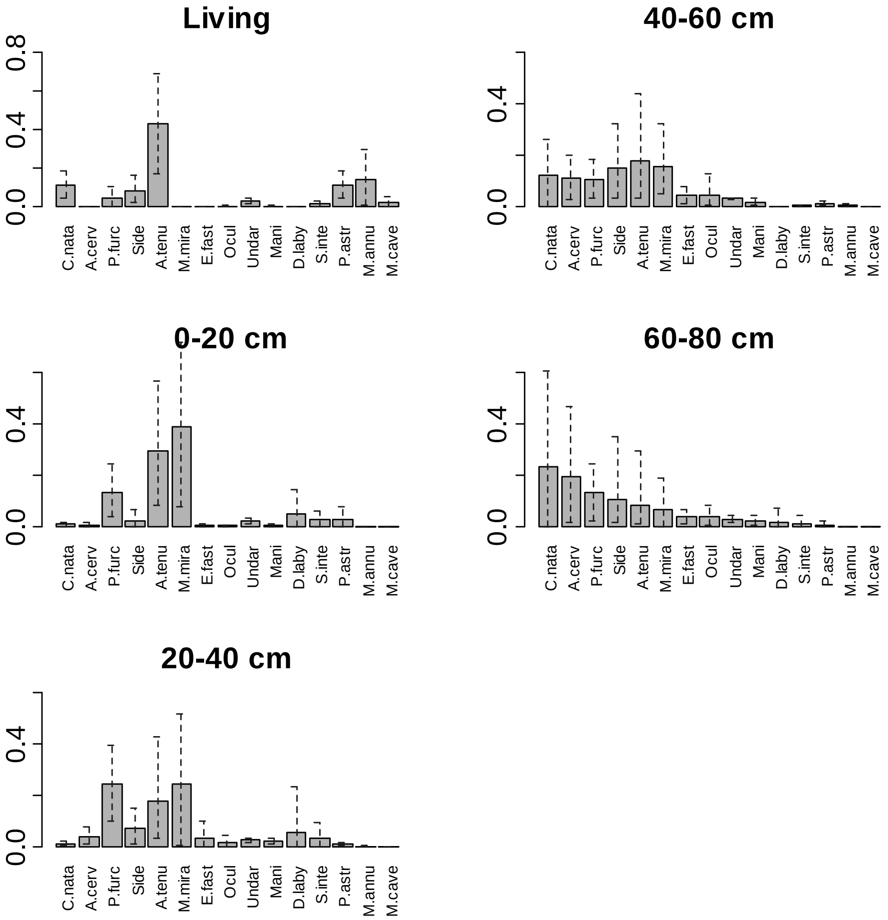


Figure 2.6. Lagoonal sites, Bocas del Toro. Mean relative abundance (proportion total weight) of species comprising at least 1% of community at any one time horizon. Dashed bars are 95% bootstrapped confidence interval. Years for death horizons are median calibrated radiocarbon dates with bootstrapped 95% confidence interval for the median.

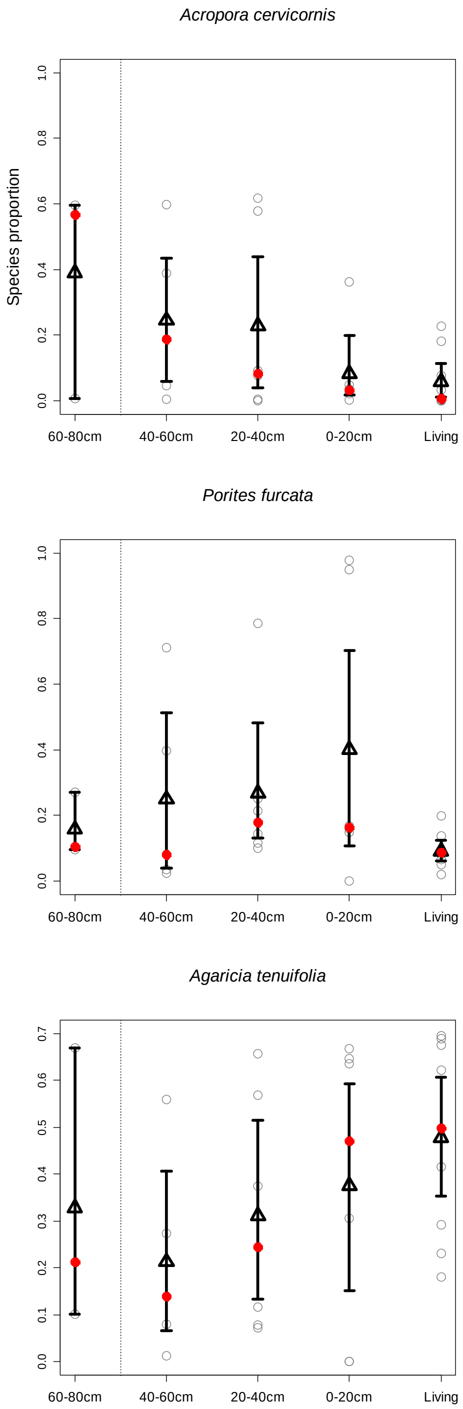


Figure 2.7. Offshore sites, Bocas del Toro. Relative abundance of dominant species over time. Open circle = individual pit, triangle = mean, closed circle = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of vertical line are pre-1960.

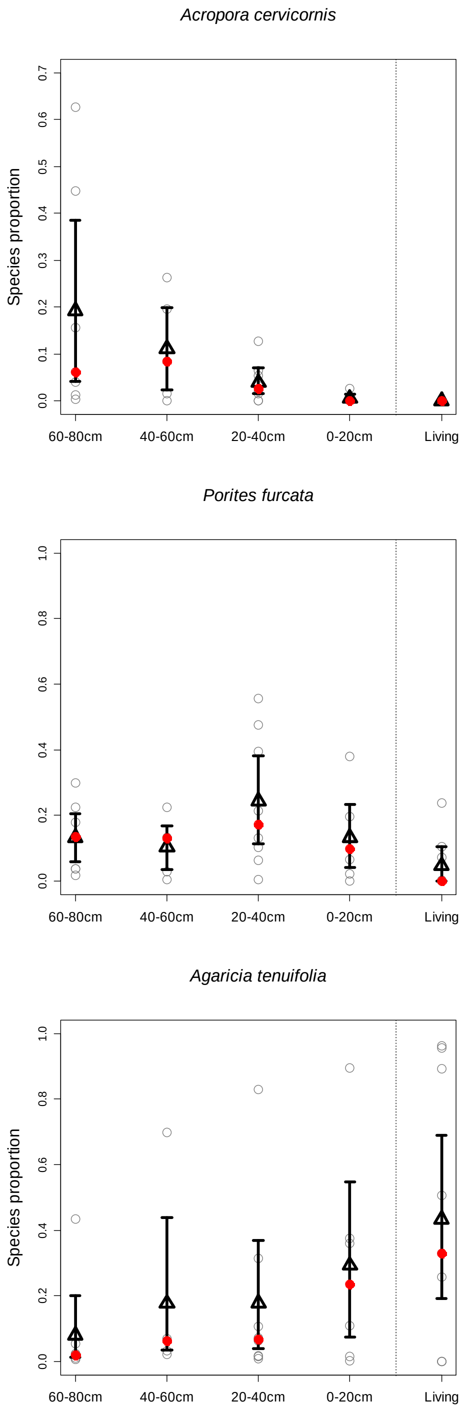


Figure 2.8. Lagoonal sites, Bocas del Toro. Relative abundance of dominant species over time. Open circle = individual pit, triangle = mean, closed circle = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of vertical line are pre-1960.

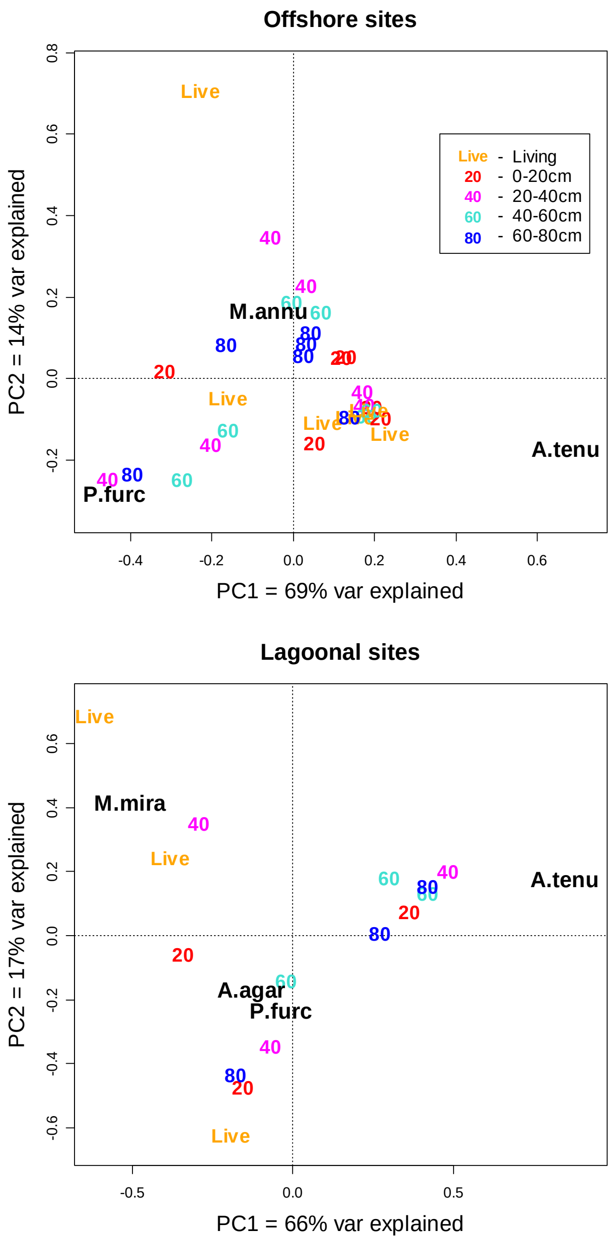
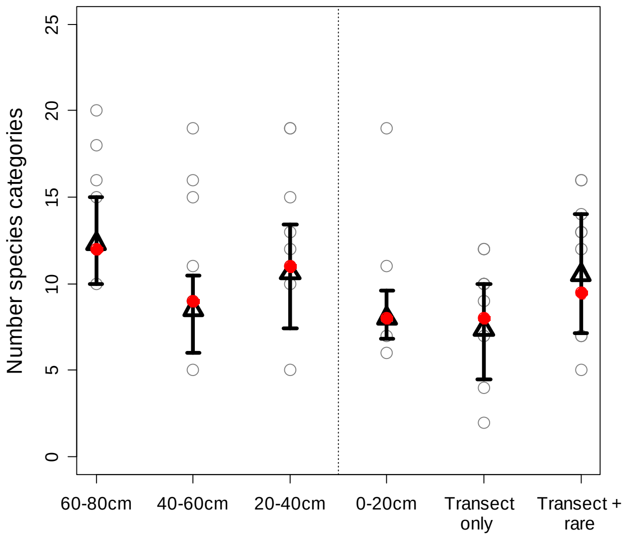


Figure 2.9. Costa Arriba. Principal Components Analysis of species proportions, offshore sites and lagoonal sites. Data points represent an individual horizon from an individual pit.

Offshore sites



Lagoonal sites

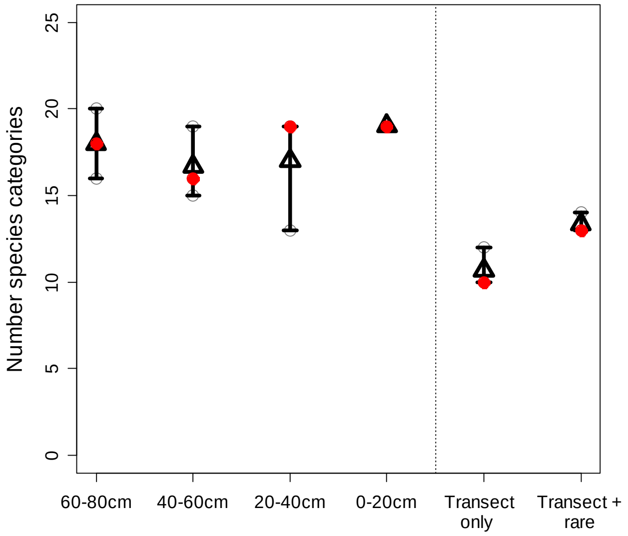


Figure 2.10. Costa Arriba. Species richness by time horizon. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960.

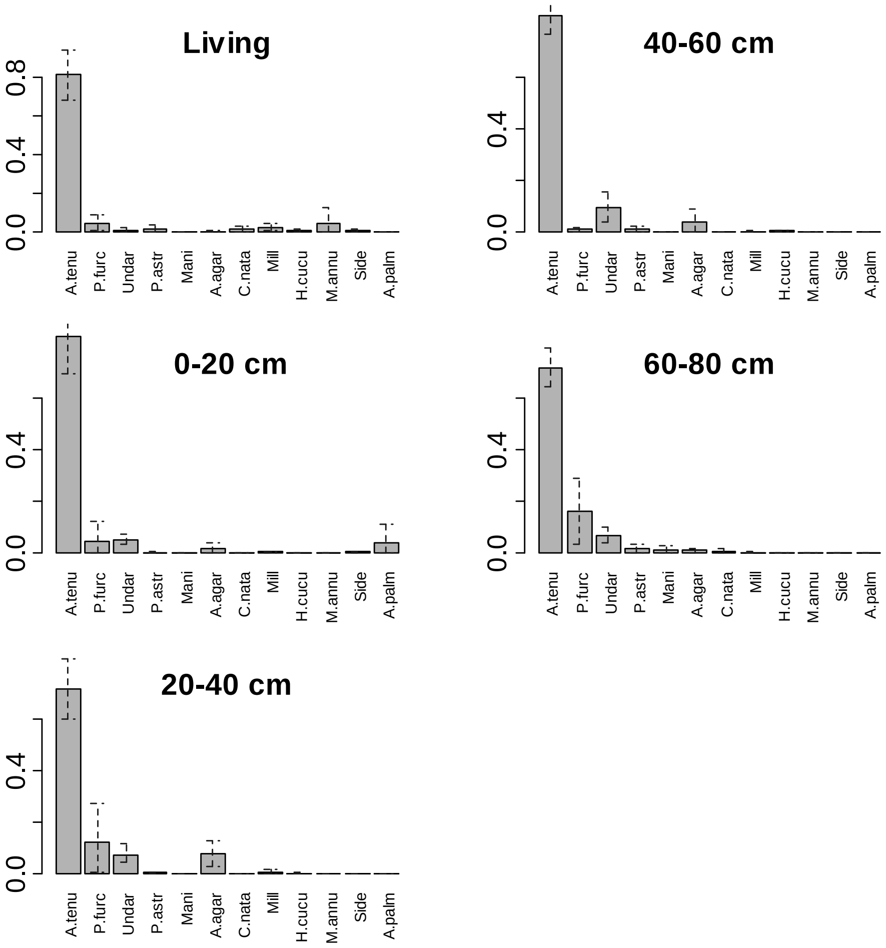


Figure 2.11. Offshore sites, Costa Arriba. Mean relative abundance (proportion total weight) of species comprising at least 1% of community at any one time horizon. Dashed bars are 95% bootstrapped confidence intervals. Years for death horizons are median calibrated radiocarbon dates with bootstrapped 95% confidence interval for the median.

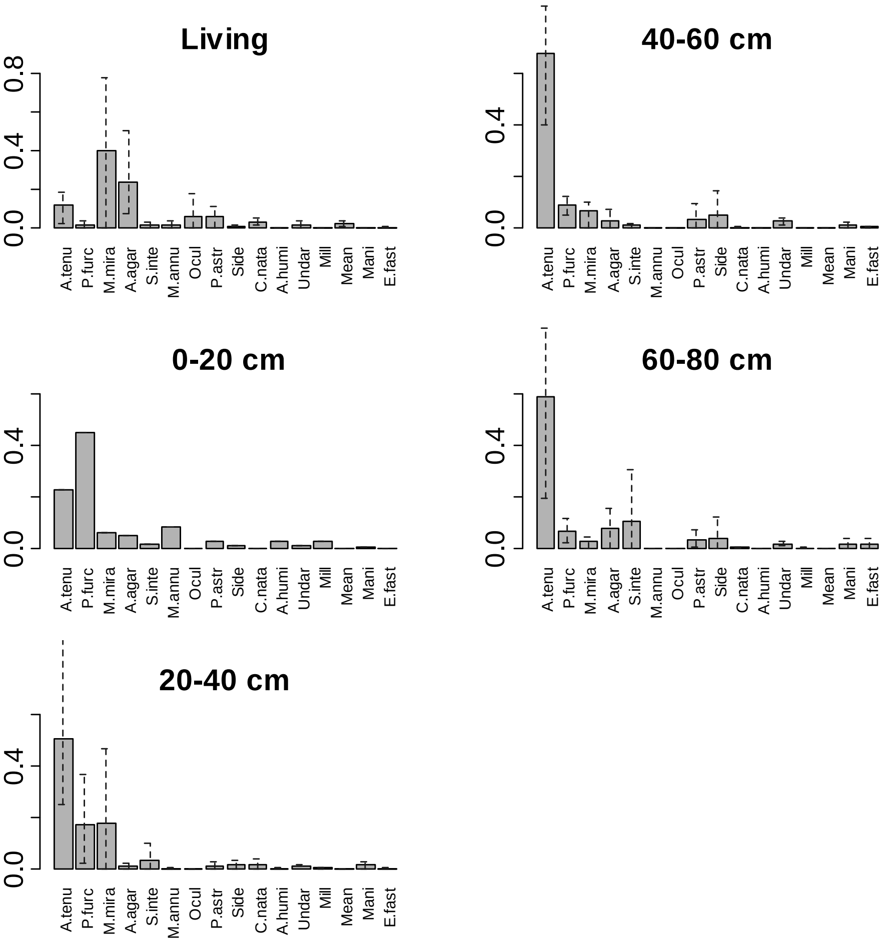


Figure 2.12. Lagoonal sites, Costa Arriba. Mean relative abundance (proportion total weight) of species comprising at least 1% of community at any one time horizon. Dashed bars are 95% bootstrapped confidence intervals. No confidence intervals for 0-20 horizon because is just one replicate.

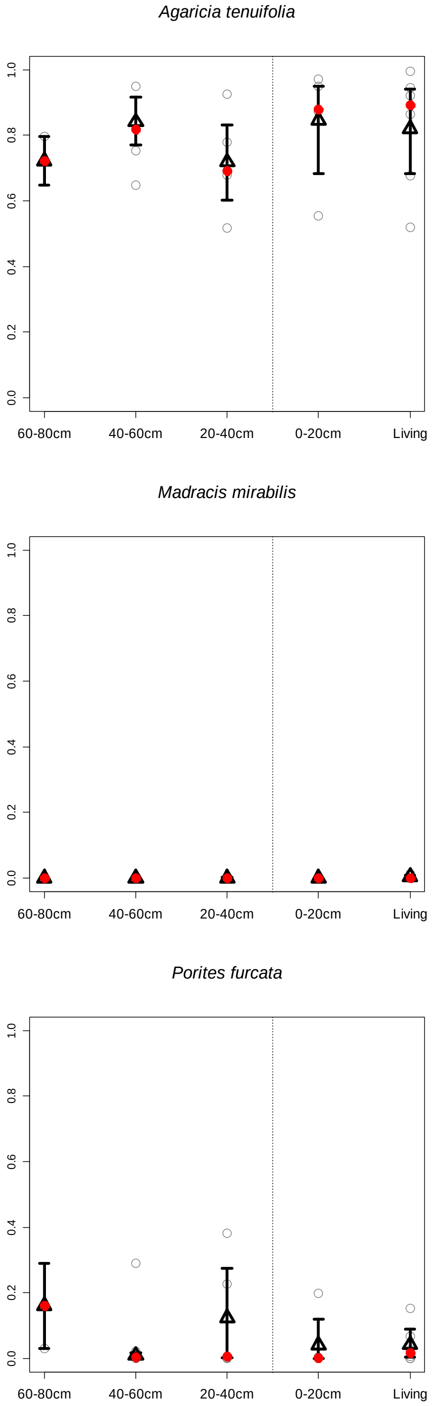


Figure 2.13. Offshore sites, Costa Arriba. Relative abundance of dominant species over time. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of vertical line are pre-1960.

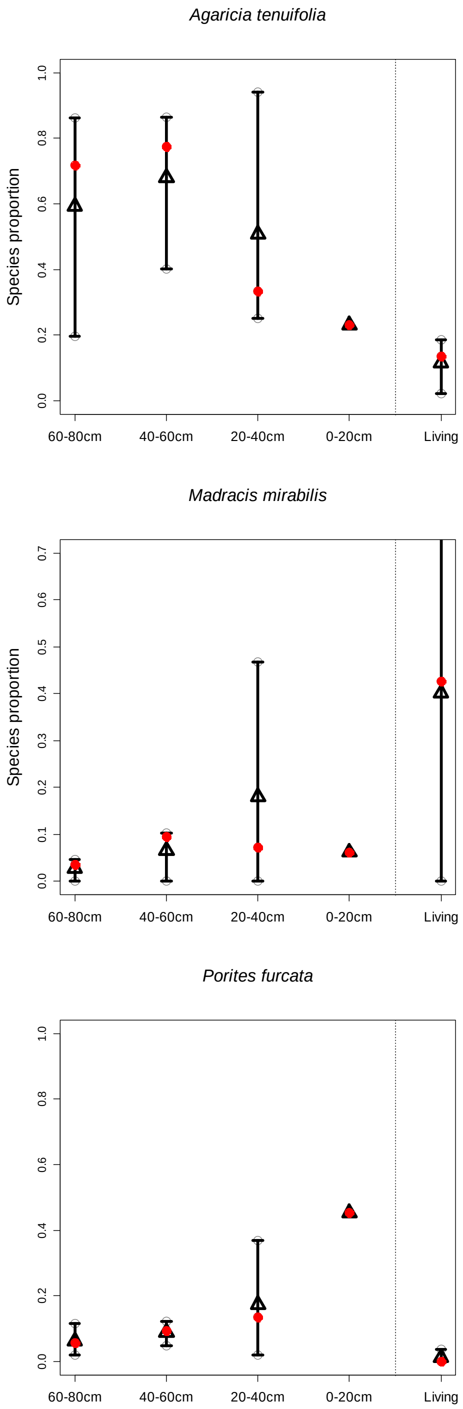


Figure 2.14. Lagoonal sites, Costa Arriba. Relative abundance of dominant species over time. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of vertical line are pre-1960.

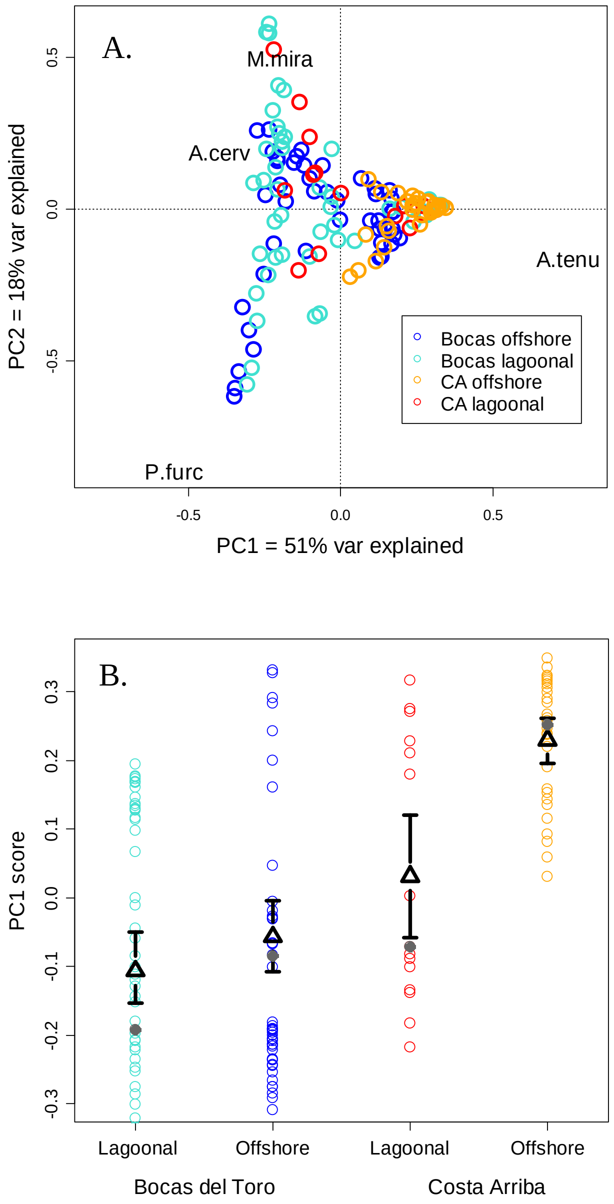


Figure 2.15. Bocas del Toro and Costa Arriba. A) Principal Components Analysis of species proportions, B) Scores for first principal component by region and environment, with triangle = mean score, bars = 95% bootstrapped CIs, grey dot = median score. Open circles represent an individual horizon from an individual pit.

CHAPTER 3: HISTORICAL CHANGE IN CORAL REEF BIVALVE AND GASTROPOD COMMUNITIES IN CARIBBEAN PANAMA

ABSTRACT

Caribbean coral reefs have undergone dramatic changes since the 1970s, including a large-scale loss of corals that has been widely attributed to human activities such as fishing, land-based pollution, and climate change. Because the known timeline of change on reefs is restricted to the past few decades, the relative role of these human-caused activities is unresolved. I used paleontological sampling techniques to extend the timeline of ecological change on reefs into the historical past by analyzing changes in coral reef molluscan death assemblages that extend back as far as 150 years. I sampled gastropod and bivalve death assemblages from pits excavated on reefs spanning a gradient of influence from land-based runoff and from human disturbances. Taxonomic and functional group composition was assessed from four death horizons extracted from pits dug underneath the living reef at 5m water depth from offshore and lagoonal sites in Boas del Toro and Costa Arriba in Caribbean Panama. The variation in molluscan taxonomic and functional groups over reef environments and regions varied primarily according to gradients in wave exposure and influence from terrestrial runoff. Temporal changes in the size and trophic structure of gastropod and bivalve communities indicated increased environmental stress extending back to the beginning of the time series. Taxonomic composition of mollusk communities was relatively stable throughout the time period, with two notable exceptions. A noticeable decline in the frond oyster *Dendostea frons* at reef sites in Bocas del Toro indicated a large-scale and previously

undocumented loss of its gorgonian and scleractinian coral hosts. A decline in the relative abundance and individual size of the conch *Strombus* spp. represented its historical over-exploitation in Costa Arriba. Changes in mollusk communities were less apparent in Costa Arriba, possibly due to the lower sampling effort and/or older history of human disturbance in this region.

INTRODUCTION

Caribbean coral reefs have undergone dramatic changes over historical time, including a loss of coral reef megafauna beginning centuries to millennia ago (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003) and a loss of architectural species such as corals documented since systematic ecological studies began in the 1970s (Gardner et al. 2003). Changes have been attributed to multiple human activities, including fishing, land-based pollution, and climate change (Keller and Jackson 1993, Jackson et al. 2001, Hughes et al. 2003, Fabricius 2005). Because the known timeline of change on reefs is restricted to the past few decades and because multiple human-caused disturbances are acting on reefs simultaneously, the relative role of these human-caused activities is unresolved (Hughes et al. 2003). It is impossible to understand the causes of the recent ecological change on Caribbean reefs without a more accurate ecological baseline of reef communities and environments from a time period predating large-scale human disturbances.

Bivalve and gastropod mollusks are abundant and diverse components of Caribbean coral reefs that have a variety of documented life habits, making them ideal indicators of coral reef environmental conditions (Todd 2001, Todd et al. 2002).

Gastropod and bivalve community compositions have been successfully utilized to infer environmental gradients in coral reef and seagrass habitats across space (Jackson 1972, 1973, Heck 1977, McClanahan 1992, McClanahan 2002a) and over geological (Todd et al. 2002, Allmon 2001) and ecological timescales (McClanahan 2002b).

The dominant feeding habits and substrate relationships exhibited by gastropods and bivalves can be used to assess various aspects of the reef environment including wave action, ecological stress, relative amount of planktonic and benthic productivity, and relative amount of hard and soft substrates. For gastropods, the dominant feeding type (carnivorous, herbivorous, suspension feeder) serves as an indicator of reef productivity and/or environmental stress. An herbivore-dominated trophic structure may signify high benthic algal productivity (Russ 2003), and short or simplified (herbivore-dominated) food chains may signify environmental stress (Odum 1985, McClanahan 1992) and/or removal of carnivorous forms via fishing. Conversely, a carnivore-dominated trophic structure may be an indication of relatively lower benthic algal productivity, lower environmental stress, and/or lower fishing pressure. A gastropod community with a prevalence of suspension feeders is an indication of high current or wave action and/or planktonic productivity (Levinton 1991, Birkeland 1987, 1988).

The dominant bivalve feeding type (suspension feeding, deposit feeding, or chemosymbiotic deposit feeding) is an indicator of water motion, amount of suspended sediments and organic matter, and/or reef productivity. As with gastropods, suspension feeding bivalves are more dominant in environments with high nutrient levels and planktonic productivity and with sufficient water motion for filtering planktonic prey (Birkeland 1987, 1988, Vermeij 1990). Dominance by deposit feeders signifies low-flow conditions and/or a relatively high abundance of particulate organic material on the reef benthos (Sanders 1958, Jackson 1972, Arruda et al. 2003) and possibly lower overall primary productivity (Birkeland 1987, 1988, Vermeij 1990). The prevalence of burrowing chemosymbiotic deposit feeders is an indication of low oxygen, reducing sediment environments which are associated with water stagnation and/or high concentrations of organic matter on the reef (Jackson 1972, 1973).

The dominant bivalve substrate relationship (epifaunal or infaunal) is an indicator of substrate type, water motion, and/or ecological stress on a reef. Dominance by epifaunal bivalves is an indication of high (live or dead) coral cover (Hauser et al. 2007, Harries and Sorauf 2010), while dominance by infaunal bivalves is an indication of high sediment and low coral cover (Leonard-Pingle et al. *in review*). Dominance by infaunal bivalves may also occur in high water-motion environments where burrowing into sediments is required to maintain stability. Dominance by these forms may also be an indication of stressful environmental conditions above the sediment-water interface, such as fluctuating oxygen concentrations, temperature, and/or salinity (Jackson 1972, 1973).

The abundance, size structure, and species richness of bivalves and gastropods are additional reliable indicators of reef environmental conditions. Within a habitat, environments with continuous or pulsed disturbances are generally composed of smaller species with short life cycles and high colonization rates (Odum 1985, Birkeland 1987). For bivalves in particular, higher environmental stress tends to result in smaller size classes of the epifaunal community and to larger size classes of the infaunal community. This pattern is due in part to the selection for smaller, rapidly-colonizing epifaunal forms and larger, quickly- and deeply-burrowing infaunal forms under high stress conditions

(Jackson 1972, 1973). Smaller gastropod and bivalve size structures can also result from prolonged human exploitation of these communities that disproportionately affect larger individuals (Hockey and Bosman 1986, de Boer et al. 2000).

I analyzed attributes of the taxonomic and functional group composition as well as the size structure of gastropod and bivalve death assemblages to investigate spatial and temporal variability in coral reef environments in Caribbean Panama spanning the past 150 years. Gastropod and bivalve shells were collected from sediments excavated from 80cm-deep pits underneath modern reefs that extended back to the mid-19th century. These data were utilized to provide a more accurate historical baseline of Caribbean coral reef environments in order to relate patterns observed in coral communities over historical time to human-caused environmental changes occurring during this period. These data were collected over natural and human-caused reef environmental gradients. Variability across environmental gradients was assessed to determine the reliability of molluscan community structure as an environmental proxy, while variability over time was assessed to determine the timing and magnitude of change due to human-caused disturbances. Together, the reconstruction of the molluscan and coral communities over the past 50-150 years in Caribbean Panama will provide a more complete picture of biological and environmental change on reefs during a time of increasing human disturbance. This study will also serve as the first complete description of modern coral reef gastropod and bivalve communities from the western and central coasts of Caribbean Panama.

METHODS

DATA COLLECTION

Bivalve and gastropod death assemblages were sampled from the Bocas del Toro region along the western coast of Caribbean Panama and from the Costa Arriba region along the central coast of Caribbean Panama. These regions have an extensive history of human exploitation and disturbance of coastal environments extending back at least 1000 years (Roberts 1827, Drolet 1980, Linares 1980, Gordon 1982, Pandolfi et al. 2003, Guzman 2003). Shells were collected from nine reef sites total, six from Bocas del Toro and three from Costa Arriba (Figure 2.1a). Reefs were selected to represent a range of environmental conditions, from lagoonal environments influenced by moderate to substantial amounts of river runoff to offshore environments more influenced by oceanic conditions including seasonally strong wind and wave action. Of the six reef sites from Bocas del Toro, three (STRIPT, PTDTO, PTLRL) were located in lagoonal environments and three (BAST, NPOPA, TOB) were located in semi-exposed offshore reef environments. Of the three reef sites from Costa Arriba, one was located in a lagoonal environment (BVTRA) and two (ISLNAR, MAME) were located in semi-exposed offshore environments. Lagoonal sites in both regions are exposed to greater annual variability in salinity and water temperature than offshore sites (Heck 1977, D’Croz et al. 2005). Due to its more direct exposure to the tradewinds, the Costa Arriba region experiences heavier wave action than Bocas del Toro (Cubit et al. 1989, Guzmán 2003). Although reef sites were separated into two distinct “offshore/lagoonal” categories, sites actually spanned a range of exposure to wind and wave action, with Costa Arriba offshore sites experiencing the highest wind and wave exposure and Bocas del Toro lagoonal sites experiencing the least exposure.

Bivalve and gastropod shells were collected by excavating four approximately 20cm-thick layers from a 60cm-diamter circular pit (Figure 2.1b). Pits were excavated from patches with little or no living coral and were adjacent to modern reef areas with living coral cover. Three replicate pits were excavated from each reef site. Excavations were carried out with the aid of a circular metal frame to prevent the collapse of material from outside the pit into the pit. Shells were extracted along with coral rubble with small gardening shovels and ice scoopers and placed into bottomless buckets lined with 7mm mesh netting to retain the >7mm fraction. Due to the dense packing of coral and mollusk material, however, many shells <7mm were retained in the samples and included in the data presented here. Material was extracted from four distinct layers extending down to 80cm below the reef surface: 0-20cm, 20-40cm, 40-60cm, and 60-80cm. Each of these 20cm-thick layers was considered a separate *time horizon*.

This sampling scheme allowed for the comparison of spatial and temporal variation in bivalve and gastropod communities. The spatial component of sampling was represented by three nested levels: regions, reef sites, and replicate pits (Figure 2.1). The temporal component of sampling was represented by four time horizons within each pit. Thus, the sampling scheme produced 27 total *replicates*, three from each of nine reef sites sampled total. Each of the 27 replicates was comprised of four time horizons, resulting in 108 separate bivalve and gastropod death assemblages. These assemblages represented the fundamental unit of sampling, hereafter called *samples*.

MOLLUSK DATA

Gastropod and bivalve shells were identified to species, subgenus, or genus level, resulting in a total of 88 gastropod and 78 bivalve taxonomic groupings. Of these groupings, hereafter called *species*, 32% was identified to species level for gastropods and 49% was identified to species level for bivalves (Tables 1-4). The abundance of gastropod and bivalve species was calculated in two ways: (1) by shell weight, and (2) by number of individual shells. Weight was computed from all shell pieces that could be positively identified to at least the genus level. The number of individuals was calculated by including only shells with an apex and/or aperture for gastropods and by including shells with a hinge for bivalves. These methods resulted in an estimate of the maximum number of individuals for each sample. Because the number of individuals was not uniform among samples, death assemblages were represented by the relative abundance of each species computed from the fraction total weight and from the fraction total individuals. For simplicity and because species proportions were similar when computed from weights and from counts of individuals, only the results from the latter will be presented here. The average weight of an individual was computed for each sample by dividing the total weight of individuals by the total number of individuals.

In order to assess environmental gradients on reef sites over space and time, species were combined into functional groups according to their feeding habits and substrate relationships as defined in Todd (2001). For gastropods, species were grouped into one of four diet categories: herbivore, carnivore, omnivore, or suspension feeder. For bivalves, species were grouped into one of three diet categories (suspension feeder, deposit feeder, chemosymbiotic deposit feeder) and one of five substrate relationship categories (epifaunal, infaunal, epifunal/infaunal, active borer within hard substrates, nestler on or within hard substrates). For species and functional group proportions, relative abundance was computed by proportion individuals and compared between time horizons, reef environments, and sampling regions.

STATISTICAL ANALYSES

Due to non-normality and heteroskedasticity of data, a combination of non-parametric statistics was used to investigate trends in abundance, richness, and species proportions over time and space. For all analyses, the unit of sampling was a single time horizon within a single replicate or pit, resulting in 6 sites x 3 pits x 4 time horizons = 72 samples total for Bocas del Toro, and 3 sites x 3 pits x 4 time horizons = 36 samples total for Costa Arriba. Trends in species proportions among time horizons was assessed for species that comprised ≥ 10% of the community on average in at least one time horizon. Temporal trends in species proportions, richness, and abundance over the entire time series (i.e. four time horizons) were assessed using the Kruskal-Wallis one-way ANOVA of ranked means. For measures that showed significant trends over the entire time series, post-hoc comparisons between individual horizons were conducted using a bootstrapping procedure that computed the probability that distributions of the measure of interested were significantly different from each other (Efron and Tibshirani 1986). The bootstrapping procedure also produced 95% confidence intervals for the mean value of the measure of interest. The boostrapping procedure was also used to assess statistical differences in bivalve and gastropod richness and abundance between reef environments.

Statistical differences in the entire bivalve and gastropod communities between regions and reef environments were assessed by computing the Bray-Curtis dissimilarity value and using the Analysis of Similarity (ANOSIM) procedure, a permutation test that compares within- versus between-group differences (Clarke 1993). This procedure computed a test statistic R which scales from -1 (within-group similarity << between-group similarity) to +1 (within-group similarity >> between-group similarity). A significance value for R was computed by permuting the data. The comparison of the spatial versus temporal component of community variation was assessed by computing the Bray-Curtis dissimilarity and then using the bootstrapping procedure to test for the difference in dissimilarity over space versus time. For all analyses, statistical significance was determined at the $p = 0.05$ level. All analyses were conducted using the R software package (R Development Core Team 2008).

RADIOCARBON DATIING

Age ranges for mollusk assemblages from each horizon and pit (i.e. sample) were estimated from radiocarbon dating of co-occurring coral material. One or two coral fragments were dated from each sample. Conventional radiocarbon ages were converted to calendar years AD using surface water $\Delta^{14}C$ reconstructions for the Caribbean from either coral or tree ring reference datasets. Post-bomb and pre-bomb radiocarbon dates, corresponding to the period before and after 1960 AD, were readily distinguished and allowed for comparisons of data from horizons on either side of the boundary.

The calibrated age ranges were used to determine whether samples within a given region, reef environment, and death horizon were coeval and could be combined for statistical analyses. Samples were pooled within a horizon only if their age ranges overlapped. For each region, horizon, and environment, the calibrated age range reported was the minimum and maximum possible age of the pooled radiocarbon dates. Horizons were assumed to be in stratigraphic order within individual pits.

POTENTIAL TAPHONOMIC BIASES

The mollusk death assemblages analyzed in this study may contain biases from processes that occurred during the period spanning the death and sampling of shells. Biases would arise if the 20cm-thick horizons within a pit do not represent a chronological sequence, if horizons represent unequal lengths of time, and if horizons to not contain all of their original community components. While the coral material excavated along with the mollusk material was generally encountered as a densely-packed matrix in life position, mollusk shells in general have a greater potential of being vertically mixed than do corals. Bivalve and gastropod shells were in general much smaller than the coral fragments collected, and infaunal bivalve individuals could have burrowed into the sediments and died within a matrix of coral material belonging to an older time period. While this bias is potentially serious, the majority of the bivalve community encountered in these samples was epifaunal forms. The 20cm-thick layers undoubtedly represent a time-averaged assemblage, but there is no reason to expect a systematic difference in averaging among horizons within a reef environment. The issue of preservational biases is probably not serious for the data presented here because it is unlikely that shells could have been completely destroyed within the historical time period sampled.

RESULTS

RADIOCARBON DATES

A total of 93 coral fragments from Bocas del Toro were radiocarbon dated and represented calendar ages that ranged from 1290 AD ± 25 to 2003 ± 3 (Table 1.1) and a total of 46 coral fragments from Costa Arriba were radiocarbon dated and represented calendar ages that ranged from 977AD ± 49 to 1983 AD ± 17 (Table 1.2). The pooling of coeval samples within a horizon resulted in the removal of all post-bomb samples from the 60-80cm layer and allowed for the determination of the 1960AD boundary within the time series for each region and environment. At offshore sites, this boundary was located between the 60-80 and 40-60cm horizons at Bocas del Toro and between the 40-60 and 20-40cm horizons at Costa Arriba. For lagoonal sites, all horizons were older than 1960 at both sampling regions. According to estimates of sediment and rubble accumulation rates from lagoonal environments in Bocas del Toro and Belize (Aronson et al. 2004, Hilbun 2009), the 60-80cm horizon represents an age of 80-140 years. With the exception of one pit from the offshore site ISLNAR in Costa Arriba, calibrated age ranges were largely in chronological order.

GASTROPODS

Gastropod data

The pit excavations produced a total of 13,666 gastropod individuals weighing 5.67 kg from Bocas del Toro and 2134 individuals weighing 1.22 kg from Costa Arriba. For both regions, the variation in gastropod community composition was greater between reef environments (i.e. offshore v lagoonal) than within reef environments (Bocas del Toro: ANOSIM $R = 0.50$, $p < 0.001$; Costa Arriba: ANOSIM $R = 0.50$, $p < 0.001$). For

Bocas del Toro the gastropod community composition was more variable over space (among pits within a single horizon) than over time (among horizons within a single pit) in either reef environment. For Costa Arriba the community composition was significantly more variable over space than time at offshore sites but was statistically equivalent at the lagoonal site (bootstrap tests: $p < 0.05$). These patterns are illustrated in the lack of clustering of samples by time horizon in both regions (Figures 3.3 and 3.9).

Bocas del Toro

A total of 83 gastropod species categories were sampled from Bocas del Toro, with 75 species sampled in offshore sites and 67 species sampled in lagoonal sites (Table 1). The quantity of gastropods was significantly greater at lagoonal sites, as measured by total shell weight and number of individuals (bootstrap tests: $p < 0.01$; Figure 3.1). Although gastropod abundance was greater at lagoonal sites, individual shell weight was significantly greater at offshore sites, indicating a higher dominance of light-shelled gastropods in lagoonal environments and heavier-shelled gastropods in offshore environments (Figure 3.1). Gastropod species richness did not vary between reef environments.

The gastropod communities (as measured by percent individuals) at offshore and lagoonal sites were composed of a small number of dominant species and a large number of rare species (Figure 3.4), a pattern observed in coral reef gastropod communities from other areas of the Caribbean (McClanahan 1992, McClanahan 2002) and western Indian Ocean (McClanahan 2002). Offshore sites contained a greater number of species that comprised $\geq 1\%$ of the community (28 species) compared to lagoonal sites (11 species), indicating greater evenness in population abundance in the offshore environment.

Therefore, although lagoonal environments had greater richness, those species were a more minor community component than at offshore reefs.

Gastropod communities in both reef environments were dominated by the herbivorous snail *Cerithium* spp. (primarily composed of *Cerithium litteratum* and *Cerithium eburneum*), which when averaged over all samples comprised 30% of individuals at offshore sites and 54% of individuals at lagoonal sites (Figure 3.4). This species is typical of more restricted reef environments and surrounding coarse carbonate sediments (Ekdale 1974, Cerridwen and Jones 1991) and is a major component of Caribbean coral reef and seagrass habitats (Jackson 1972, Heck 1977, McClanahan 1992). The remaining two species that comprised ≥5% of individuals at both reef environments were the herbivorous *Hemitoma octoradiata* and *Astraea tecta*. *A. tecta* is commonly found in hard and soft substratum environments such as coral reefs and seagrass beds (McClanahan 1992), while *H.octoradiata* is commonly found in higher energy environments (Glynn 1997) where it is able to graze tough macroalgae and crustose coralline algae growing on hard substrates (Steneck and Watling 1982). The identity of other subdominant species differed between environments, with the herbivorous *Columbella mercatoria* and corallivorous *Coralliophila* spp. important at offshore sites and the herbivorous *Modulus modulus* important at lagoonal sites. *Coralliophila* spp. lives and feeds on hermatypic corals and is indicative of relatively high cover of living coral, and *C. mercatoria* is commonly found in both exposed and restricted reef environments (Ekdale 1974). *M. modulus* is indicative of relatively high turbidity and high productivity environments and is tolerant of salinity fluctuations from freshwater runoff (Houbrick 1980, McClanahan 1992). Therefore, dominant and subdominant members accurately reflected the different hydrodynamic regimes at offshore and lagoonal sites.

The analysis of gastropod communities by diet category revealed an important difference between offshore and lagoonal sites. While all diet categories (carnivorous, herbivorous, omnivorous, suspension feeder) were present at each environment, gastropod richness was dominated by carnivorous species at offshore sites and by herbivorous species at lagoonal sites. Of the species that constituted ≥1% of gastropod individuals on average at one or more horizons, 46% were carnivorous at offshore sites and 27% were carnivorous at lagoonal sites. Although gastropod abundance was dominated by herbivores, a significantly higher proportion of carnivores was present at offshore sites (26% of individuals) compared to lagoonal sites (9% of individuals; bootstrap test: $p < 0.001$). These differences in the dominant diet category may reflect the higher benthic productivity, greater degree of salinity and/or temperature stress (McClanahan 1992), and/or lower habitat complexity (Kohn and Leviten 1976) in lagoonal sites.

Significant changes occurred in the abundance of the gastropod community at lagoonal sites prior to 1960. Between the 60-80 and 20-40cm horizons (pre-1960), the number of individual gastropods significantly increased (K-W $X^2 = 13.7$, $p < 0.001$) and individual shell weight significantly decreased (K-W $X^2 = 9.72$, $p < 0.05$; Figure 3.2). Therefore, the abundance and richness increase at lagoonal sites during this period was due to a disproportionate increase in lighter-shelled (i.e. smaller and/or thinner-shelled) species such as the carnivorous *Bursa*, *Mitra nodulosa*, *Pilsbryspira alboncincta*, the herbivorous *Heliacus bisculatus*, *Smaragdia viridis*, *Zafrona pulchella*, and suspension feeding *Acmaea* spp. and *Cheilea* spp. (Table 1). Species proportions remained stable among time horizons at both reef environments (Figure 3.5). A progressive and nearly statistically significant increase (K-W $X^2 = 7.2$, $p = 0.07$) in the relative abundance of *Cerithium* spp. occurred over time at offshore sites (Figure 3.5a).

The proportion of carnivorous individuals declined progressively and significantly over the time series at offshore sites (K-W $X^2 = 9.16$, $p < 0.05$) but not at lagoonal sites. This decline was driven by the significantly lower proportion of carnivores at the 0-20cm horizon compared to the 60-80cm horizon (bootstrap test: $p < 0.05$; Figure 3.6), indicating a decline between the pre-1960 and post-1960 periods. Therefore, the proportion carnivores at offshore sites declined sometime during this period until by the end of the 21st century it was statistically equivalent to the proportion carnivores in the earliest horizon at lagoonal sites (Figure 3.6; bootstrap test: $p < 0.05$). The decline in proportion carnivorous individuals at offshore sites was accompanied by a nearly significant increase in herbivorous individuals during the same time period (K-W $X^2 = 6.9$, $p = 0.08$). As these species are not harvested for consumption (Carpenter 2002), the change in trophic structure signaled a change in reef environment rather than a response to fishing pressure. The proportion omnivores and suspension feeders did not show any significant trends over the time series.

In order to relate temporal trends in gastropod community size structure to trends in trophic structure, individual shell weight was computed separately for each feeding type. No trends were found over the time series for average shell weight for carnivores, herbivores, omnivores, or suspension feeders, signifying that the decline in individual shell weight at lagoonal sites was due to a loss of the relatively larger carnivores and did not involve a decline in size of remaining carnivores. The greater weight on average of carnivores is responsible for the higher individual shell weight at offshore sites, which had a greater proportion of carnivorous individuals.

Costa Arriba

A total of 88 species categories were sampled in any of the time horizons, with 58 species sampled in offshore sites and 55 species sampled in lagoonal sites (Table 2). As in Bocas del Toro, gastropod abundance measured by total weight and number of individuals was greater at lagoonal sites than at offshore sites (Figure 3.7). Neither gastropod richness nor average shell weight varied between reef environments.

As in Bocas del Toro, the gastropod community was composed of a small number of abundant and a large number of rare species, and offshore sites contained a greater number of species that comprised ≥ 1% of the community (34 species) compared to lagoonal sites (24 species), indicating greater evenness in population abundance at offshore sites (Figure 3.10).

Also similar to Bocas del Toro, both reef environments were dominated by the herbivorous snail *Cerithium* spp. This species comprised an average of 21% of individuals at offshore sites and 42% of individuals at lagoonal sites (Figures 3.10,3.11). Dominance by this species was less at offshore sites in Costa Arriba than at the lagoonal site in Costa Arriba or in either environment in Bocas del Toro. In both Costa Arriba reef environments, two species comprised ≥5% of individuals, the corallivorous snail *Coralliophila* spp. and the herbivorous conch *Strombus* spp. Other subdominant species included the suspension feeding snails *Turritella* spp. and *Cheilea* spp. and the carnivorous snail *Bailya* spp. at offshore sites and the herbivorous snail *Astraea tecta* at lagoonal sites only (Figures 3.10, 3.11). The importance of suspension feeding gastropods at offshore sites is an indication of the relatively higher energy (Sanders 1958, Levinton 1991) and/or higher planktonic productivity in this environment (Birkeland 1987, 1988). The greater relative abundance of *Strombus* spp. at offshore sites may be due to the relatively lower levels of fishing pressure resulting from the lower accessibility of these more turbulent reefs. Although this species has been over-exploited throughout the Caribbean (Stoner 1996, Appeldoorn 1996), including in Bocas del Toro (Tewfik and Guzman 2003), rough waters may provide a refuge from fishing since it is caught primarily by free-diving in Panama (Martans 1996). The greater importance of the algae/detritus-eating and coral and seagrass dwelling *Astrea tecta* and *Cerithium* spp. (McClanachan 1992, Jackson 1973) at the lagoonal site is an indication of relatively higher benthic productivity there.

The gastropod functional group composition did not vary between reef environments in Costa Arriba as much as it did in Bocas del Toro. The percent of carnivorous species comprising ≥ 1% of individuals at any horizon was greater at offshore sites (46%) than at lagoonal sites (36%). However, the proportion of *individuals* that were carnivores was not significantly different between offshore sites (37%) and lagoonal sites (31%). This pattern may reflect the smaller difference in hydrodynamic conditions between offshore and lagoonal sites along the relatively more exposed coastline of Costa Arriba.

Significant temporal trends occurred in gastropod weight and abundance at the $p = 0.1$ level. Although a progressive increase in total weight and abundance is apparent at the lagoonal site, the number of coeval replicates (1-3) at this site provided very low statistical power for assessing trends (Figure 3.8). Declines in total weight and number of individuals occurred over the time series at offshore sites (total weight: K-W $X^2 = 6.7$, $p = 0.08$, average shell weight: K-W $X^2 = 6.4$, $p < 0.09$), driven by a significant decline in both measures between pre-1960 and post-1960 horizons (bootstrap test: $p < 0.05$; Figure 3.8).

Species proportions remained stable among the time horizons at both reef environments (Figure 3.11). A generally progressive but non-significant decrease in the relative abundance of *Strombus* spp. occurred between the pre- and post-1960 horizons at offshore sites (K-W $X^2 = 5.6$, $p = 0.13$; Figure 3.11a). The proportion of individuals from the four feeding types (carnivores, herbivores, omnivores, suspension feeders) did not change over time (Figure 3.12). However, the individual shell weight of herbivores decreased over time at offshore sites (K-W $X^2 = 9.7$, $p < 0.05$), driven by a significant decline between the 60-80cm and all other horizons (bootstrap test: $p < 0.05$). This trend was due to a decline in the individual shell weight of the conch *Strombus* spp. that occurred before 1960. This and the non-significant but noticeable decline in relative abundance suggest that conchs were overexploited in Costa Arriba by the middle of the 20th century.

Comparison of regions

Gastropod community composition varied significantly between Bocas del Toro and Costa Arriba, with-between region community dissimilarity greater than within-region dissimilarity (ANOSIM: $R = 0.33$, $p < 0.001$). Although both regions contained essentially the same community members, their assemblages differed with respect to the relative abundance of members. The most conspicuous differences in community composition between regions were the greater dominance by *Cerithium* spp. in Bocas del Toro and the higher relative abundance of subdominant species such as *Turritella*, *Coralliophila*, and *Strombus* spp. in Costa Arriba (Figure 3.13). The ordination of samples from both regions together revealed that the majority of variation in coral community composition (55%) was explained by the first principal component (PC1) and that samples grouped by region and reef environment closely tracked PC1 (Figure 3.13). Differences in species composition between regions were greatest between Bocas del Toro lagoonal sites and Costa Arriba offshore sites, which represent the sites subjected to the least and most wave exposure, respectively (Figure 3.13). It is possible that these patterns were also driven by the differing time periods represented by each of these four groups, although neither the range nor median midpoint of the oldest time horizon (60-80 cm) from these groups are ordered sequentially along PC1 (Tables 2.3 and 2.4).

BIVALVES

Bivalve data

The pit excavations produced a total of 23,658 bivalve individuals weighting 11 kg from Bocas del Toro and 1,739 individuals weighing 0.6 kg from Costa Arriba. Within each study region, bivalve communities from offshore and lagoonal environments differed significantly (Bocas del Toro: ANOSIM R = 0.31, $p < 0.001$; Costa Arriba: ANOSIM R = 0.31, $p < 0.001$). The bivalve community varied significantly more over space (among pits at a given horizon) than over time (among horizons within a given pit) in both reef environments at Bocas del Toro and Costa Arriba (bootstrap tests: $p < 0.05$). The high degree of spatial variation was illustrated by the wide spread of replicates within a time horizon in the ordination biplots (Figures 3.16, 3.21).

Bocas del Toro

A total of 73 bivalve species categories were sampled from Bocas del Toro, with 50 species sampled at offshore sites and 68 species sampled at lagoonal sites (Table 3). Bivalve abundance (measured by total weight and number of individuals) and richness were significantly higher at lagoonal than offshore sites (bootstrap tests: $p < 0.05$; Figure 3.15). Average individual shell weight was also significantly higher at lagoonal sites (bootstrap test: $p < 0.05$). In general, bivalves were heavier (i.e. bigger), more abundant and more diverse at lagoonal sites, likely due to the greater nutrient availability and primary productivity in this environment (Vermeij 1978, 1990).

The bivalve communities were composed of a small number of dominant species and a larger number of rare species, although species dominance was in general less than that for gastropods. Lagoonal sites had greater evenness in bivalve population abundance, with 23 species that comprised ≥ 1% of individuals compared to 19 species at offshore sites (Figure 3.17). Thus, bivalve richness, abundance, and species evenness was higher at lagoonal sites.

Assemblages from reef environments were dominated by the epifaunal suspension feeders *Dendostrea frons*, *Chama congregata/macerophylla*, and *Barbatia cancellaria* at one or more time horizons. Together, these species comprised an average of 47% of individuals over all horizons at offshore sites and 54% of individuals at lagoonal sites (Figure 3.17). The dominance of epifaunal suspension feeding bivalves in both environments was indicative of a relatively high-productivity coral reef environment dominated by hard substrates and influenced by terrigenous nutrients from river runoff (Birkeland 1987, Todd et al. 2002). The prevalence of *Chama macerophylla,* typically found cemented to coral or other limestone debris (Jackson 1972, Harries and Sorauf 2010), indicated a relatively high abundance of live or dead coral substrate. The prevalence of *Dendrostrea frons* was a clear indication of the presence of branching colonies of the plexaurid and gorgoniid corals that are the primary hosts on which this oyster lives (Forbes 1971).

The differences in relative abundance of dominant and subdominant species between offshore and lagoonal sites revealed finer differences between these environments. The epifaunal suspension feeder *Ctenoides* was dominant at lagoonal sites but only subdominant at offshore sites. This bysally-attached species is normally typical of high energy environments (Hauser et al. 2007). Subdominant species (comprising between 5-10% of individuals at any horizon) included epifaunal suspension feeders *Lima lima* and *Caribachlamys imbricata* at offshore sites, *Brachtechlamys antillarum* at lagoonal sites, and *Arca imbricata* at both environments, highlighting the prevalence of hard substrata and relatively high plankton productivity in both environments. However, the greater importance at lagoonal sites of infaunal chemosymbiotic deposit feeder *Lucina nassula/muricata* – which can tolerate high temperature, low salinity, high suspended sediment, and stagnant conditions – indicates that lagoonal environments were more stressful in terms of these factors (Jackson 1972, Hauser et al. 2007).

The analysis of bivalves by substrate relationship and feeding type in offshore versus lagoonal sites revealed subtle differences in reef environments. Both environments were dominated by suspension feeding bivalves, which comprised 93% of individuals at offshore and 90% of individuals at lagoonal sites, averaged over all pits and horizons (Figure 3.19). The mean proportion of individuals that were deposit feeders was significantly higher at lagoonal sites (3%) compared to offshore sites (2%; bootstrap test: $p = 0.05$), reflecting the quieter, lower flow conditions and higher availability of organic material deposited on the benthos at lagoonal sites (Levinton 1991). Although both reef environments were dominated by epifaunal bivalves living on hard substrates, offshore sites had a significantly higher proportion of epifaunal individuals (90%) than lagoonal sites (86%) averaged over pits and horizons (bootstrap test: $p < 0.05$, Figure 3.19). This pattern indicated a higher availability of live or dead coral at offshore sites and/or higher sediment or algal cover at lagoonal sites.

Neither bivalve richness nor abundance changed over the time period in either reef environment. However, the individual average shell weight declined significantly across the 1960 boundary at offshore sites (K-W $X^2 = 13.7$, $p < 0.01$) and during the earliest part of the pre 1960 period (from as early as the mid 19th century) at lagoonal sites (K-W $X^2 = 13.3$, $p < 0.01$; Figure 3.15). The decline in individual average weight occurred for epifaunal species (K-W $X\ 2 = 8.0$, $p < 0.05$) but not for infaunal species, indicating an increase in stressful conditions above the sediment surface that disproportionately affected bivalves living in this zone (Jackson 1972, Stanley 1970).

The species composition at offshore sites remained stable over the time period, with no significant trends in any of the dominant or subdominant species (Figure 3.18a). At lagoonal sites, the relative abundance of the epifaunal suspension feeder *B. cancellaria* increased progressively during the pre-1960 period (K-W $X\ 2 = 10.5$, $p < 0.05$), culminating in a significant increase between the 60-80 and 0-20cm horizons (Figure 3.18b).

Although not statistically significant, a notable and generally progressive decline in relative abundance occurred over the time series for the epifaunal suspension feeding oyster *D. frons*, declining from an average of 42-17% of individuals between the 60-80 and 0-20cm horizons at offshore sites and from 27-10% of individuals at lagoonal sites (Figure 3.18). This decline appears to have continued to the present, as this species is not a conspicuous component of coral reefs in Bocas del Toro today (KL Cramer, *pers. obs*). *D. frons* lives primarily on branching gorgonian corals from the Plexauridae and Gorgoniidae families and secondarily on the branching scleractinian *Acropora cervicornis* (Forbes 1971). It is not harvested for human consumption today (Carprenter 2002) nor has it been in the past (Wake, Linares 1980). Therefore, the decline of this species likely represents a large scale loss of its coral hosts. The proportion of bivalve life habit categories remained stable over the time series.

Costa Arriba

A total of 51 species categories were sampled from Costa Arriba, with 38 species sampled at offshore and lagoonal sites (Table 4). Bivalve species richness and abundance as measured by total number of individuals was significantly higher at lagoonal sites (bootstrap tests: $p < 0.05$; Figure 3.20). However, bivalve total weight and individual shell weight did not differ between environments. Thus, the greater number of bivalves at the lagoonal site was not accompanied by a significant increase in weight, signifying that this site was composed of lighter (i.e. smaller) individuals than the offshore sites. However, the difference in individual weight was not statistically significant between reef environments.

As in Bocas del Toro, the bivalve communities in Costa Arriba were composed of a small number of dominant species and a larger number of rare species. Species evenness was essentially equivalent between lagoonal and offshore sites: 27 species comprised ≥ 1% of individuals at offshore sites and 28 species comprised ≥ 1% of individuals at lagoonal sites (Figure 3.23). Averaged over all samples, the bivalve community in both environments was dominated by the epifaunal suspension feeders *Chama congregata / macerophylla* and *Brachtechlamys antillarum*, which together comprised 41% of individuals at offshore sites and 39% of individuals at lagoonal sites. The dominance of these species indicated a prevalence of hard substrates in both environments. Other abundant species (comprising ≥10% of individuals at a horizon) included infaunal deposit feeder *Tellina tampensis* at offshore sites and epifaunal suspension feeder *Anomia simplex* and infaunal suspension feeder *Chione* at lagoonal sites.

Subdominant species (comprising 5-10% of individuals at a horizon) differed between environments as well. At offshore sites epifaunal suspension feeders *Ctenoides*, *Barbatia tenera*, and *A. simplex*, chemosymbiotic deposit feeder *Lucina nassula/muricata*, and the epi and infaunal suspension feeder *Modiolus americanus* were subdominant at offshore sites. Epifaunal suspension feeders *Acar*, *Chama macerophylla*, and *Plicatula* spp. were subdominant at lagoonal sites. The epifaunal suspension feeder *Arca imbricata* was subdominant in both environments (Figure 3.23).

Differences in the composition of dominant and subdominant bivalves between offshore and lagoonal sites were likely related to the relative degree of water motion and proximity to seagrass habitats. Offshore sites had a higher prevalence of forms resistant to heavy wave action: the infaunal *T. tampensis* and *L. nassula/muricata* maintain stability in energetic environments by burrowing below the sediment-water interface, while *B. tenera*, *Ctenoides* spp., and *M. americanus* attach to the substrate by means of strong byssal threads that provide resistance to detachment (Jackson 1972, Hauser et al. 2007). Abundant species in lagoonal sites included a greater variety of life habits, with bysally-attaching coral-associated epifaunal suspension feeders *Acar* spp. and *C. macerophylla*, coral and seagrass-associated epifaunal suspension feeder *Plicatula* spp. (Yonge 1973, Daley 2002, Harries and Sorauf 2010), and the infaunal suspension feeder *Chione* spp. The *Chione* genus contains species that are typical of restricted lagoonal environments as well as species typical of more open lagoonal environments (Jackson 1973, Ekdale 1974, Hauser et al. 2007).

As in Bocas del Toro, the analysis of bivalves by substrate relationship and feeding type identified subtle differences in environmental conditions between offshore and lagoonal sites. Both environments were dominated by epifaunal bivalves living on hard substrates, which comprised 80% of individuals at offshore sites and 85% of individuals at the lagoonal site (Figure 3.25). Also similar to Bocas del Toro, both environments were dominated by suspension feeders, comprising 79% of individuals at offshore sites and 84% of individuals at the lagoonal site. Costa Arriba lagoonal sites contained a significantly higher proportion of suspension feeding individuals (lagoonal = 96%, offshore = 82%) and offshore sites contained a significantly higher proportion of deposit feeding individuals (lagoonal = 4%, offshore = 9%), the opposite of the pattern observed in Bocas del Toro (bootstrap tests: $p < 0.05$). Offshore sites also had a higher proportion of chemosybiotic deposit feeding individuals (lagoonal = <1%, offshore =

7%; bootstrap test: $p < 0.05$). The lower prevalence of (primarily epifaunal) suspension feeders in Costa Arriba offshore sites is likely due to heavy wave action preventing effective attachment onto hard substrate (Jackson 1972). The higher prevalence of suspension feeders at Costa Arriba lagoonal sites may also reflect the higher planktonic productivity in the less restricted and more oceanic conditions in Costa Arriba lagoonal environments (Birkeland 1987).

Neither bivalve richness nor abundance changed over the time period at either reef environment. In contrast to Bocas del Toro, the average individual shell weight also remained constant over the time period in both environments (figure 3.22). In addition, proportions of dominant and subdominant species remained stable over the time in both environments (Figure 3.24).

Comparison of regions

Bivalve community composition varied significantly between Bocas del Toro and Costa Arriba, with between-region community dissimilarity significantly greater than within-region dissimilarity (ANOSIM $R = 0.35$, $p < 0.001$). Although both regions were composed of similar species assemblages, the relative abundance of assemblage members differed, most notably with a higher proportion of the epifaunal suspension feeding oyster *D. frons* in Bocas del Toro and a higher proportion of the epifaunal suspension feeding scallop *B. antillarum* in Costa Arriba (Figure 3.26). The ordination of samples from both regions together revealed that 33% of the variation in bivalve community composition was explained by the first principal component (PC1) and that samples grouped by region and environment had significantly different PC1 scores (bootstrap test: $p < 0.05$; Figure 3.26). The distribution of scores along PC1 of each of the four groups (Bocas del Toro offshore, Bocas del Toro lagoonal, Costa Arriba offshore, Costa Arriba lagoonal) revealed that regional differences were greater than environmental differences in bivalve community composition.

The analysis of gastropod and bivalve assemblages together revealed that molluscan assemblages were distinct between regions and reef environments. The principal components biplot showed a moderate amount of separation in communities according to region and environment, with differences driven mainly by the relative abundance of the gastropods *Cerithium* spp., *C. mercatoria*, *H. octoradiata* and the bivalves *D. frons*, *C. congregata/macerophylla*, *B.cancellaria*, *L. nassula.muricata*, *B. antillarum* (Figure 3.27). As with the separate analyses of gastropod and bivalve assemblages, the combined gastropod/bivalve community was significantly more similar within a region and environment than among regions and environments (ANOSIM R = 0.6, $p < 0.001$). Variation in molluscan community composition within a region and environment was in general too large for the detection of obvious assemblages of gastropod and bivalves that occurred together consistently (Figure 3.28).

DISCUSSION

The gastropod and bivalve death assemblages sampled from modern reefs in Caribbean Panama were typical of coral reefs with a high availability of hard substrates and relatively high productivity due to the influence of river runoff. Common community members were consistent across regions and environments, and variation in the taxonomic community composition was due to differences in the relative abundance of members. These communities showed a high amount of variation in the relative abundance of common species within and between reef environments and sampling regions, revealing subtle and localized differences in natural and/or human-caused environmental conditions.

The variation in gastropod and bivalve life habits over reef environments and regions varied in a coherent way according to gradients in wave exposure and influence from terrestrial runoff. The numerical abundance and mass of bivalves and gastropods was greater at lagoonal sites, signifying that these quieter, higher productivity coral reef environments were the preferred habitat for both groups. This pattern was also reflected in higher bivalve species richness but was not reflected in gastropod species richness. For gastropods, the proportion of the community comprised of carnivores increased with wave exposure and more oceanic reef conditions, while the proportion of herbivores increased with greater protection from wave action and higher influence from river runoff. For bivalves, life habits varied in a more complex way according to wave exposure and reef productivity, with infaunal and deposit feeding forms most abundant at sites with the highest exposure to waves and lowest exposure to river runoff, and epifaunal and suspension feeding forms most abundant at sites with moderate wave and river runoff exposure. These patterns illustrate the response of coral reef gastropod and bivalves to a complex suite of environmental stressors that include food availability, dislodgement, clogging of filtering mechanisms by suspended sediments, and variation in sediment and water temperature, salinity, and oxygen content. Because none of these stressors was measured directly in this study, it was not possible to determine their relative importance in the structuring of the molluscan communities.

The temporal changes observed in the relative abundance of taxonomic and life habit categories of bivalves and gastropods suggest that these reefs were undergoing human-caused ecological changes before 1960 and possibly as far back as the 19th century. The weight of both bivalve and gastropod individuals declined significantly over the time series, with the decline in individual gastropod weight occurring at offshore sites only and the decline in individual bivalve weight occurring in Bocas del Toro only. Bocas del Toro reefs also underwent a decline in their proportion carnivorous gastropods, indicating heightened ecological change in this region during the 20th century. As the importance of carnivorous coral reef gastropods has been found to be higher in environments with higher habitat complexity (Kohn and Leviten 1976), this decline could be due to a loss of living coral habitat over this time period.

Reef mollusk communities with short food chains and with a dominance of small individuals and low trophic levels are an indication of high environmental stress from terrestrial runoff and restricted water flow (Jackson 1972, McClanahan 1992) and/or fishing pressure (Hockey and Bosman 1986, de Boer et al. 2000, Roy et al. 2003) that disproportionately affect larger and higher trophic level species. Therefore, the observed decline in size structure for gastropods and bivalves and the simplification of trophic structure for gastropods could be the result of an increase in environmental stress and/or fishing pressure over historical time. Because none of the common species that underwent these declines have typically been consumed by humans, the changes appear to be caused primarily from a change in the reef environment.

Temporal changes that occurred in the relative abundance and individual weight of common mollusk species provided further evidence of environmental change. In Bocas del Toro the dominance of the oyster *Dendostrea frons* from the oldest time horizons (corresponding to approximately the 1960s at offshore sites and before from the 19th century to mid-20th century at lagoonal sites) was striking because today this species is not conspicuous on reefs (KL Cramer, *pers. obs*). Because it is not consumed by humans, the loss of this species signifies a change in the reef environment. Increased nutrients in terrestrial runoff would not be expected to result in a decline in this suspension-feeding oyster because it would increase food availability. Increased sediments in terrestrial runoff that clog the filtering apparatus of this species would be expected to negatively impact this oyster, however. Therefore, the decline in *D. frons* is likely due to increased sedimentation and/or a change in the availability of its branching gorgonian and scleractinian coral hosts. Gorgonian corals underwent drastic declines in abundance from disease epidemics during the 1980s and 1990s across the Caribbean (Guzman and Cortes 1984, Harvell et al. 1999). However, the species that were the most affected by disease (*Gorgonia* spp.) are not common hosts of *D. frons* (Forbes 1971). Thus, the decline in *D. frons* may signify an undocumented mortality event of the preferred gorgonian hosts *Pseudopterogorgia*, *Muricea*, and *Muriceopsis* spp. and/or of the scleractinian host *Acropora cervicornis* that began from 50-150 years ago on some reefs.

Lastly, the significant temporal decline in the individual size of the heavily-exploited conch *Strombus* spp. coupled with its non-significant but noticeable decline in relative abundance at Costa Arriba is an indication of historical fishing effects that extend back at least 50 years to the first half of the 20th century in this region.

This data showed that coral reef mollusk communities in Caribbean Panama underwent noticeable changes in taxonomic, trophic, and size structure over the past 50-

150 years or more. While spatial patterns in community composition can be explained by gradients in natural environmental stress, temporal patterns are more likely a result of human-induced stress. The shifts in mollusk community structure at offshore sites in Bocas del Toro that occurred over the past half-century –towards increased dominance by smaller individuals and lower trophic levels – resulted in these communities becoming more similar to communities from Bocas del Toro lagoonal environments. This pattern strongly implicates terrestrial runoff as a driving factor of change in these communities.

Human population and deforestation have increased substantially over the past century in both regions, increasing the amount of sediments, nutrients, and pollutants to adjacent coral reef environments (summarized in Guzman 2003). Negative effects of sediments and pollutants have been documented in bivalves and gastropods (Donohue and Irvine 2003, McIntyre et al. 2003, Salanki et al. 2003). Declines in water quality also negatively impact the scleractinian corals which form the habitat in which these mollusks live (Fabricius 2005). Thus, the shifts in mollusk trophic and size structure in Bocas del Toro may be a response to declines in live coral habitat from the increased eutrophication of reefs.

CONCLUSIONS

This study revealed that complex changes occurred within gastropod and bivalve communities extending back a century or more on reefs in Caribbean Panama. These changes were characterized generally by a decline in the individual size and a simplification of the trophic structure of organisms but not in overall molluscan abundance or richness, indicating a community shift rather than a loss of mollusks on reefs during a time of increased human disturbance. Mollusk communities in Bocas del Toro underwent more noticeable changes than did those in Costa Arriba, likely due to the older time period sampled in Bocas del Toro and/or the older history of human disturbance in Costa Arriba. The paleontological data analyzed here therefore support the view that the recent dramatic shifts seen on Caribbean reefs are the legacy of ecological change caused by human disturbance over historical time. Gastropod and bivalve assemblages served as reliable proxies of environmental gradients over space and time but their high degree of variability within and among reefs did not allow for clear-cut correlations between specific environmental factors and species assemblages. Nevertheless, the molluscan death assemblage data presented here provided a more accurate historical baseline of reef communities and environments from which to assess causes of the recent dramatic decline of Caribbean reefs.

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Table 3.1. Gastropod species categories and life habits, Bocas del Toro.

BOCAS DEL TORO			Offshore sites				Lagoonal sites			
Species category	Abbreviation	Diet category	0-20cm	20-40cm	40-60cm	60-80cm	0-20cm	20-40cm	40-60cm	60-80cm
Acmea	Acmaea	HERB	+	+	+	+		+		
Anachis	Anachis	CARN	+	+	+	+	+	+	+	
Antillophos	Antillo	CARN	+	+	+	+	+	+	+	+
Arene bitleri / riseii	A.bit/rise	HERB		+		+	+	+	+	+
Arene cruentata	A.cruen	HERB	+	+	+	+				
Aspella	Aspella	CARN	+	+	+	+	+	+	+	+
Astraea americana	A.ameri	HERB	+			+	+	+	+	+
Astraea caellata	A.caell	HERB	+		+					+
Astraea phoebia	A.phoeb	HERB	+	+	+	+	+	+		+
Astraea tecta	A.tecta	HERB	+	+	+	+	+	+	+	+
Attiliosa	Attilio	CARN	+		+		+	+	+	+
Bailya	Bailya	CARN	+	+	+	+	+	+	+	+
Buchema	Buchem	CARN				+				
Bulla	Bulla	HERB	+		+		+	+	+	+
Bursa	Bursa	CARN	+	+	+	+	+	+		
Calliostoma	Callio	CARN	+	+	+	+	+	+	+	+
Cerithiopsis	Cerithiop	CARN					+	+	+	
Cerithium	Cerith	HERB	+	+	+	+	+	+	+	+
Charonia	Charon	CARN			+					
Cheilea	Cheilea	SUSP	+	+	+	+		+	+	
Chicoreus	Chicor	CARN		+			+	+	+	+
Collisella	Collis	HERB			+	+	+	+	+	+
Colubriaria	Colub	CARN	+	+		+	+	+	+	
Columbella mercatoria	C.merc	HERB	+	+	+	+	+	+	+	+
Conella	Conella	CARN	+	+	+	+				
Conus	Conus	CARN	+	+	+	+				+
Coralliophila	Coral	CARN	+	+	+	+	+	+	+	+
Crassispira	Crassis	CARN	+	+	+	+	+	+	+	+
Crepidula	Crepid	SUSP								
Cymatium	Cymat	CARN	+	+	+	+	+	+	+	+
Cyphoma	Cyphoma	CARN	+	+	+	+				
Cypraea	Cypraea	CARN	+	+	+	+			+	
Cypraecassis	Cypraecas	CARN		+	+	+				+
Daphnella	Daphne	CARN	+				+			+
Dermomurex	Dermo	CARN						+		+
Diodora	Diodora	OMNI	+	+	+	+	+	+	+	+
Dolicholatirus pauli	D.pauli	CARN								+
Drillia	Drillia	CARN	+							
Emarginula	Emarg	OMNI	+	+	+	+	+	+	+	+
Engina	Engina	CARN	+		+	+	+	+	+	+
Epitonium	Epiton	CARN		+						
Fasciolaria tulipa	F.tulip	CARN	+	+	+		+	+	+	+
Favartia	Favart	CARN		+		+		+	+	
Fissurella	Fissur	HERB			+		+	+	+	+
Haplocochlias	Haplo	HERB		+						
Heliacus bisculatus	H.bisul	CARN						+		
Heliacus cylindricus	H.cylind	CARN					+	+	+	+
Hemitoma emarginata	H.emarg	HERB	+	+	+	+	+	+	+	+
Hemitoma octoradiata	H.octo	HERB	+	+	+	+	+	+	+	+
Hipponix	Hippon	SUSP	+	+	+	+			+	
Latirus	Latirus	CARN	+	+	+	+	+	+	+	+
Leucozonia nassa	L.nassa	CARN	+	+	+	+	+	+	+	+
Lucapina	Lucap	OMNI	+	+	+	+	+	+	+	+
Marginella	Margin	CARN	+					+	+	
Melanella	Melan	CARN			+					
Melongena melongena	M.melong	CARN								
Mitra nodulosa	M.nodul	CARN	+	+	+	+		+		
Modulus modulus	M.modu	HERB	+	+	+	+	+	+	+	+
Morula	Morula	CARN	+		+		+	+		+
Morum	Morum	CARN	+	+	+	+				
Murexiella	Murexie	CARN				+				
Muricopsis	Murico	CARN	+	+	+	+	+	+	+	+
Nassarius	Nassar	CARN	+	+	+	+	+	+	+	+
Naticarius canrena	N.canr	CARN					+	+	+	+
Nitidella nitida	N.nitida	HERB	+		+					
Oliva	Oliva	CARN	+		+	+				
Olivella	Olivella	CARN			+					
Parviphos	Parvi	CARN								
Pilsbryspira alboncincta	P.alboc	CARN	+		+		+	+	+	
Pisania pusio	P.pusio	CARN	+	+	+	+				
Polinices lacteus	P.lact	CARN	+	+	+				+	
Prunum	Prunum	CARN			+	+	+	+	+	+
Pterotyphis pinnatus	P.pinna	CARN	+	+		+	+	+	+	+
Pterotyphis triangularis	P.triang	CARN	+							+
Rissoina	Rissoi	HERB	+			+	+	+	+	
Sinum	Sinum	CARN								+
Smaragdia viridis	S.virid	HERB						+		
Strombus	Stromb	HERB	+	+	+	+	+	+	+	+
Tegula fasciata	T.fasci	HERB	+	+	+	+	+	+	+	+
Tonna	Tonna	CARN	+	+	+	+			+	
Trivia	Trivia	CARN	+	+	+	+				
Turbo	Turbo	HERB	+	+	+	+	+	+	+	+
Turritella	Turrit	SUSP	+	+	+	+				
Vasum	Vasum	CARN					+	+		+
Vermetidae	Vermet	SUSP	+	+	+	+	+	+	+	+
Vermicularia fargoi	Vermic	SUSP								
Vexillum	Vexill	CARN	+	+	+	+				
Xenophora conchyliophora	X.conchy	HERB								
Zafrona pulchella	Z. pulch	HERB	+		+		+	+	+	
Total			61	52	60	55	48	55	50	48
Median / pit			14	20	24	22	23	26	21	20
Mean / pit			16.78	19.11	20.67	18.33	22.11	25.33	22.11	19.44

Table 3.2. Gastropod species categories and life habits, Costa Arriba.

COSTA ARRIBA			Offshore sites				Lagoonal sites			
Species category	Abbreviation	Diet category	0-20cm	20-40cm	40-60cm	60-80cm	0-20cm	20-40cm	40-60cm	60-80cm
Acmea	Acmaea	HERB	+	+	+	+	+	+	+	+
Anachis	Anachis	CARN						+		
Antillophos	Antillo	CARN	+	+	+	+				+
Arene bitleri / riseii	A.bit/rise	HERB		+					+	
Arene cruentata	A.cruen	HERB	+	+	+	+	+	+	+	
Aspella	Aspella	CARN								
Astraea americana	A.ameri	HERB								
Astraea caellata	A.caell	HERB			+	+				
Astraea phoebia	A.phoeb	HERB						+		
Astraea tecta	A.tecta	HERB	+	+	+	+	+	+	+	+
Attiliosa	Attilio	CARN								
Bailya	Bailya	CARN	+	+	+	+	+	+	+	+
Buchema	Buchem	CARN								
Bulla	Bulla	HERB		+	+	+				
Bursa	Bursa	CARN	+	+	+	+	+	+		+
Calliostoma	Callio	CARN	+	+	+	+	+	+	+	+
Cerithiopsis	Cerithiop	CARN	+	+	+	+				
Cerithium	Cerith	HERB		+			+	+	+	+
Charonia	Charon	CARN								
Cheilea	Cheilea	SUSP	+	+	+	+	+	+	+	+
Chicoreus	Chicor	CARN	+			+	+	+		+
Collisella	Collis	HERB								
Colubriaria	Colub	CARN	+	+	+		+	+	+	+
Columbella mercatoria	C.merc	HERB	+	+	+	+		+		
Conella	Conella	CARN		+	+	+				
Conus	Conus	CARN	+	+	+	+	+			
Coralliophila	Coral	CARN	+	+	+	+	+	+	+	+
Crassispira	Crassis	CARN	+	+	+	+	+	+		
Crepidula	Crepid	SUSP	+			+	+		+	
Cymatium	Cymat	CARN	+	+	+		+	+	+	+
Cyphoma	Cyphoma	CARN								
Cypraea	Cypraea	CARN	+	+	+	+	+	+	+	+
Cypraecassis	Cypraecas	CARN		+	+			+	+	+
Daphnella	Daphne	CARN						+	+	
Dermomurex	Dermo	CARN	+	+				+		+
Diodora	Diodora	OMNI		+	+	+	+	+	+	+
Dolicholatirus pauli	D.pauli	CARN				+				
Drillia	Drillia	CARN						+		
Emarginula	Emarg	OMNI		+	+	+	+		+	+
Engina	Engina	CARN	+	+				+	+	+
Epitonium	Epiton	CARN								
Fasciolaria tulipa	F.tulip	CARN								+
Favartia	Favart	CARN						+	+	
Fissurella	Fissur	HERB		+	+					
Haplocochlias	Haplo	HERB								
Heliacus bisculatus	H.bisul	CARN								
Heliacus cylindricus	H.cylind	CARN								
Hemitoma emarginata	H.emarg	HERB					+	+	+	+
Hemitoma octoradiata	H.octo	HERB		+	+	+	+	+	+	+
Hipponix	Hippon	SUSP		+	+	+				
Latirus	Latirus	CARN		+	+	+	+	+	+	+
Leucozonia nassa	L.nassa	CARN	+		+				+	
Lucapina	Lucap	OMNI	+	+	+	+	+	+	+	+
Marginella	Margin	CARN				+		+	+	
Melanella	Melan	CARN								
Melongena melongena	M.melong	CARN					+			
Mitra nodulosa	M.nodul	CARN		+	+	+	+	+	+	+
Modulus modulus	M.modu	HERB	+	+		+	+	+	+	+
Morula	Morula	CARN		+	+		+		+	
Morum	Morum	CARN						+	+	
Murexiella	Murexie	CARN								
Muricopsis	Murico	CARN	+	+	+	+	+	+	+	+
Nassarius	Nassar	CARN		+	+	+	+	+	+	
Naticarius canrena	N.canr	CARN								
Nitidella nitida	N.nitida	HERB	+							
Oliva	Oliva	CARN		+						
Olivella	Olivella	CARN			+					
Parviphos	Parvi	CARN		+		+				
Pilsbryspira alboncincta	P.alboc	CARN	+	+	+			+		+
Pisania pusio	P.pusio	CARN		+	+	+				
Polinices lacteus	P.lact	CARN			+	+				
Prunum	Prunum	CARN								
Pterotyphis pinnatus	P.pinna	CARN		+	+	+	+	+		+
Pterotyphis triangularis	P.triang	CARN					+	+	+	+
Rissoina	Rissoi	HERB		+	+					
Sinum	Sinum	CARN								
Smaragdia viridis	S.virid	HERB								
Strombus	Stromb	HERB	+	+	+	+	+	+	+	+
Tegula fasciata	T.fasci	HERB	+	+	+	+				
Tonna	Tonna	CARN	+	+	+	+			+	+
Trivia	Trivia	CARN		+	+	+		+	+	+
Turbo	Turbo	HERB								+
Turritella	Turrit	SUSP	+	+	+	+	+	+	+	+
Vasum	Vasum	CARN								
Vermetidae	Vermet	SUSP	+		+	+	+	+	+	+
Vermicularia fargoi	Vermic	SUSP						+	+	+
Vexillum	Vexill	CARN			+			+	+	
Xenophora conchyliophora	X.conchy	HERB					+	+		
Zafrona pulchella	Z. pulch	HERB	+	+		+				
Total			32	47	45	42	34	44	39	36
Median / pit			12.5	15.5	14	17	19	27	28	17
Mean / pit			11	17	15.7	15.5	19.3	26.7	23.3	19.7

Table 3.3. Bivalve species categories and life habits, Bocas del Toro

BOCAS DEL TORO					Offshore sites				Lagoonal sites			
Species category	Abbreviation	Diet category	Substrate relationship	Attachment	0-20cm	20-40cm	40-60cm	60-80cm	0-20cm	20-40cm	40-60cm	60-80cm
Acar	Acar	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Americardia	Americ	SUSP	IN	UNATTACH	+	+	+	+	+	+	+	+
Amusium	Amusi	SUSP	EPI	UNATTACH							+	+
Anadara	Anadara	SUSP	IN	UNATTACH		+		+	+		+	+
Angulus	Angu	DEPOS	IN	UNATTACH								
Anodontia	Anodo	CHEMO	IN	UNATTACH					+	+	+	+
Anomia simplex	A.simpl	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Arca imbricata	A.imbri	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Arca zebra	A.zebra	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Arcinella Arcinella	Arcinella	SUSP	EPI	ATTACH							+	
Arcopsis adamsi	A.adamsi	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Argopecten	Argopec	SUSP	EPI	BOTH	+				+	+	+	+
Barbatia cancellaria	B.cancel	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Barbatia candida	B.cand	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Barbatia tenera	B.tenera	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Botula fusca	B.fusca	SUSP	NESTLER	ATTACH		+	+		+	+	+	+
Brachtechlamys antillarum	B.antill	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Caribachlamys imbricata	C.imbric	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Caribachlamys mildredae	C.mildred	SUSP	EPI	ATTACH			+		+			
Caribachlamys ornata	C.ornat	SUSP	EPI	ATTACH		+				+	+	+
Caribachlamys sentis	C.sentis	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	
Caryocarbula	Caryoc	SUSP	IN	ATTACH	+	+	+	+	+	+	+	+
Chama congregata/macerophylla	C.cong/mace	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Chama macerophyllia	C.mace	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Chione	Chione	SUSP	IN	UNATTACH	+	+	+	+	+	+	+	
Chlamys multisquamata	C.multi	SUSP	EPI	ATTACH								
Codakia	Codakia	CHEMO	IN	UNATTACH	+	+	+	+				
Coralliophaga	Corallio	SUSP	BORER	UNATTACH					+		+	
Crassinella	C.lunu	SUSP	EPI / IN	BOTH					+	+		
Crassostrea rhizophorae	C.rhizo	SUSP	EPI	ATTACH							+	+
Ctenoides	Ctenoid	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Cumingia sp	Cuming	DEPOS	IN	UNATTACH			+		+		+	
Dendostrea frons	D.frons	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Diplodonta	Diplod	SUSP	IN	UNATTACH				+	+	+	+	+
Dosinia	Dosinia	SUSP	IN	UNATTACH							+	
Gouldia cerina	G.cerina	SUSP	IN	UNATTACH		+		+	+	+	+	+
Gregariella coralliophaga	G.corallio	SUSP	EPI	ATTACH		+	+		+	+	+	+
Hyotissa sp	Hyotissa	SUSP	EPI	ATTACH		+						
Isognomun	Isognom	SUSP	EPI	ATTACH		+			+	+	+	+
Laevicardium laevigatum	L.laevig	SUSP	IN	UNATTACH					+	+	+	+
Lima Lima	L.lima	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Lirophora	Liroph	SUSP	IN	UNATTACH					+	+	+	
Lithophaga	Lithophag	SUSP	BORER	UNATTACH	+	+		+	+	+	+	
Lucina nassula/muricata	L.nass/muri	CHEMO	IN	UNATTACH	+	+	+	+	+	+	+	+
Lucina pensilvanica	L.pensilv	CHEMO	IN	UNATTACH						+		
Lyropecten (Nodipecten)	Lyro	SUSP	EPI	ATTACH					+	+	+	+
Macoma	Macoma	DEPOS	IN	UNATTACH					+			
Macrocallista maculata	M.macul	SUSP	IN	UNATTACH					+	+	+	+
Mactra	Mactra	SUSP	IN	UNATTACH		+						
Merisca	Merisca	DEPOS	IN	UNATTACH							+	
Modiolus americanus	M.ameri	SUSP	EPI / IN	ATTACH		+			+	+		+
Musculus	Muscul	SUSP	EPI	UNATTACH	+	+		+				
Nuculana	Nuculan	DEPOS	IN	UNATTACH					+			
Papyridea soleniformes	P.soleni	SUSP	IN	UNATTACH	+		+		+	+	+	+
Parvilucina multilineata	P.multilin	CHEMO	IN	UNATTACH	+	+	+	+	+	+	+	+
Periglypta listeri	P.listeri	SUSP	IN	UNATTACH			+	+	+	+	+	+
Petricola	Petric	SUSP	BORER	UNATTACH				+	+	+	+	+
Pinctada imbricata	P.imbric	SUSP	EPI	ATTACH					+	+	+	+
Pinna	Pinna	SUSP	IN	ATTACH					+	+		
Pitar fulminatus	P.fulm	SUSP	IN	UNATTACH					+		+	+
Pitar simpsoni	P.simps	SUSP	IN	UNATTACH							+	
Pleurolucina leucocyma	Pleuroluc	CHEMO	IN	UNATTACH	+	+						
Plicatula	Plicat	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	
Pseudochama	Pseudoch	SUSP	EPI	ATTACH		+			+		+	
Pteria	Pteria	SUSP	EPI	ATTACH		+			+	+	+	+
Saccella	Sacc	DEPOS	IN	UNATTACH						+		
Scissula sp	Scissula	DEPOS	IN	UNATTACH					+			
Semele	Semele	DEPOS	IN	UNATTACH	+	+	+		+	+	+	+
Solena	Solena	SUSP	IN	UNATTACH								
Spathochlamys	Spathochl	SUSP	EPI	ATTACH		+	+	+	+	+		
Spengleria rostrata	S.rostrat	SUSP	BORER	UNATTACH					+	+		+
Spondylus americanus	S.americ	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Tellina fausta	T.fausta	DEPOS	IN	UNATTACH	+	+	+	+	+	+	+	+
Tellina tampensis	T.tampen	DEPOS	IN	UNATTACH	+	+	+	+	+	+	+	+
Tivela floridana	T.florid	SUSP	IN	UNATTACH						+		
Trachycardium dallocardia	Trachy	SUSP	IN	UNATTACH	+		+		+	+	+	
Tucetona	Tucet	SUSP	EPI / IN	UNATTACH								
Ventricolaria rugatina	V.ruga	SUSP	IN	UNATTACH								
Total					33	42	35	34	58	53	56	45
Median / pit					13	11	16	12	27	27	26	23
Mean / pit					12	13.8	15	13.2	27.3	28	25.4	22.1

Table 3.4. Bivalve species categories and life habits, Costa Arriba

COSTA ARRIBA					Offshore sites				Lagoonal Sites			
Species category	Abbreviation	Diet category	Substrate relationship	Attachment	0-20cm	20-40cm	40-60cm	60-80cm	0-20cm	20-40cm	40-60cm	60-80cm
Acar	Acar	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Americardia	Americ	SUSP	IN	UNATTACH		+			+		+	+
Amusium	Amusi	SUSP	EPI	UNATTACH							+	
Anadara	Anadara	SUSP	IN	UNATTACH		+	+	+	+	+		+
Angulus	Angu	DEPOS	IN	UNATTACH			+	+				
Anodontia	Anodo	CHEMO	IN	UNATTACH								
Anomia simplex	A.simpl	SUSP	EPI	ATTACH		+	+	+	+	+	+	+
Arca imbricata	A.imbri	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Arca zebra	A.zebra	SUSP	EPI	ATTACH			+	+			+	+
Arcinella Arcinella	Arcinella	SUSP	EPI	ATTACH								
Arcopsis adamsi	A.adamsi	SUSP	EPI	ATTACH								
Argopecten	Argopec	SUSP	EPI	BOTH				+				
Barbatia cancellaria	B.cancel	SUSP	EPI	ATTACH						+		
Barbatia candida	B.cand	SUSP	EPI	ATTACH	+	+	+	+		+		
Barbatia tenera	B.tenera	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Botula fusca	B.fusca	SUSP	NESTLER	ATTACH								
Brachtechlamys antillarum	B.antill	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Caribachlamys imbricata	C.imbric	SUSP	EPI	ATTACH	+	+	+	+		+	+	+
Caribachlamys mildredae	C.mildred	SUSP	EPI	ATTACH								
Caribachlamys ornata	C.ornat	SUSP	EPI	ATTACH								
Caribachlamys sentis	C.sentis	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Caryocarbula	Caryoc	SUSP	IN	ATTACH					+	+	+	
Chama congregata/macerophylla	C.cong/mace	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Chama macerophyllia	C.mace	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Chione	Chione	SUSP	IN	UNATTACH		+	+	+	+	+	+	+
Chlamys multisquamata	C.multi	SUSP	EPI	ATTACH					+	+	+	
Codakia	Codakia	CHEMO	IN	UNATTACH				+				
Coralliophaga	Corallio	SUSP	BORER	UNATTACH					+			
Crassinella	C.lunu	SUSP	EPI / IN	BOTH								
Crassostrea rhizophorae	C.rhizo	SUSP	EPI	ATTACH								
Ctenoides	Ctenoid	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Cumingia sp	Cuming	DEPOS	IN	UNATTACH								
Dendostrea frons	D.frons	SUSP	EPI	ATTACH		+	+		+	+	+	+
Diplodonta	Diplod	SUSP	IN	UNATTACH								
Dosinia	Dosinia	SUSP	IN	UNATTACH								
Gouldia cerina	G.cerina	SUSP	IN	UNATTACH								+
Gregariella coralliophaga	G.corallio	SUSP	EPI	ATTACH					+	+	+	+
Hyotissa sp	Hyotissa	SUSP	EPI	ATTACH							+	
Isognomun	Isognom	SUSP	EPI	ATTACH	+			+				
Laevicardium laevigatum	L.laevig	SUSP	IN	UNATTACH			+					+
Lima Lima	L.lima	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Lirophora	Liroph	SUSP	IN	UNATTACH				+				
Lithophaga	Lithophag	SUSP	BORER	UNATTACH								
Lucina nassula/muricata	L.nass/muri	CHEMO	IN	UNATTACH	+	+	+	+				+
Lucina pensilvanica	L.pensilv	CHEMO	IN	UNATTACH								
Lyropecten (Nodipecten)	Lyro	SUSP	EPI	ATTACH				+				+
Macoma	Macoma	DEPOS	IN	UNATTACH								
Macrocallista maculata	M.macul	SUSP	IN	UNATTACH								
Mactra	Mactra	SUSP	IN	UNATTACH				+				
Merisca	Merisca	DEPOS	IN	UNATTACH								
Modiolus americanus	M.ameri	SUSP	EPI / IN	ATTACH							+	
Musculus	Muscul	SUSP	EPI	UNATTACH								
Nuculana	Nuculan	DEPOS	IN	UNATTACH			+					
Papyridea soleniformes	P.soleni	SUSP	IN	UNATTACH						+	+	
Parvilucina multilineata	P.multilin	CHEMO	IN	UNATTACH				+				
Periglypta listeri	P.listeri	SUSP	IN	UNATTACH								
Petricola	Petric	SUSP	BORER	UNATTACH			+					
Pinctada imbricata	P.imbric	SUSP	EPI	ATTACH					+	+		
Pinna	Pinna	SUSP	IN	ATTACH								
Pitar fulminatus	P.fulm	SUSP	IN	UNATTACH								
Pitar simpsoni	P.simps	SUSP	IN	UNATTACH								
Pleurolucina leucocyma	Pleuroluc	CHEMO	IN	UNATTACH	+	+	+	+				
Plicatula	Plicat	SUSP	EPI	ATTACH	+		+		+	+	+	+
Pseudochama	Pseudoch	SUSP	EPI	ATTACH								
Pteria	Pteria	SUSP	EPI	ATTACH								+
Saccella	Sacc	DEPOS	IN	UNATTACH								
Scissula sp	Scissula	DEPOS	IN	UNATTACH								
Semele	Semele	DEPOS	IN	UNATTACH		+		+				
Solena	Solena	SUSP	IN	UNATTACH			+					
Spathochlamys	Spathochl	SUSP	EPI	ATTACH								
Spengleria rostrata	S.rostrat	SUSP	BORER	UNATTACH								
Spondylus americanus	S.americ	SUSP	EPI	ATTACH	+	+	+	+	+	+	+	+
Tellina fausta	T.fausta	DEPOS	IN	UNATTACH	+	+	+	+	+		+	+
Tellina tampensis	T.tampen	DEPOS	IN	UNATTACH	+	+	+	+	+	+	+	+
Tivela floridana	T.florid	SUSP	IN	UNATTACH								
Trachycardium dallocardia	Trachy	SUSP	IN	UNATTACH	+	+	+	+		+		
Tucetona	Tucet	SUSP	EPI / IN	UNATTACH			+					
Ventricolaria rugatina	V.ruga	SUSP	IN	UNATTACH						+		
Total					19	23	29	30	23	26	26	26
Median / pit					8.5	11	11	12	16	17	20	18
Mean / pit					7.5	10.8	12	11.5	16.3	16.7	18	16.7

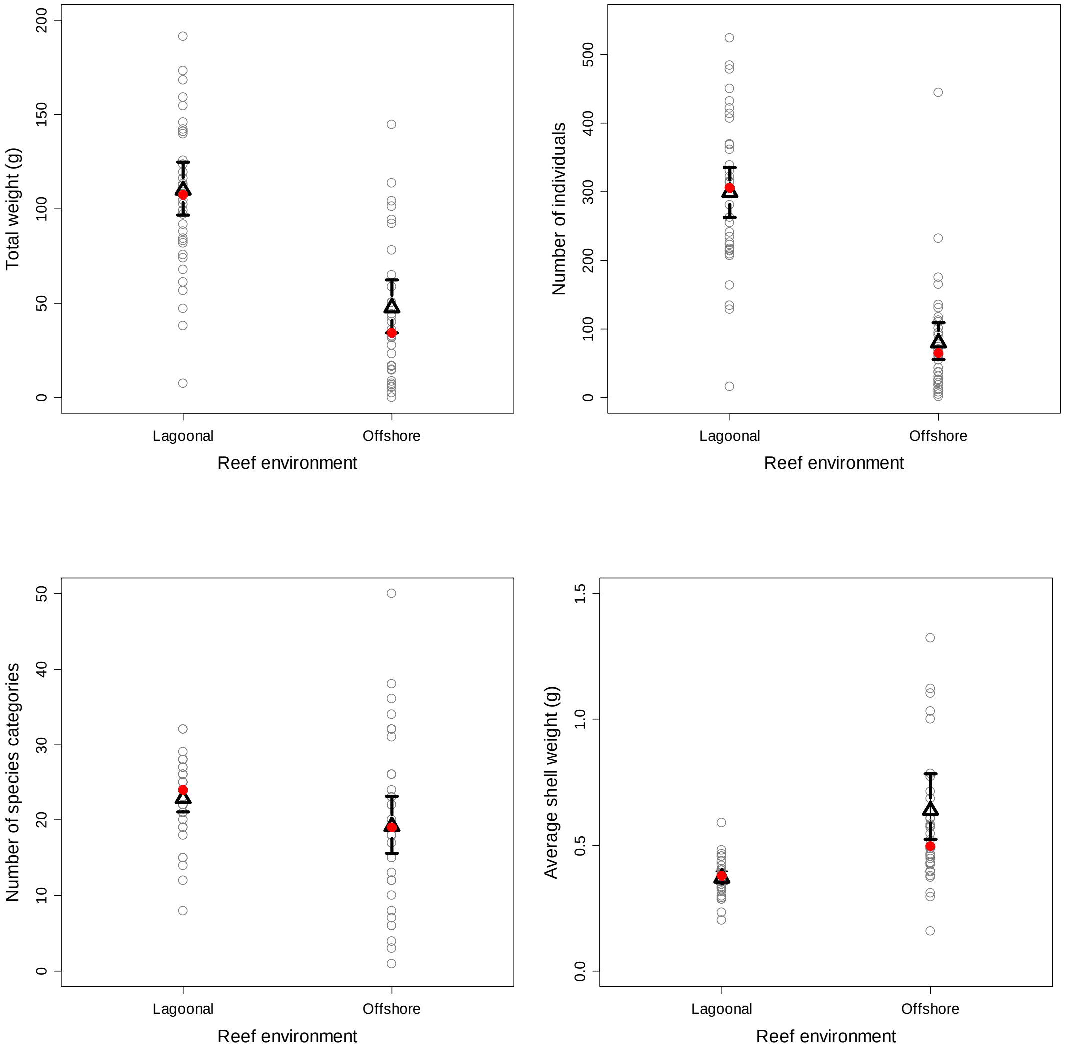


Figure 3.1. Gastropods, Bocas del Toro. Richness, total weight, total abundance, and average individual weight of gastropod shells. Grey points = data by pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. One point ~2.5g not shown in plot for individual shell weight from offshore environment.

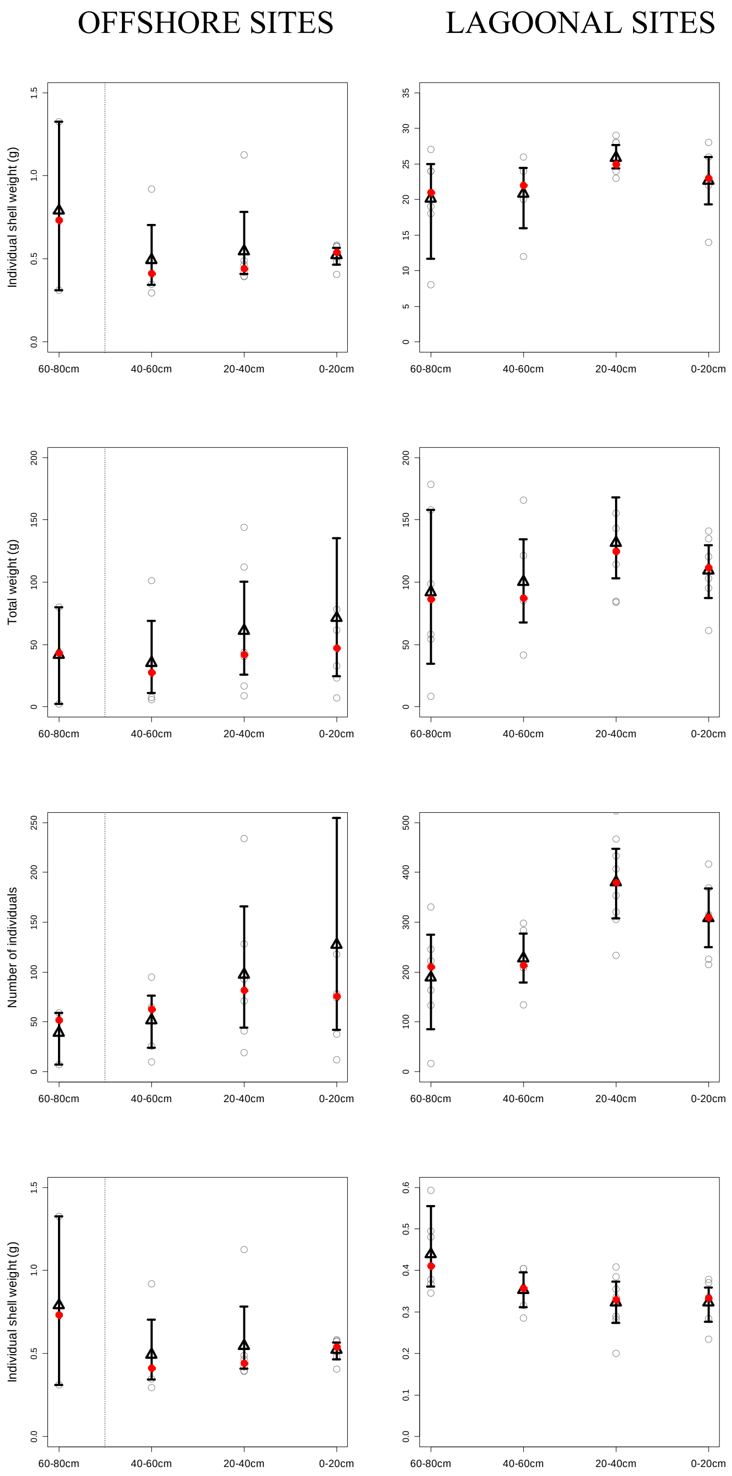


Figure 3.2. Gastropods, Bocas del Toro. Richness, total weight, number of individuals, and individual shell weight by time horizon. Grey points = individual pit, triangle =mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960. All horizons from lagoonal sites are pre-1960 AD.

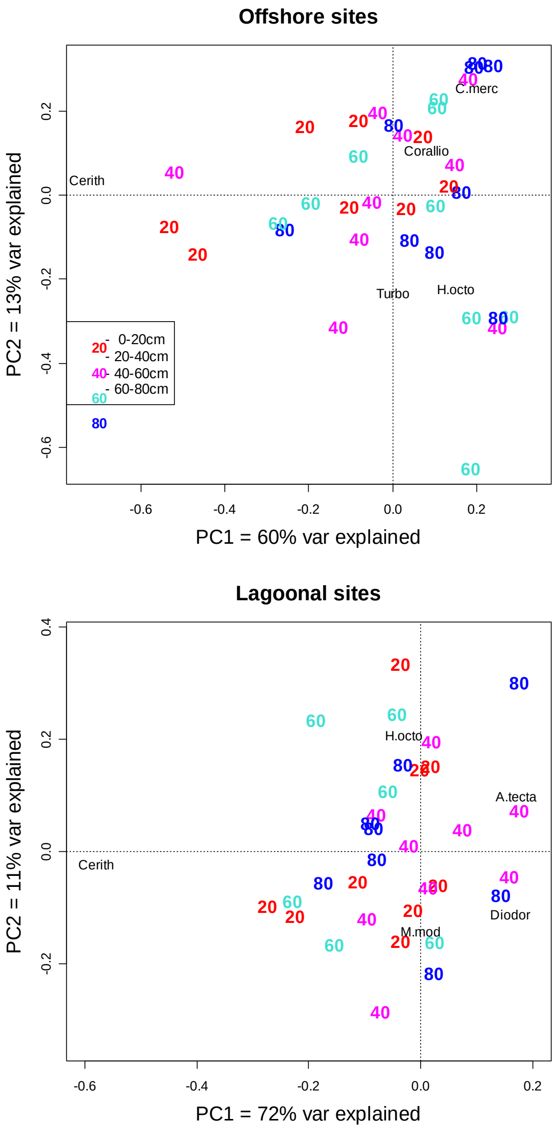
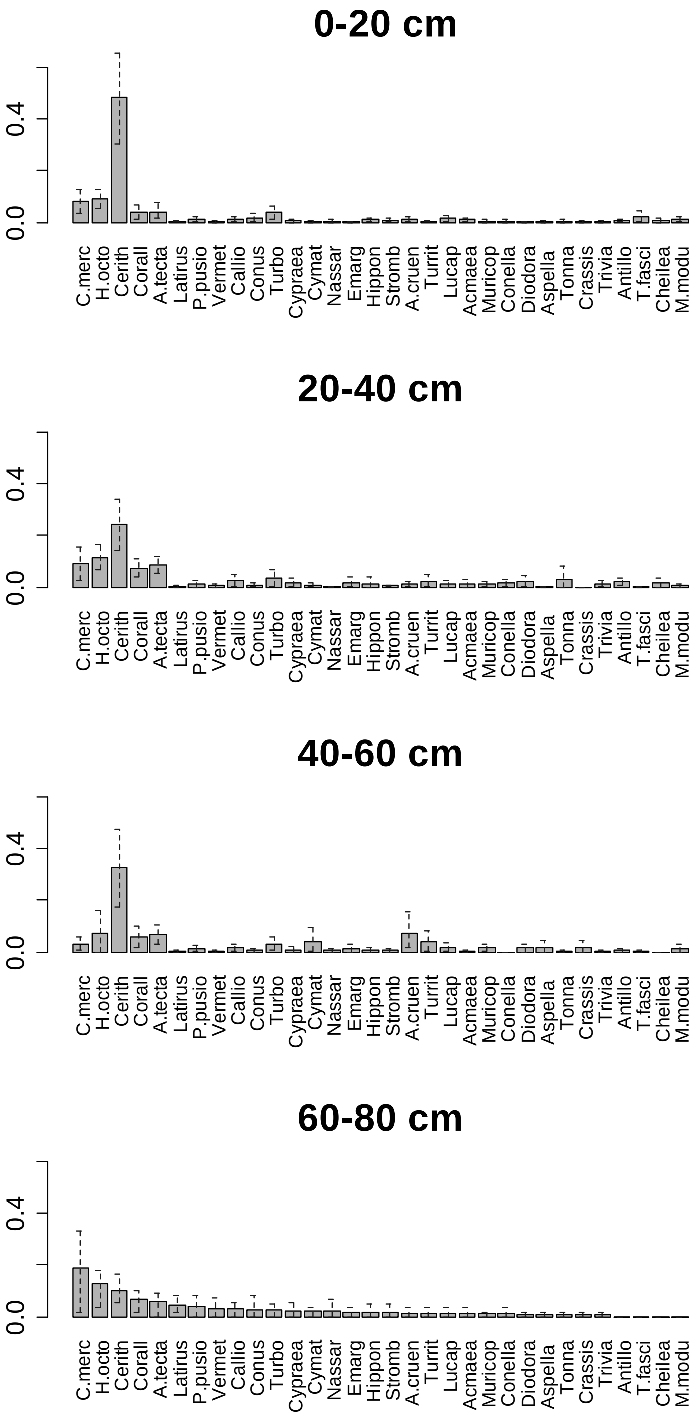


Figure 3.3. Gastropods, Bocas del Toro. Principal Components Analysis of species proportion by abundance (number of individuals), offshore and lagoonal sites. Data points represent an individual horizon from an individual pit.



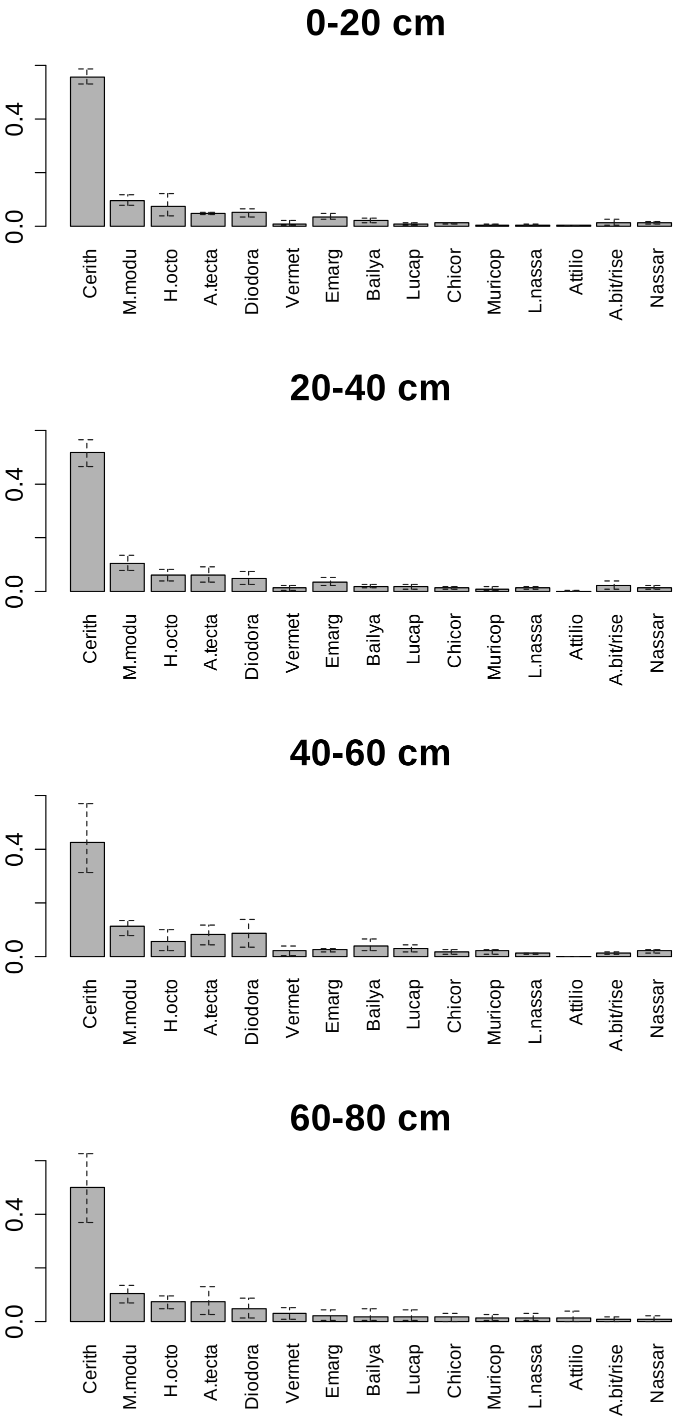
0-20 cm

20-40 cm

40-60 cm

60-80 cm

Figure 3.4. Gastropods, offshore sites, Bocas del Toro. Mean relative abundance (proportion individuals) of species comprising ≥1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.



0-20 cm

20-40 cm

40-60 cm

60-80 cm

Figure 3.5. Gastropods, lagoonal sites, Bocas del Toro. Mean relative abundance (proportion individuals) of species comprising ≥1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.

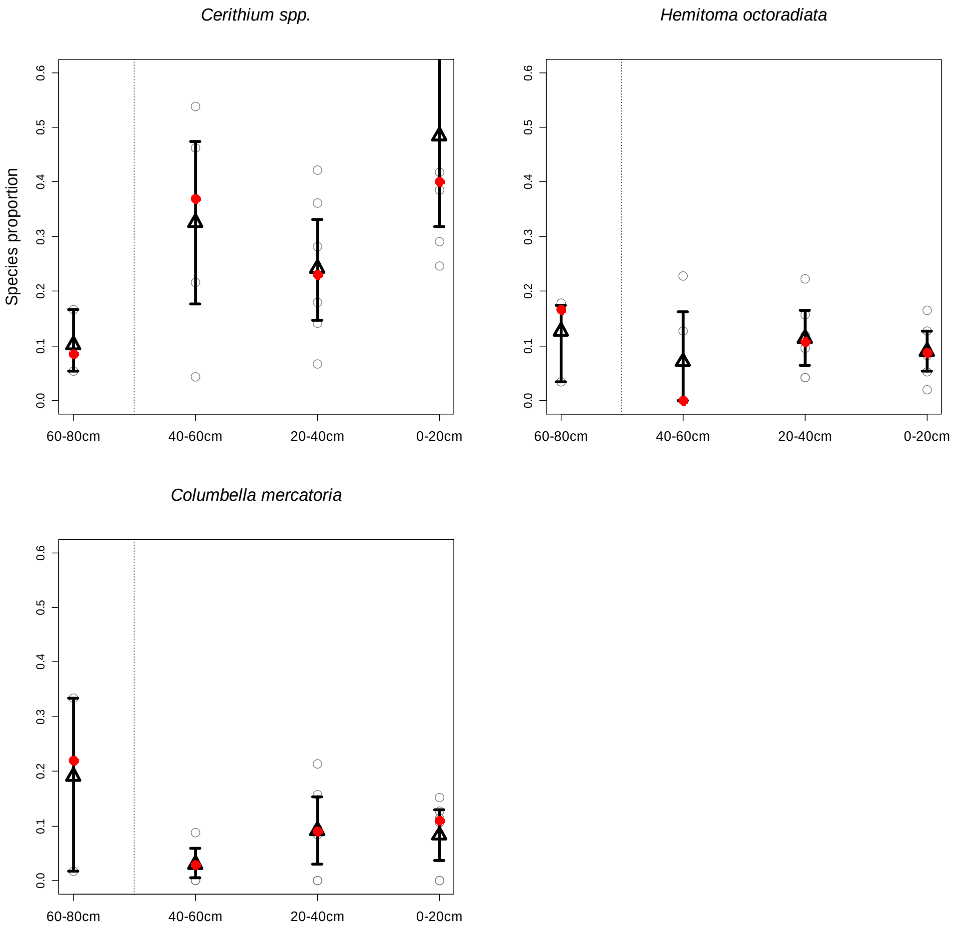


Figure 3.6. Gastropods, offshore sites, Bocas del Toro. Proportion over time of common gastropod species (>5% of community on average). Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960.

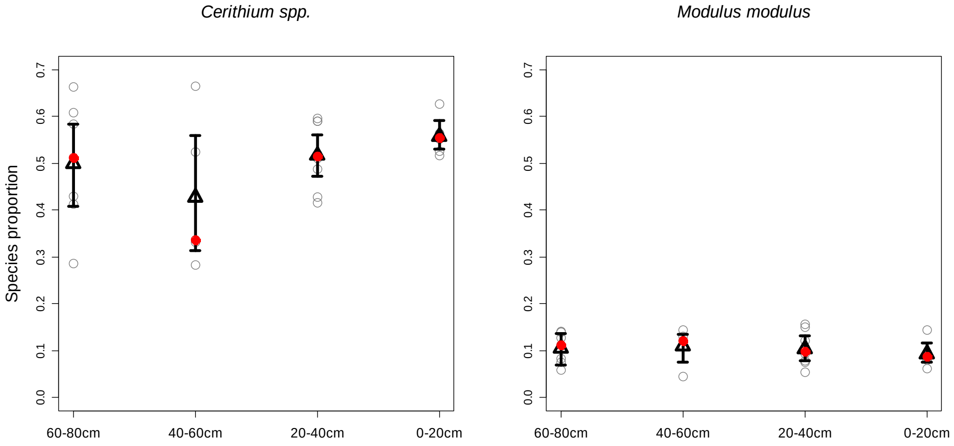


Figure 3.7. Gastropods, lagoonal sites, Bocas del Toro. Proportion over time of common gastropod species (>5% of community on average). Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. All horizons are pre-1960 AD.

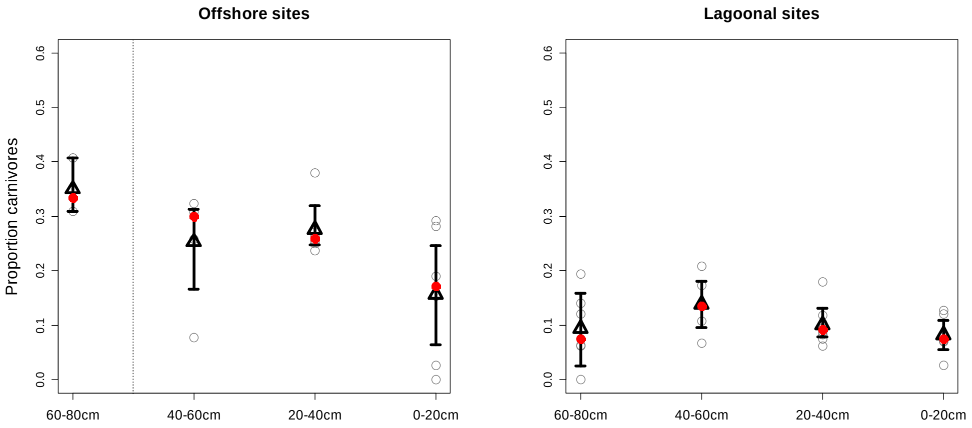


Figure 3.8. Gastropods, Bocas del Toro. Proportion carnivorous individuals. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960. All horizons from lagoonal sites are pre-1960 AD.

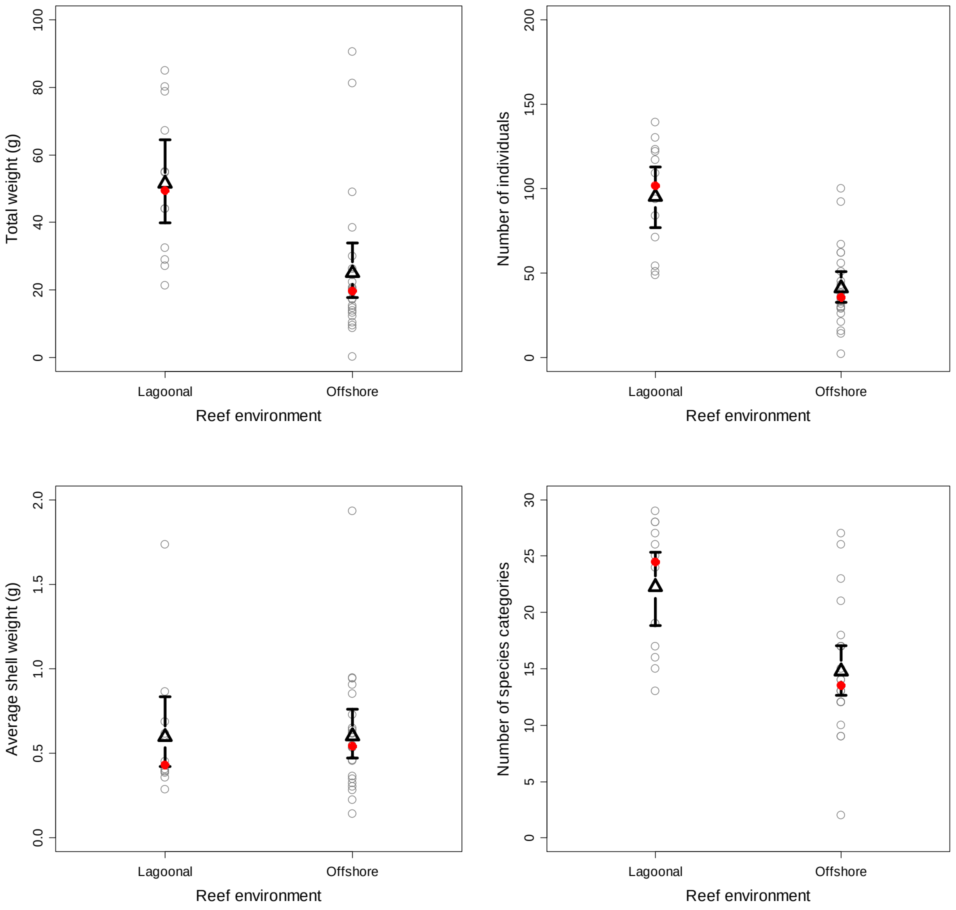
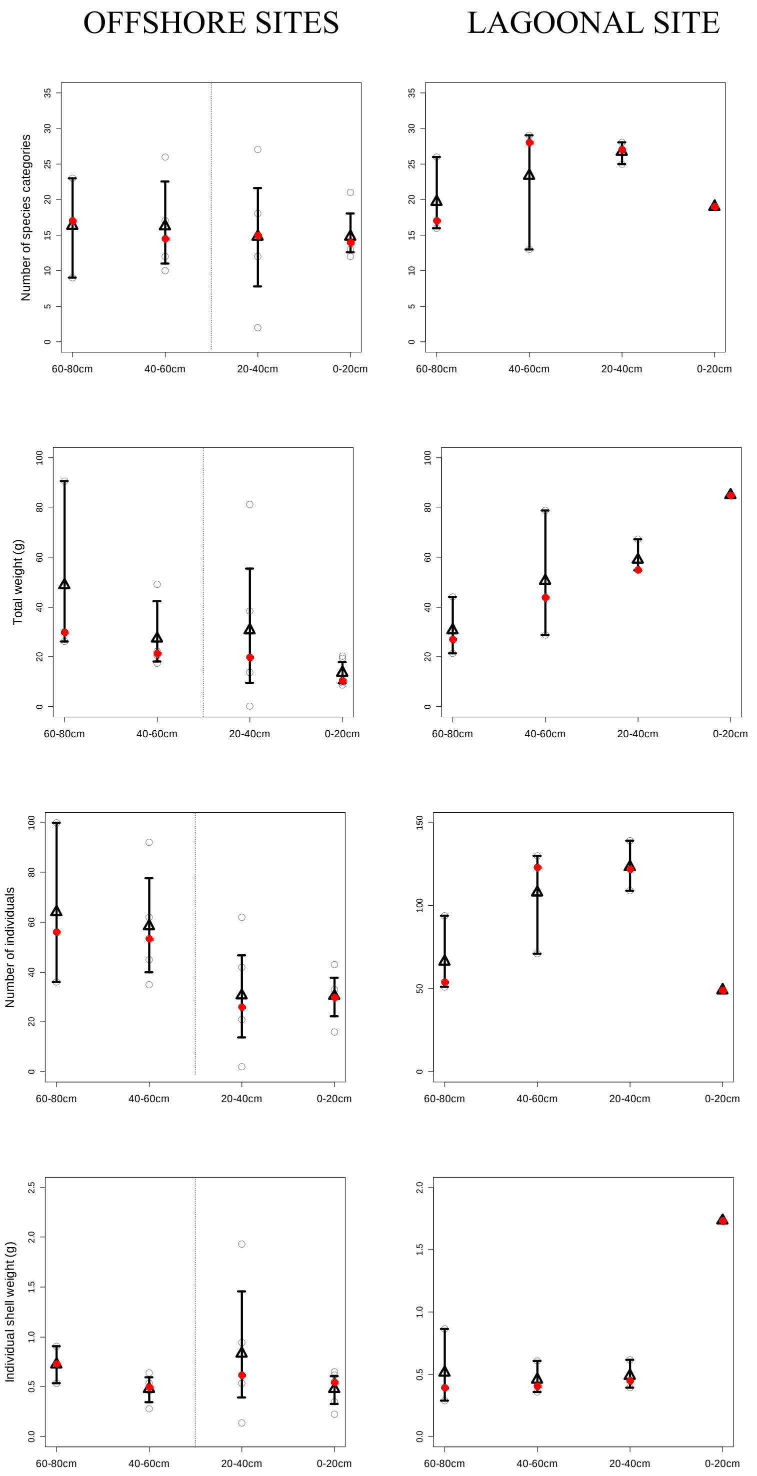
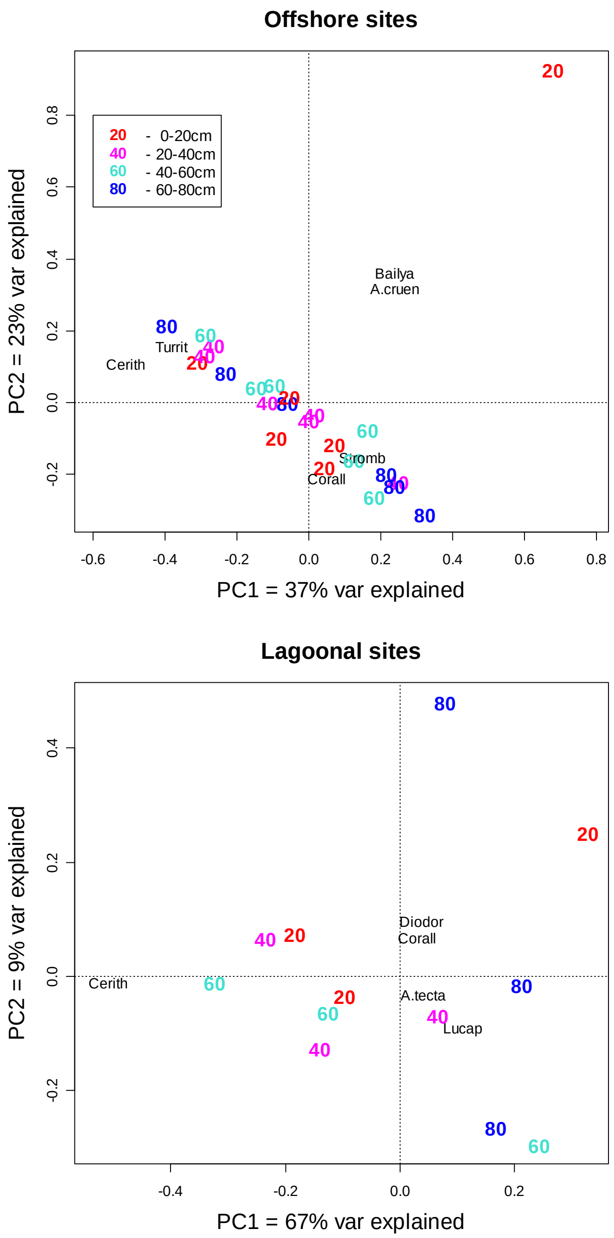


Figure 3.9. Gastropods, Costa Arriba. Total weight, total abundance, and average individual weight of shells. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals.


OFFSHORE SITES

LAGOONAL SITE

Figure 3.10. Gastropods, Costa Arriba. Richness, total weight, number of individuals, and individual shell weight by time horizon. Grey points = individual pit, triangle =mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960. All horizons from lagoonal sites are pre-1960 AD.


Offshore sites

Lagoonal sites

Figure 3.11. Gastropods, Costa Arriba. Principal Components Analysis of species proportion by abundance (number of individuals). Data points represent an individual horizon from an individual pit.

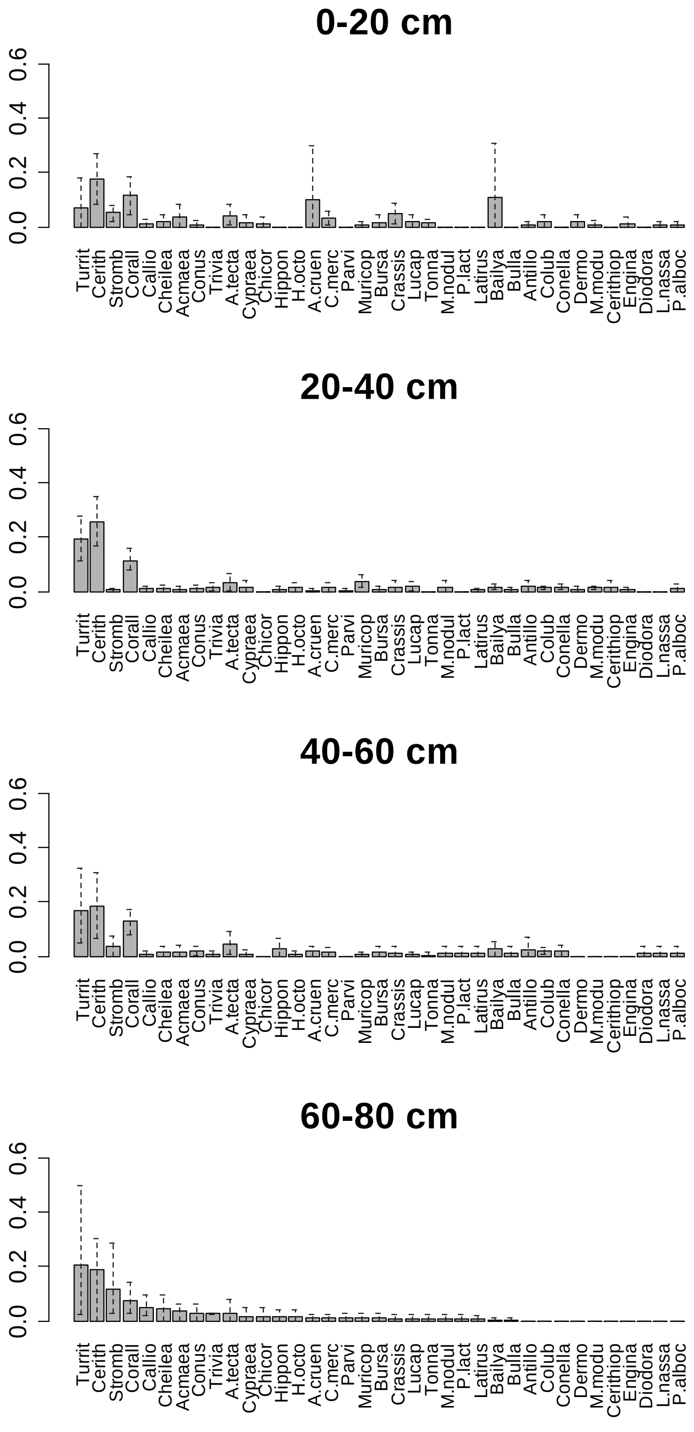


Figure 3.12. Gastropods, offshore sites, Costa Arriba. Mean relative abundance (proportion individuals) of species comprising ≥ 1% of gastropod community in one or more time horizons. Dashed bars are 95% bootstrapped confidence intervals.

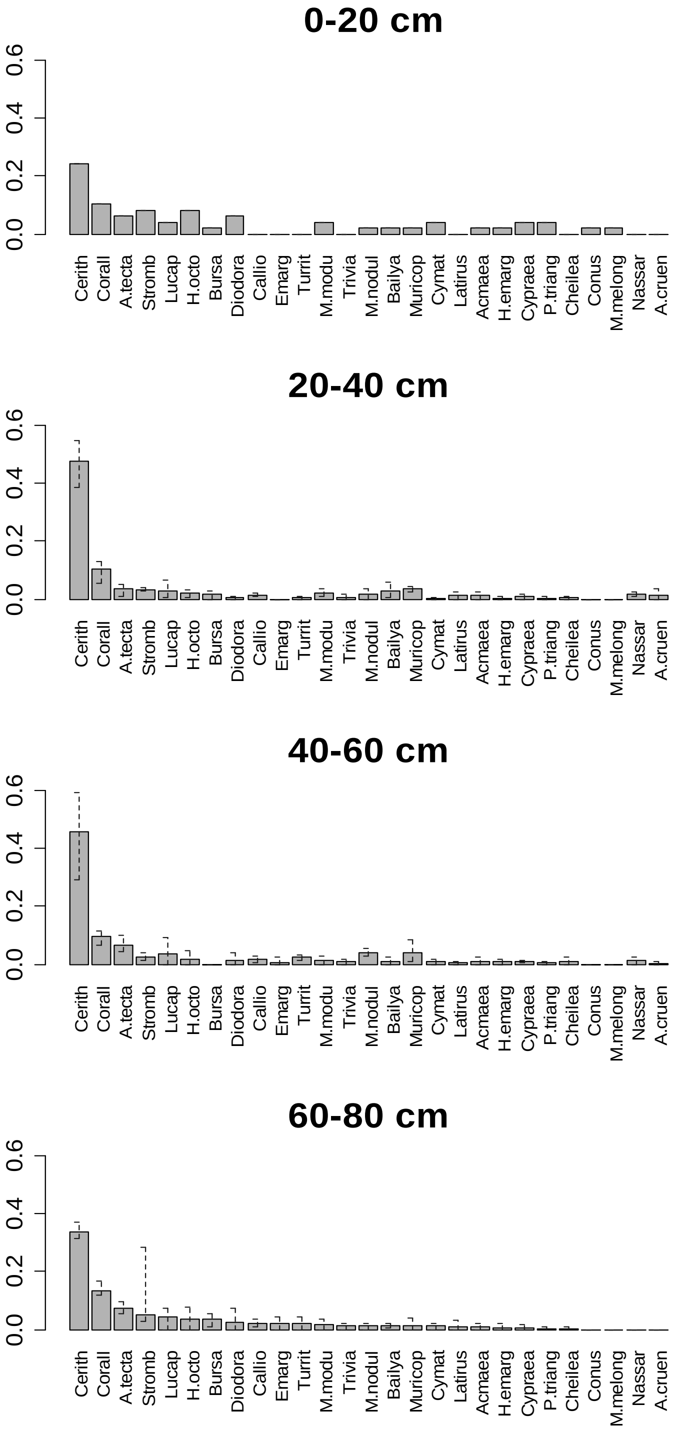


Figure 3.13. Gastropods, lagoonal sites, Costa Arriba. Mean relative abundance (proportion individuals) of species comprising ≥ 1% of gastropod community in one or more time horizons. Dashed bars are 95% bootstrapped confidence intervals.

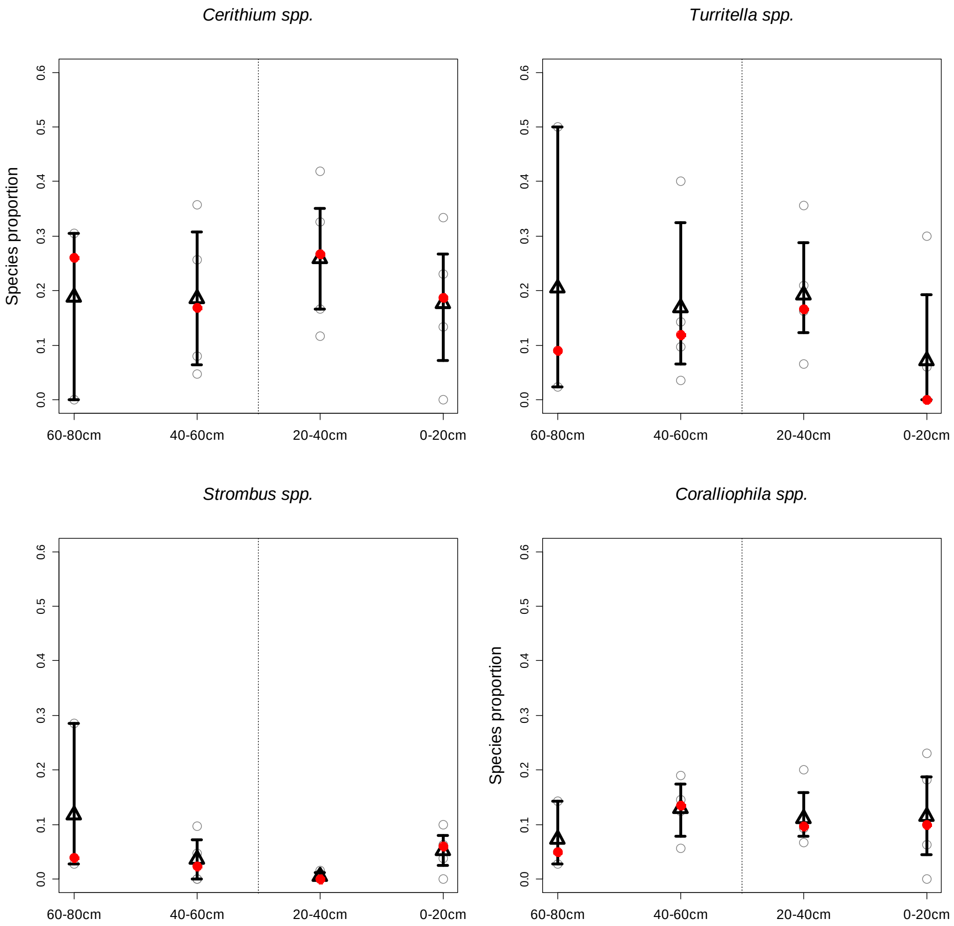


Figure 3.14. Gastropods, offshore sites, Costa Arriba. Relative abundance by time horizon for species comprising ≥5% of community at any one horizon. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960.

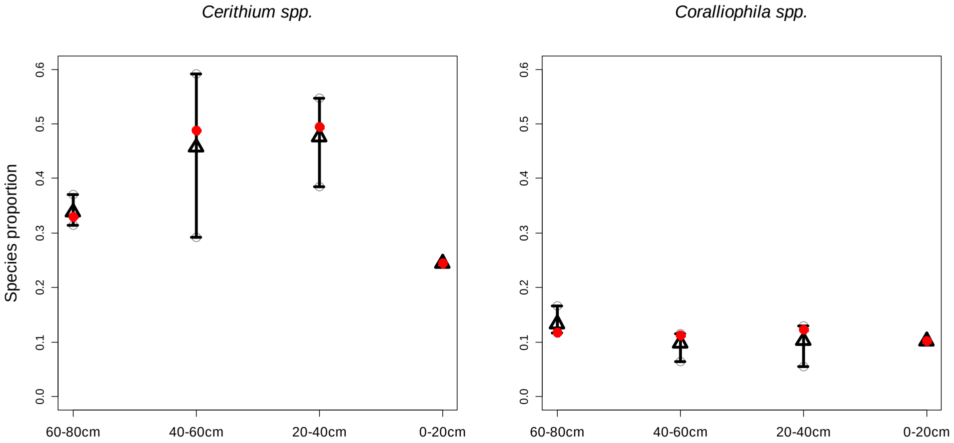


Figure 3.15. Gastropods, lagoonal sites, Costa Arriba. Relative abundance by time horizon for species comprising ≥5% of community at any one horizon. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. All horizons are pre-1960 AD.

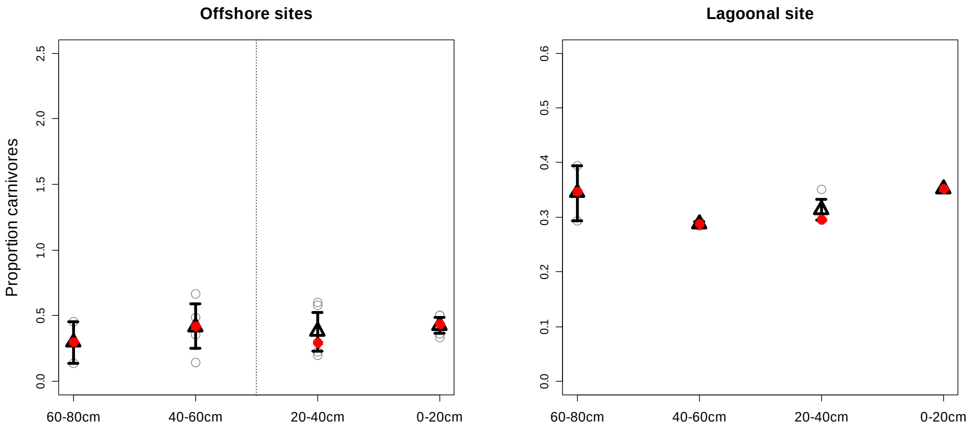


Figure 3.16. Gastropods, Costa Arriba. Proportion carnivorous individuals. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960.

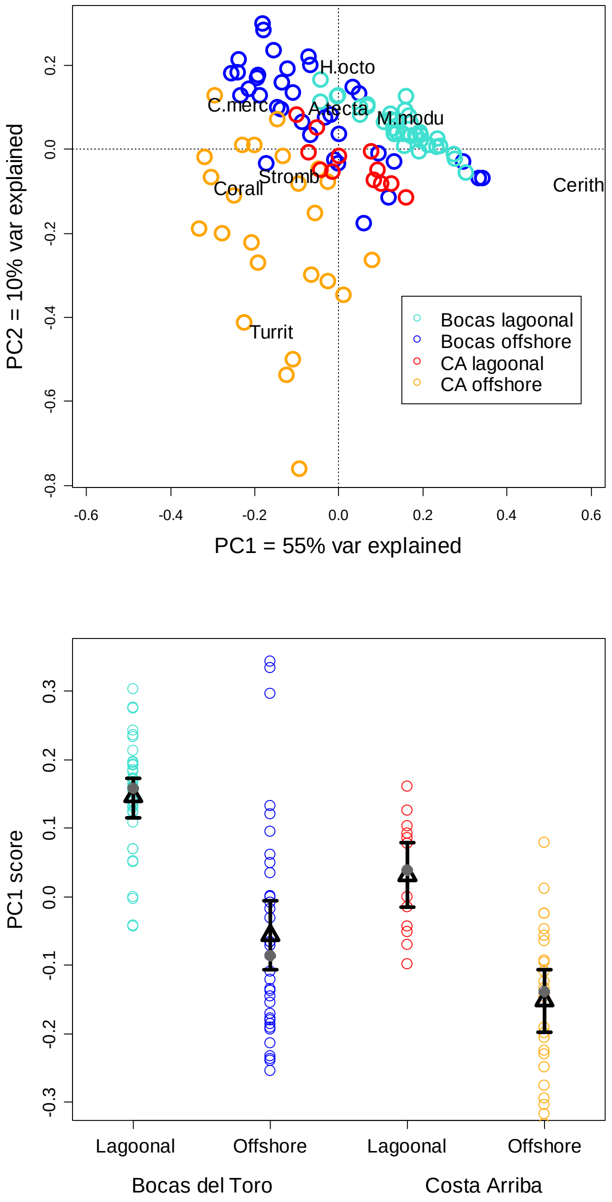


Figure 3.17. Gastropods, Bocas del Toro and Costa Arriba combined. Principal Components Analysis of species proportions and scores for first principal component by region and environment. Triangle = mean scores, bars = 95% bootstrapped confidence intervals, closed circles = median store. Open circles represent an individual horizon from an individual pit.

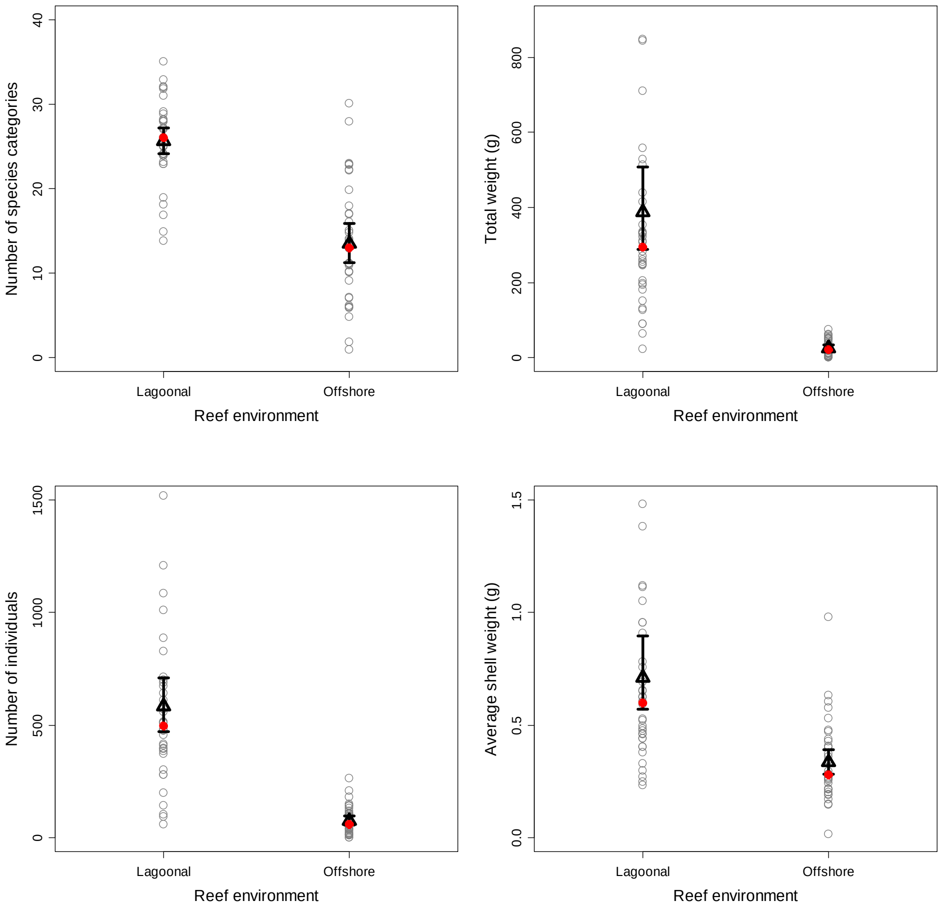


Figure 3.18. Bivalves, Bocas del Toro. Richness, total weight, total abundance, and average individual weight by reef environment. Open circles = individual pit, triangle = mean, closed circle = median, black bars = 95% bootstrapped confidence intervals.

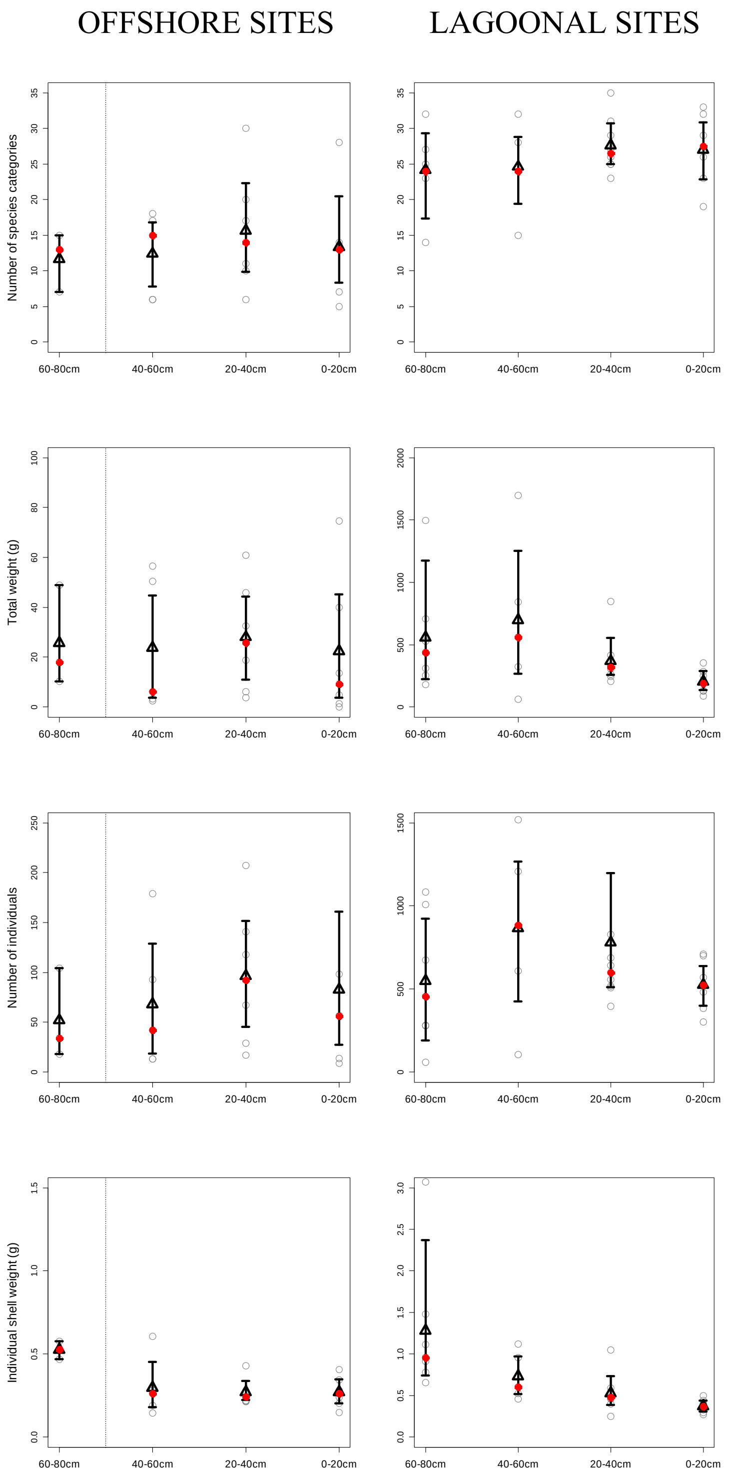


Figure 3.19. Bivalves, Bocas del Toro. Species richness, total weight, number of individuals, and individual shell weight by time horizon. Open circles = pit, triangle = mean, closed circle = median, bars = 95% bootstrapped confidence intervals. Horizons to left of dotted line are pre-1960. All horizons from lagoonal sites are pre-1960 AD.

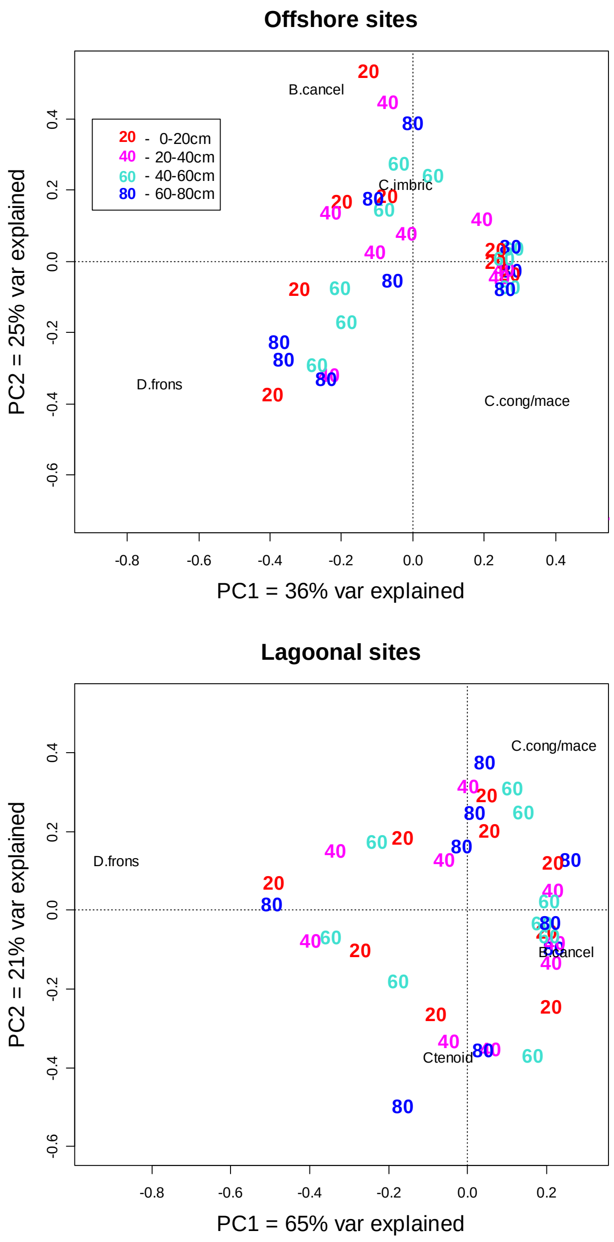
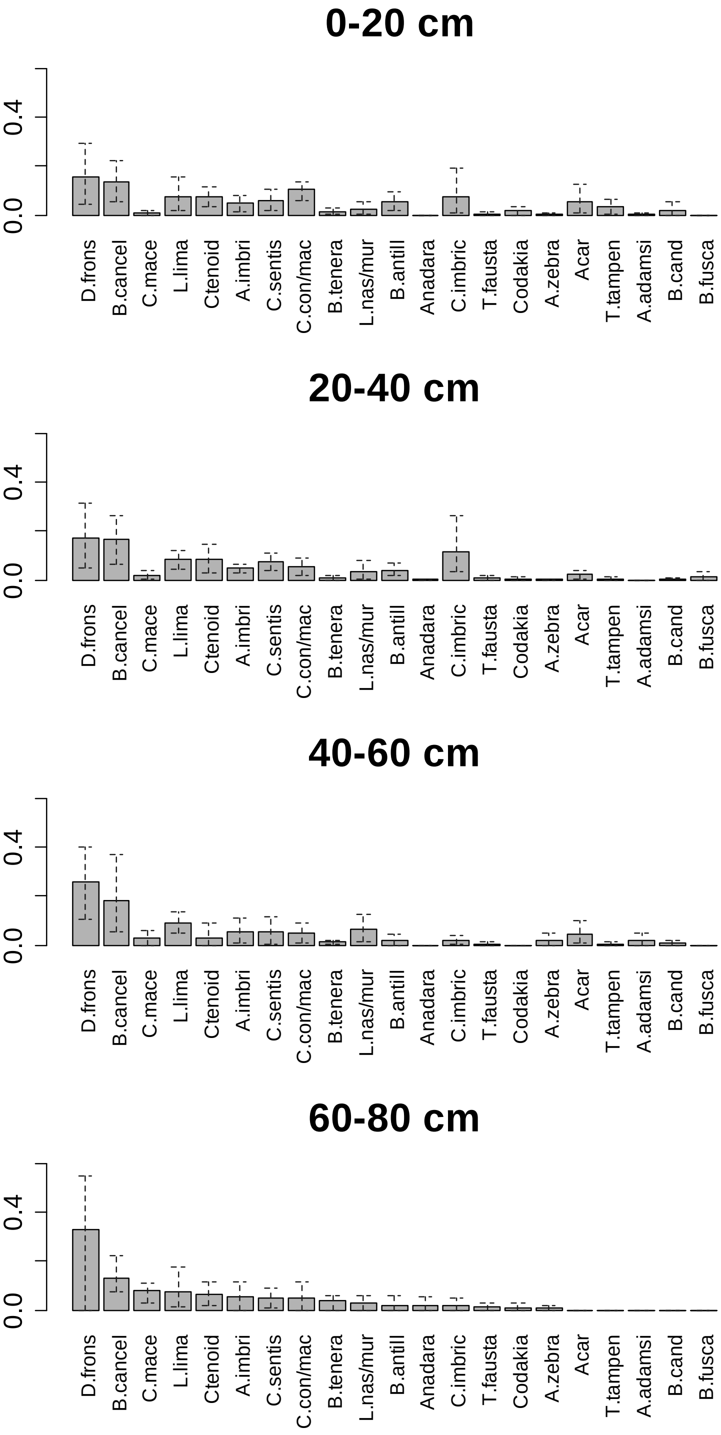


Figure 3.20. Bivalves, Bocas del Toro. Principal Components Analysis of species proportion by abundance (number of individuals). Data points represent an individual horizon from an individual pit.



0-20 cm

20-40 cm

40-60 cm

60-80 cm

Figure 3.21. Bivalves, offshore sites, Bocas del Toro. Mean relative abundance (proportion individuals) of species comprising >= 1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.

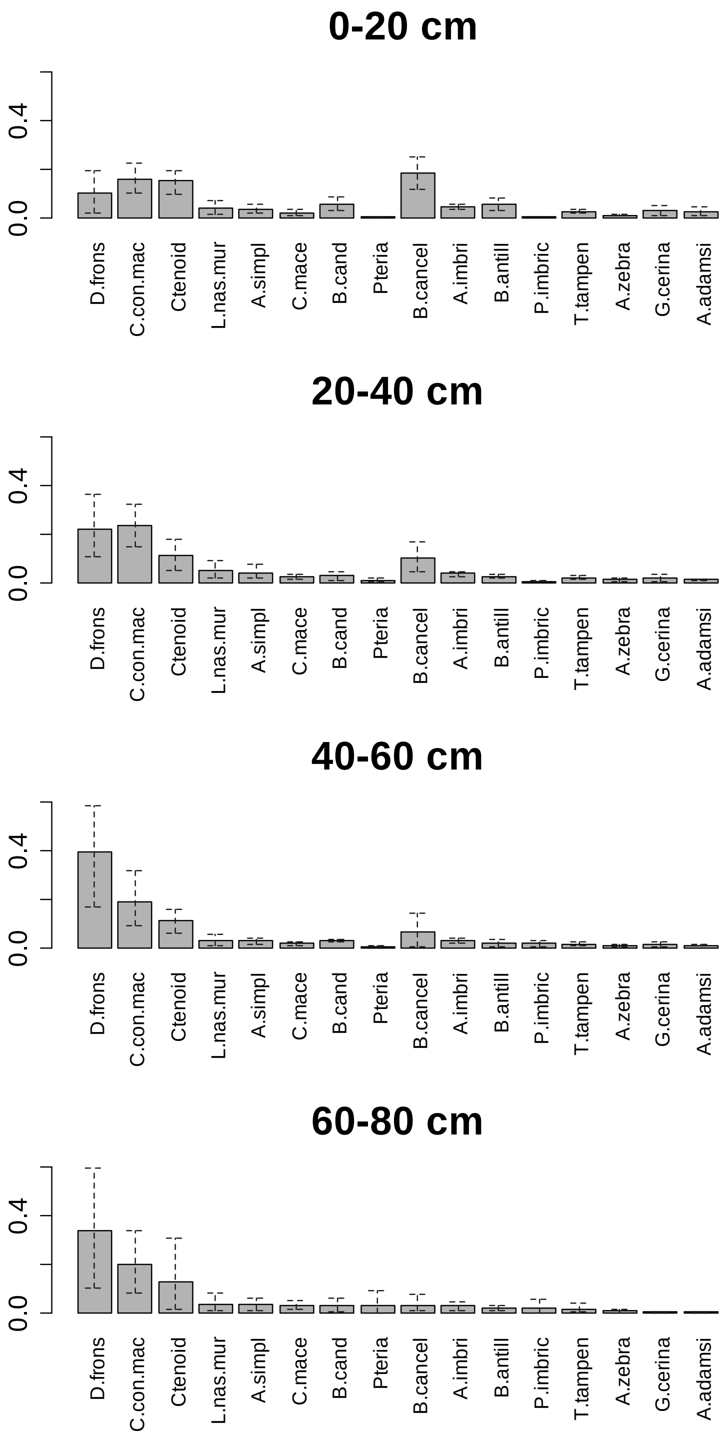


Figure 3.22. Bivalves, lagoonal sites, Bocas del Toro. Mean relative abundance (proportion individuals) of species comprising >= 1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.

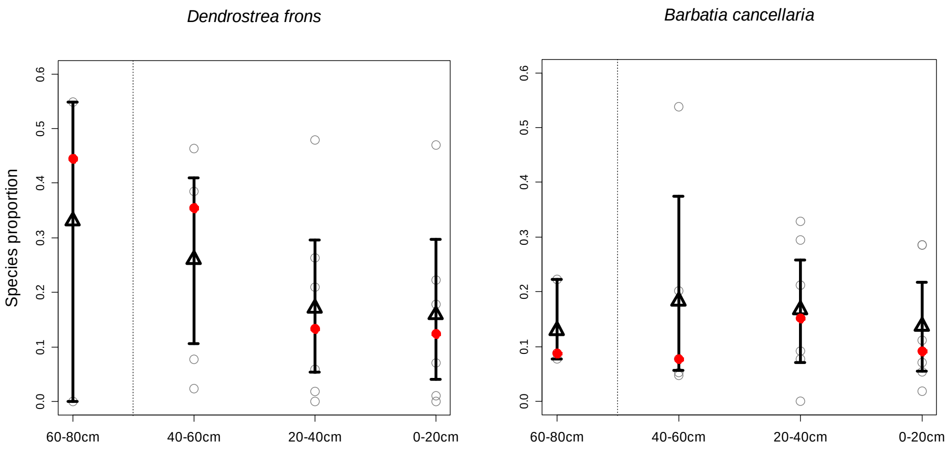


Figure 3.23. Bivalves, offshore sites, Bocas del Toro. Proportions for common gastropod species (>10% of community at any horizon). Open circles = individual pit, triangle = mean, closed circles = median, bars = 95% bootstrapped confidence intervals. One data point > 0.7 from 20-40cm horizon excluded from *Chama congragata/macerophylla* plot.

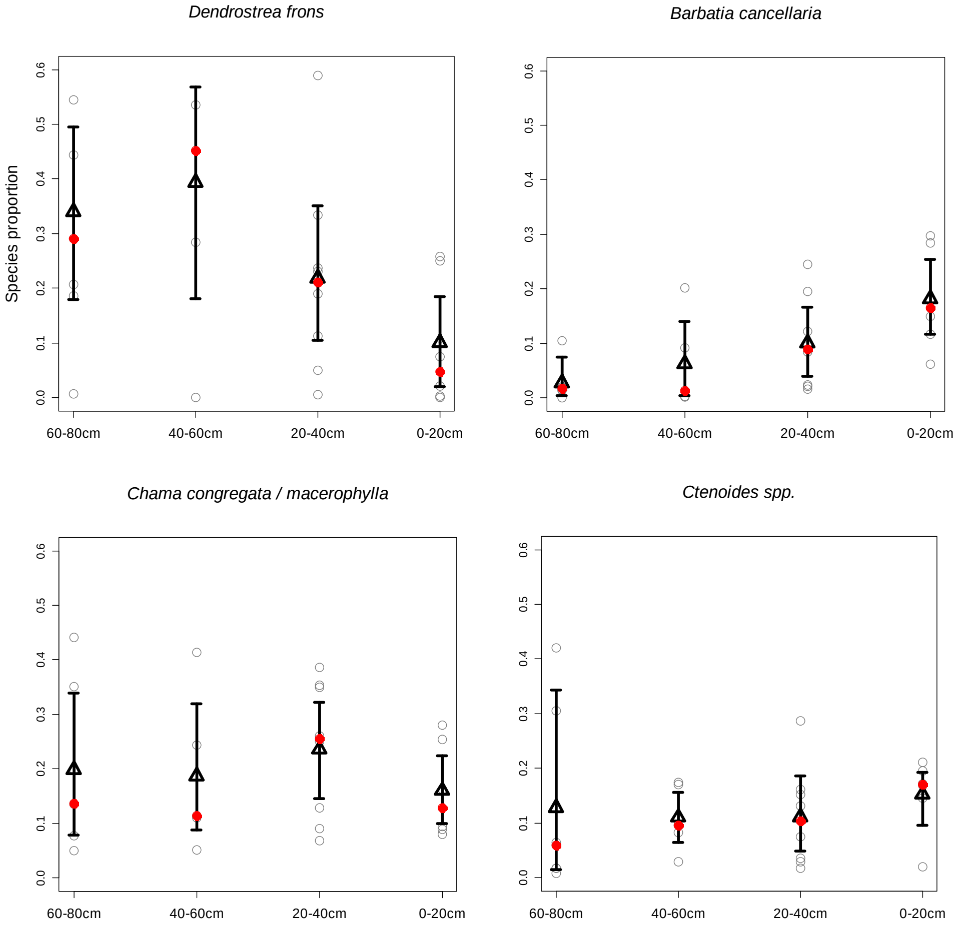


Figure 3.24. Bivalves, lagoonal sites, Bocas del Toro. Proportions for common gastropod species (>10% of community at any horizon). Open circles = individual pit, triangle = mean, closed circles = median, bars = 95% bootstrapped confidence intervals. One data point > 0.7 from 20-40cm horizon excluded from *Chama congragata/macerophylla* plot.

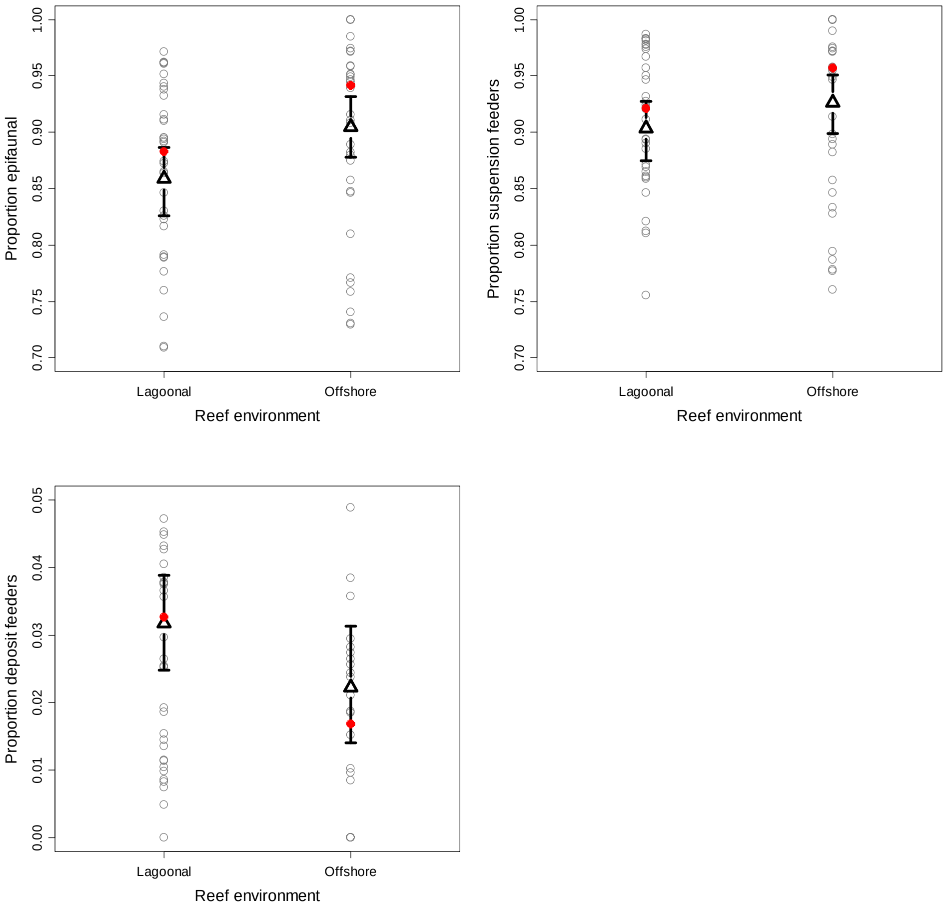


Figure 3.25. Bivalves, Bocas del Toro. Proportion individuals by feeding type and substrate relationship. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals.

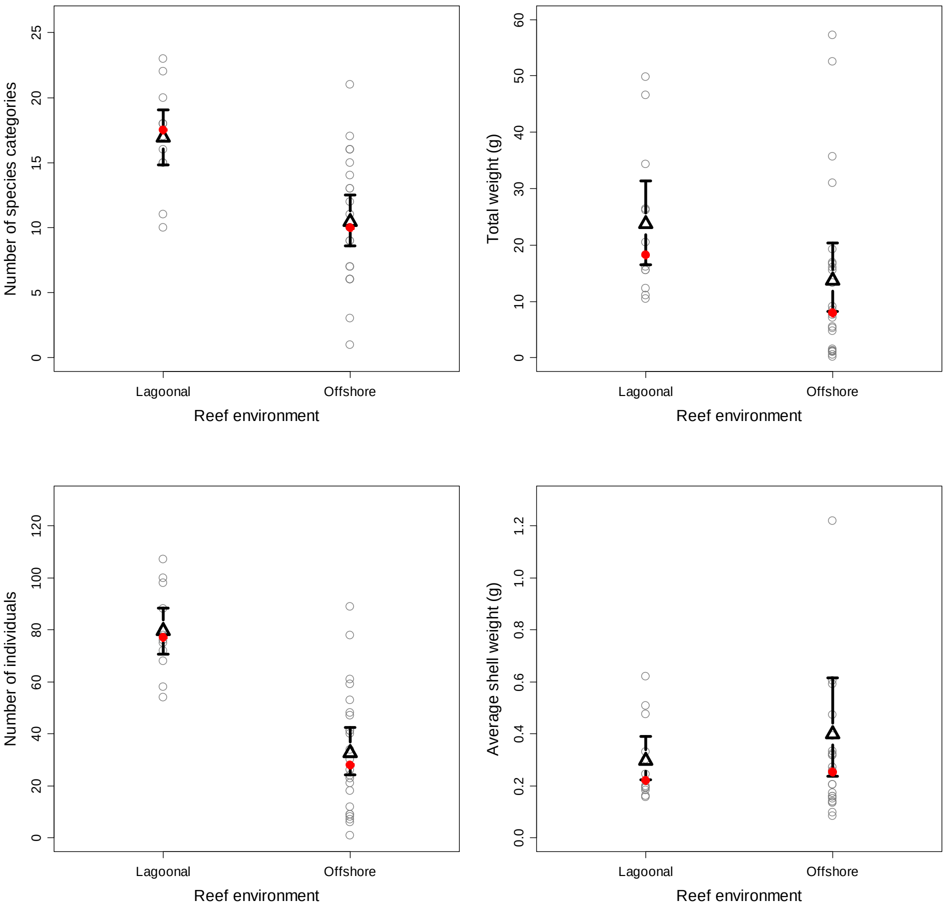


Figure 3.26. Bivalves, Costa Arriba. Richness, total weight, total abundance, and average individual weight. Open circles = individual pit, triangle = mean, closed circle = median, black bars = 95% bootstrapped confidence intervals.

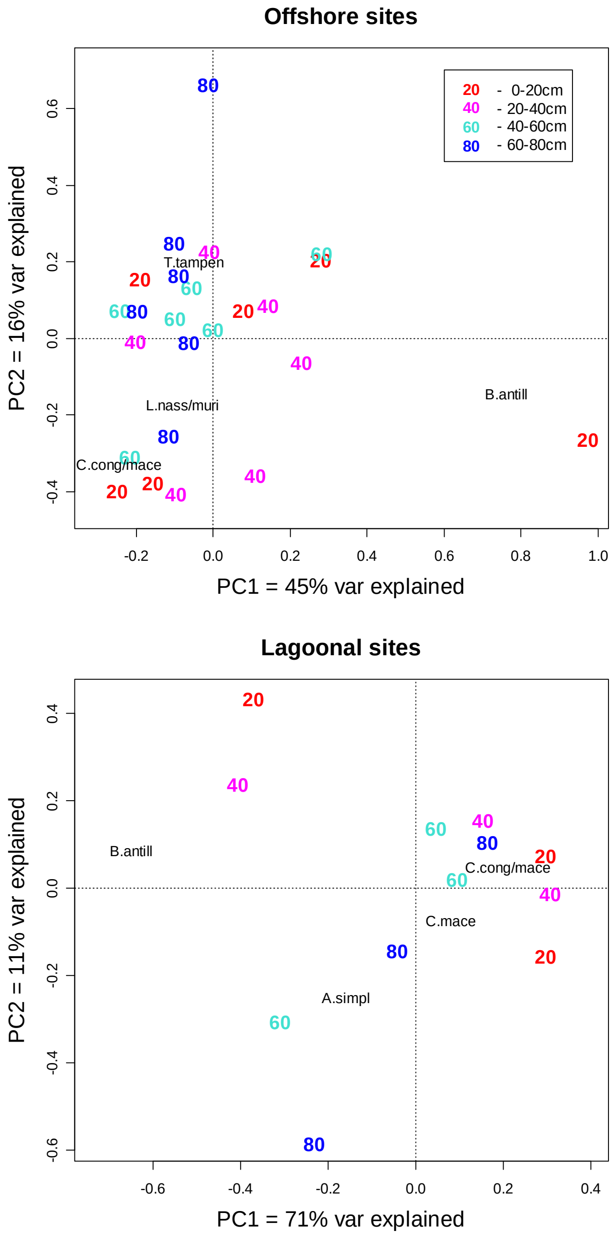


Figure 3.27. Bivalves, Costa Arriba. Principal Components Analysis of species proportion by abundance (number of individuals). Data points represent an individual horizon from an individual pit.

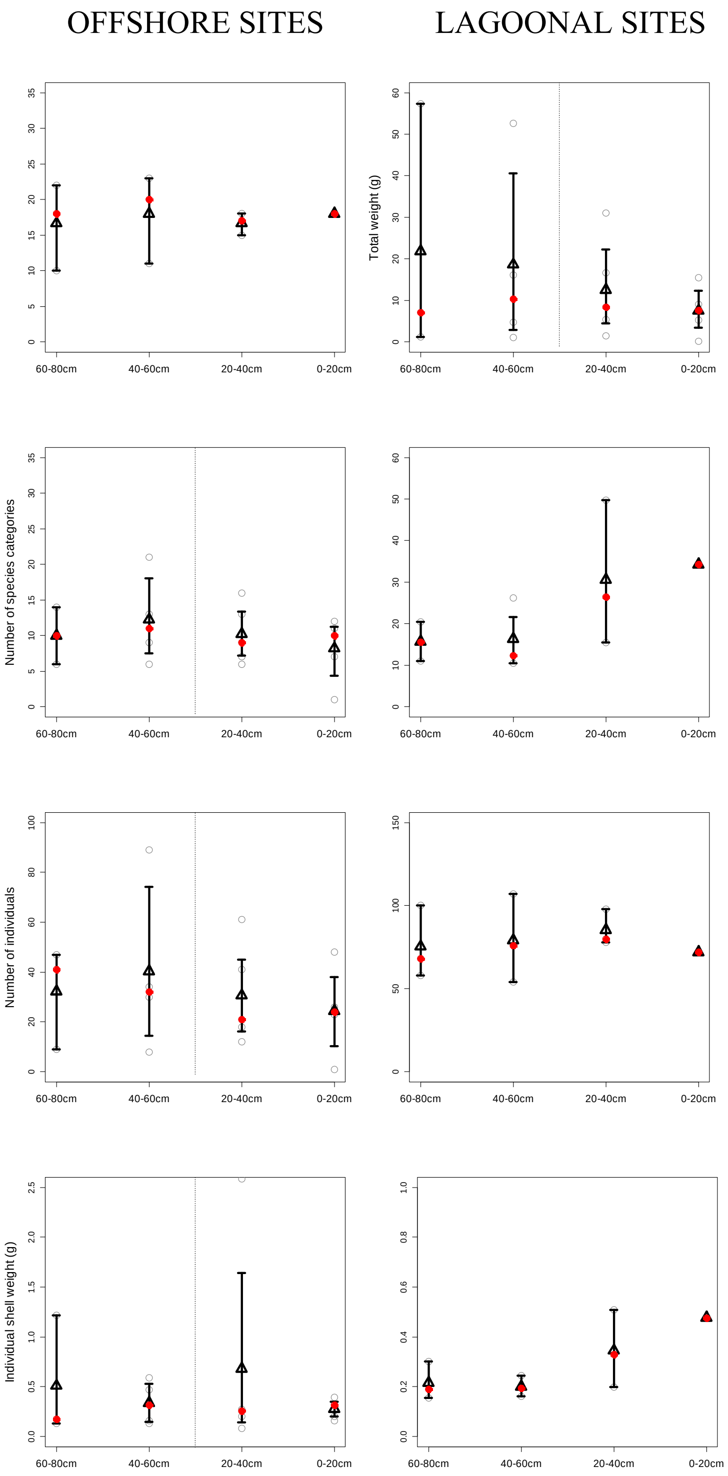


Figure 3.28. Bivalves, Costa Arriba. Richness, total weight, number of individuals, and individual shell weight by time horizon. Open circles = individual pit, triangle = mean, closed circles = median, black bars = 95% bootstrapped confidence intervals.

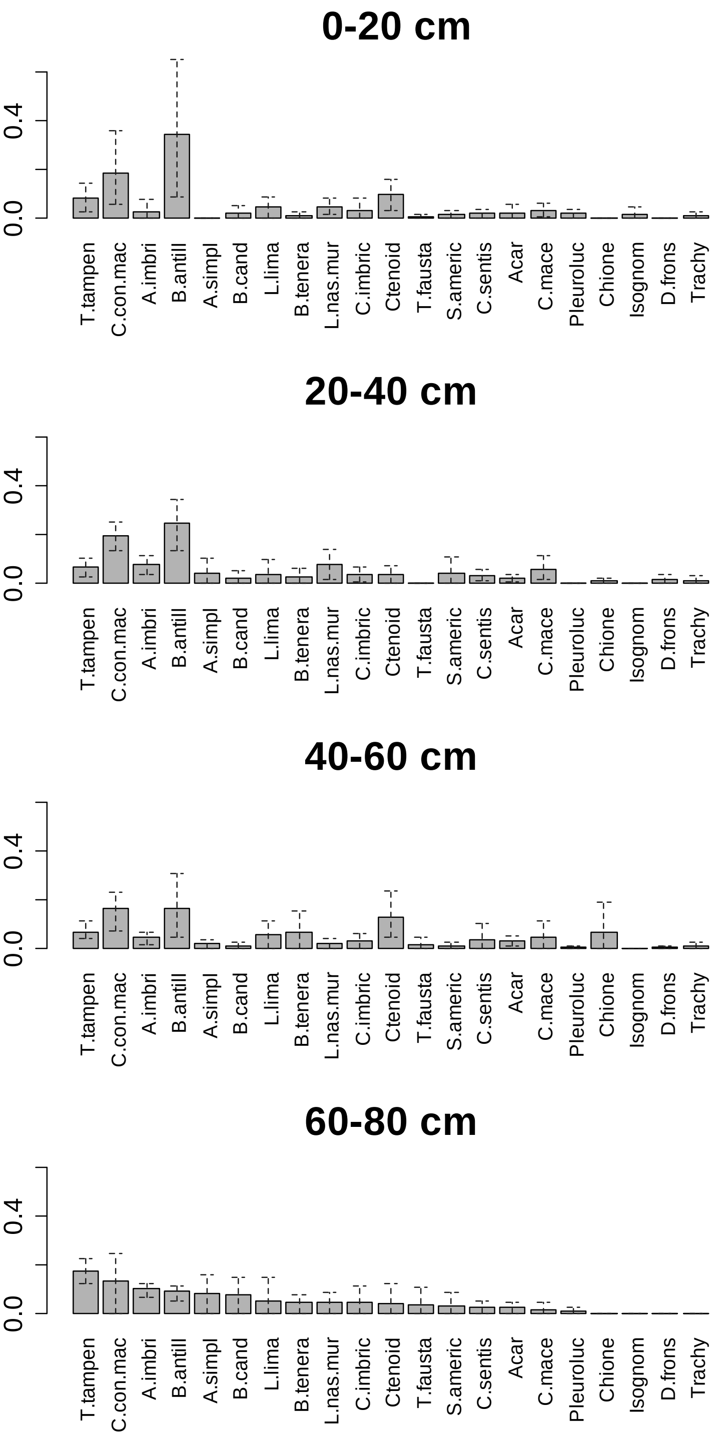


Figure 3.29. Bivalves, offshore sites, Costa Arriba. Mean relative abundance (proportion individuals) of species comprising ≥1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.

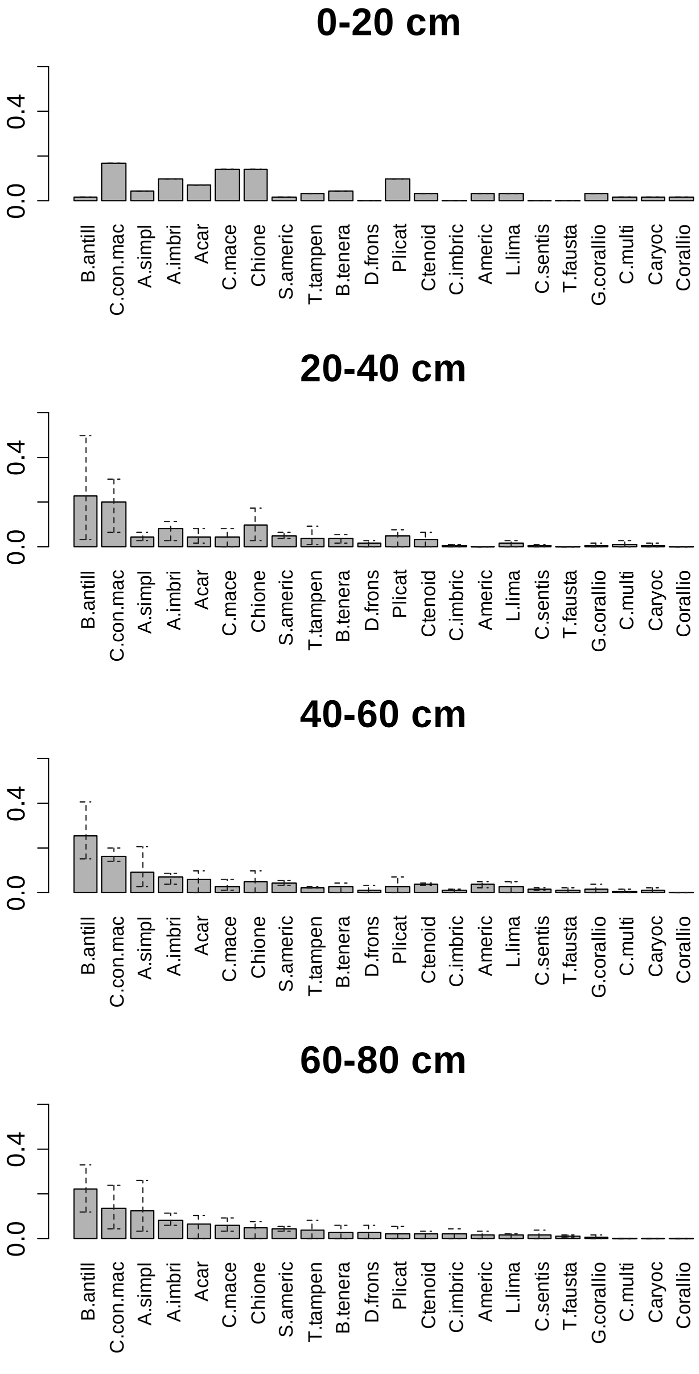


Figure 3.30. Bivalves, lagoonal sites, Costa Arriba. Mean relative abundance (proportion individuals) of species comprising ≥1% of community in at least one time horizon. Dashed bars are 95% bootstrapped confidence intervals.

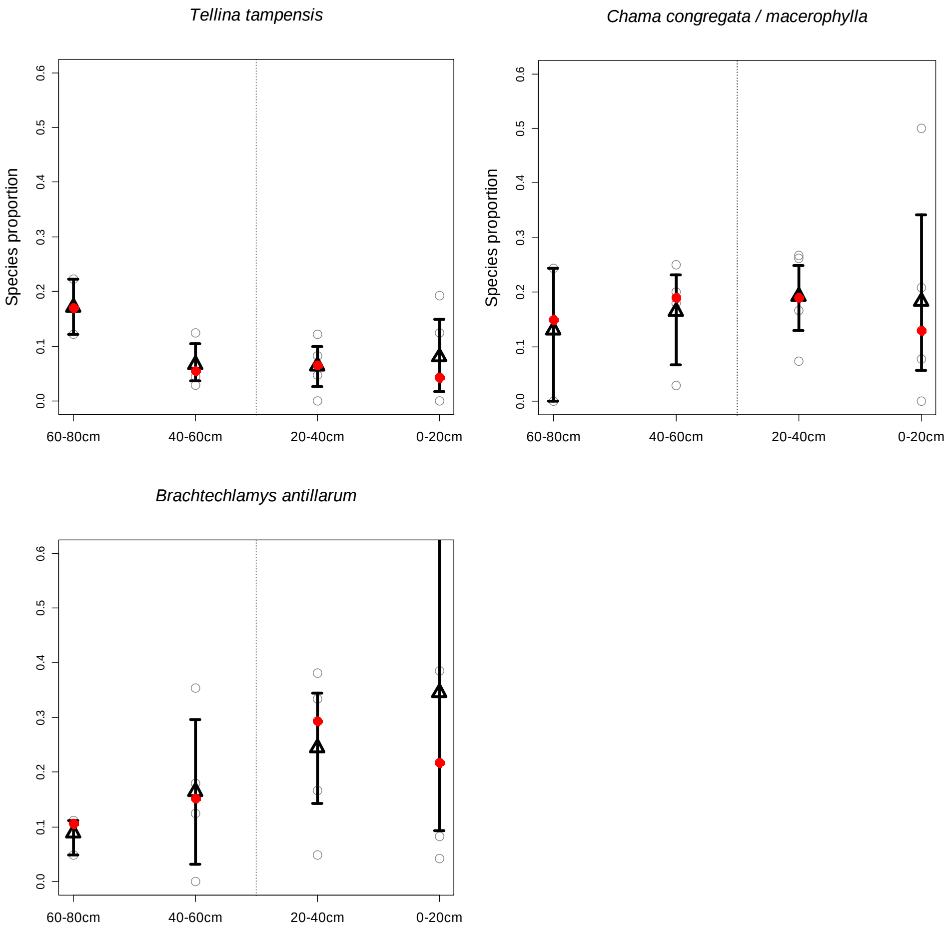


Figure 3.31. Bivalves, offshore sites, Costa Arriba. Relative abundance of dominant species. Open circles = individual pit, triangle = mean, closed circles = median, black bars = 95% bootstrapped confidence intervals. One data point > 0.7 from 0-20cm horizon excluded from *Brachtechlamys antillarum* plot.

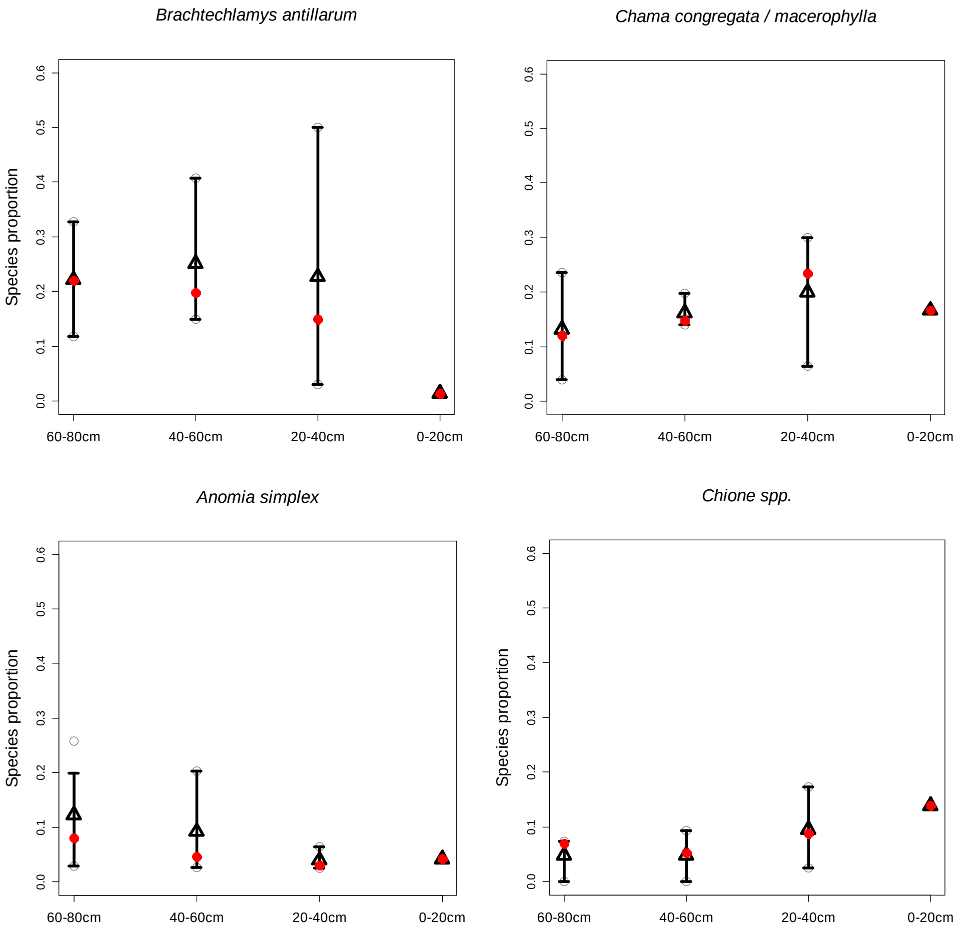


Figure 3.32. Bivalves, lagoonal sites, Costa Arriba. Relative abundance of dominant species. Open circles = individual pit, triangle = mean, closed circles = median, black bars = 95% bootstrapped confidence intervals. One data point > 0.7 from 0-20cm horizon excluded from *Brachtechlamys antillarum* plot.

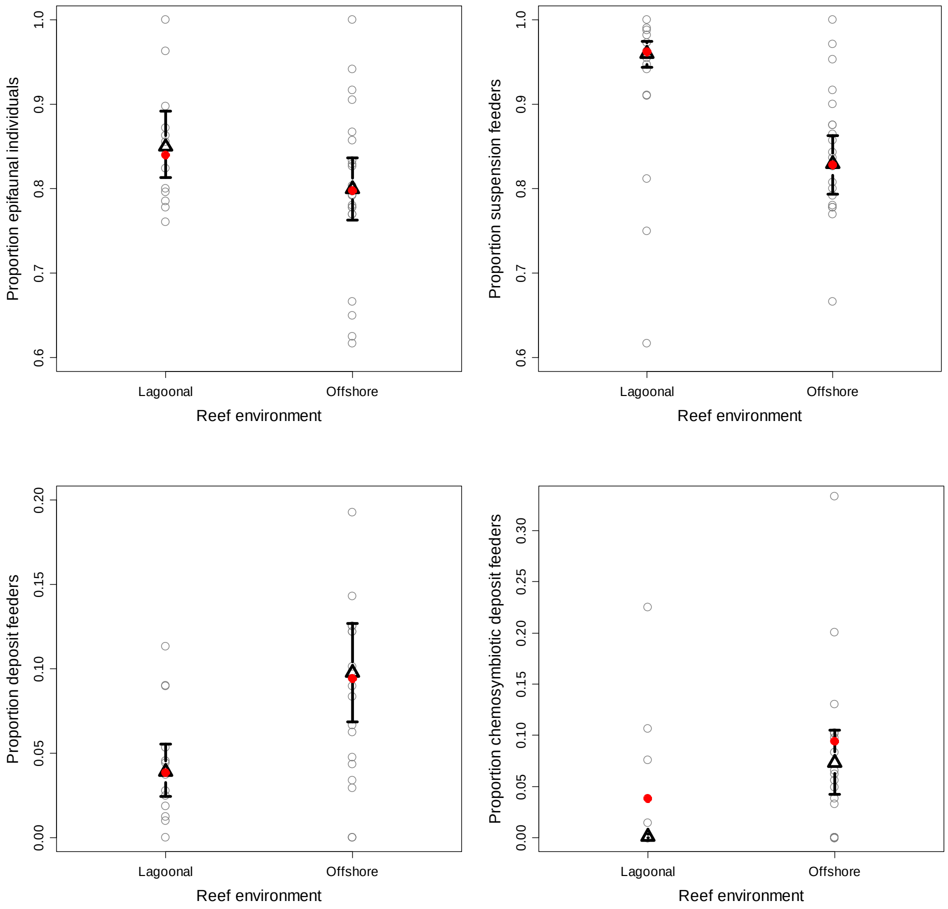


Figure 3.33. Bivalves, Costa Arriba. Proportion individuals by feeding type and substrate relationship. Grey points = individual pit, triangle = mean, red point = median, black bars = 95% bootstrapped confidence intervals.

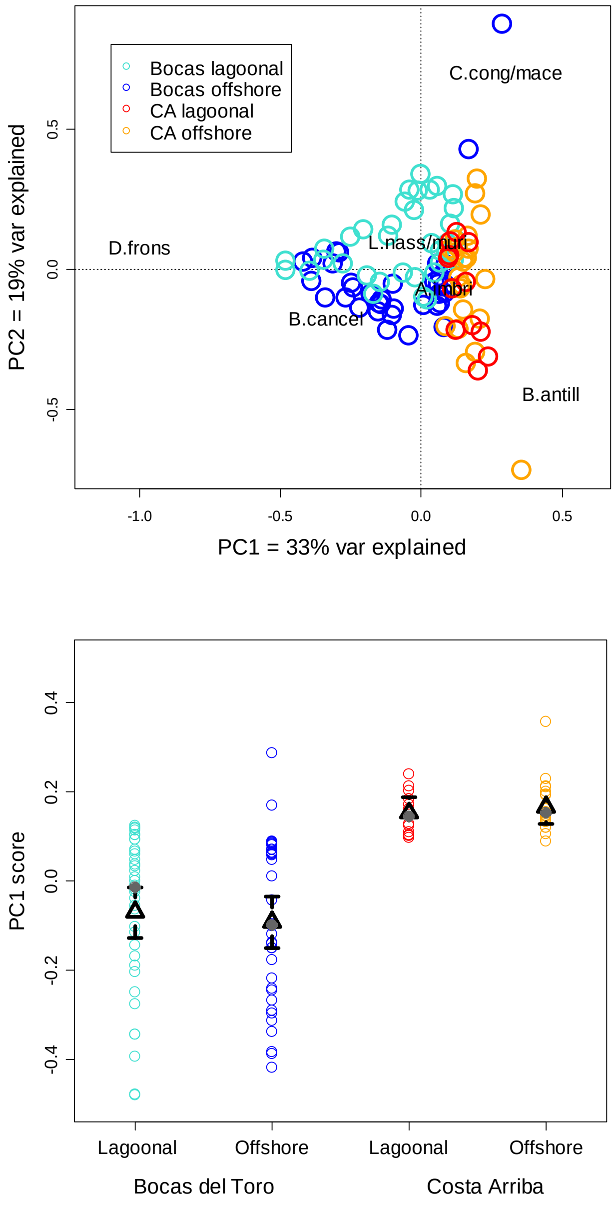


Figure 3.34. Bivalves, Bocas del Toro and Costa Arriba combined. Principal Components Analysis of species proportions and scores for first principal component by region and environment, triangle = mean scores, bars = 95% bootstrapped confidence intervals, closed circles=median score. Open circles represent an individual horizon from an individual pit.

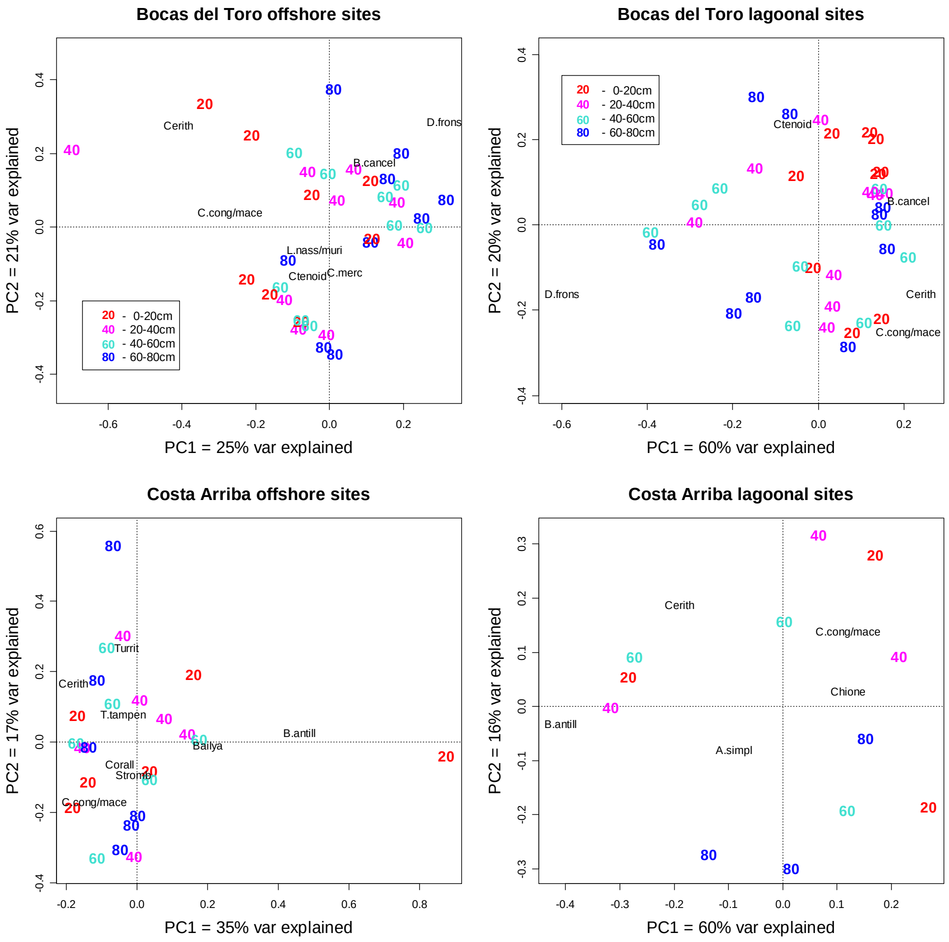


Figure 3.35. Bocas del Toro and Costa Arriba, Gastropods and bivalves combined. Principal Components Analyses by region and by environment.

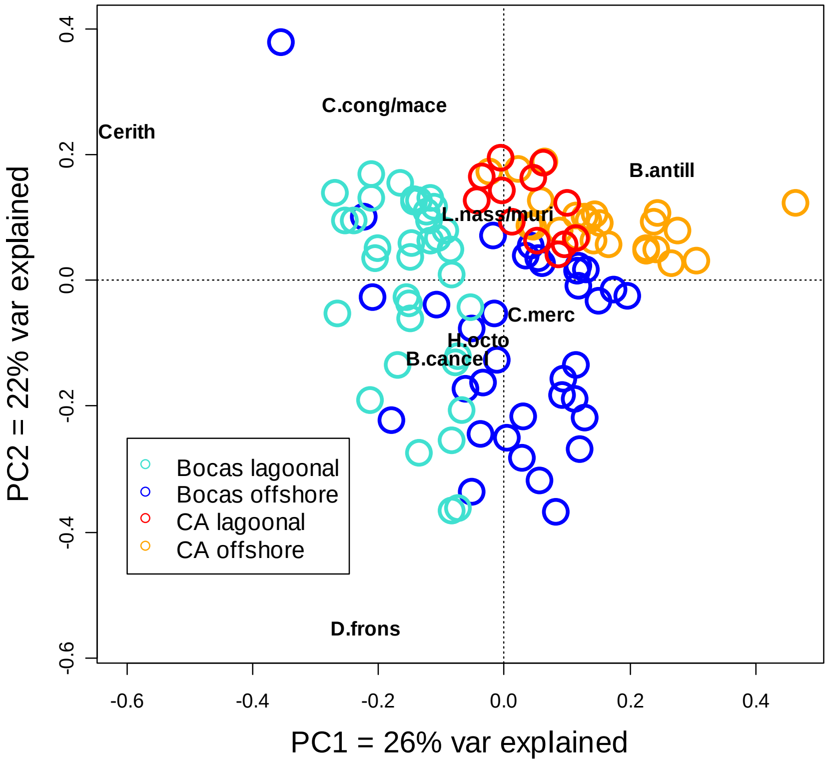


Figure 3.36. Bocas del Toro and Costa Arriba, Gastropods and bivalves combined. Principal components analysis of all death assemblages.

CHAPTER 4: ECOLOGICAL CHANGE ON CARIBBEAN CORAL REEFS BEFORE CORAL DISEASE AND BLEACHING

ABSTRACT

Caribbean coral reefs have deteriorated dramatically since the 1980s, and it is uncertain if ecological change is mainly a response to modern disturbances such as coral disease and bleaching or if change was initiated by historical disturbances such as fishing and land clearing. To help resolve this issue, I sampled coral and mollusk death assemblages from Caribbean Panama and reconstructed a timeline of ecological change in these groups extending from the 19th century to the present. The previously-dominant coral *Acropora cervicornis* and oyster *Dendrostrea frons* were in decline before 1960 and very likely during the 19th century in lagoonal reef environments exposed to terrestrial runoff and continued to decline after 1960 in offshore reef environments. Changes in taxonomic composition were accompanied by a decline in bivalve size structure and a simplification of gastropod trophic structure, indicating increasing environmental stress on these reefs over time. The most dramatic changes in coral and mollusk communities occurred at least decades before reported outbreaks of coral disease and bleaching.

TEXT

Caribbean coral reefs have been severely altered by human activities over historical time, beginning with the loss of coral reef megafauna at least centuries ago from fishing (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003, McClenachan et al. 2006, McClenachan and Cooper 2008) and followed by the loss of architectural species such as reef-building corals that has been documented since quantitative ecological studies of reefs began in the 1980s (Connell 1997, Gardner et al. 2003). Recent changes in coral communities include a widespread loss of coral abundance and a replacement of previously dominant branching species (staghorn and elkhorn *Acropora* spp. and branching *Porites* spp.) with non-branching early successional species (*Agaricia* spp. and *Porites astreoides*; Aronson et al. 2004, 2005, Green et al. 2008). Because the taxonomic composition of reef-building corals remained remarkably stable over intervals of 10,000s-100,000s years during the late Pleistocene-middle Holocene despite dramatic changes in sea level and climate (Lighty et al. 1982, Geister 1980, Jackson 1992, Aronson and Precht 1997, Pandolfi and Jackson 2001, 2006, 2007, Aronson et al. 2002, Greer et al. 2009), recent ecological shifts must be a result of novel (i.e. anthropogenic) disturbances.

Coral community shifts have been attributed to disease epidemics of corals and other reef invertebrates (Aronson et al. 1998, Harvell et al. 1999) and to coral bleaching (Aronson et al. 2000, 2002) that were first documented in the 1980s. However, the long time period of human disturbance on Caribbean reefs as well as evidence of declines in *Acropora* coral dominance coinciding with European settlement and land-clearing activities centuries ago (Lewis 1984) suggest that coral communities were changing prior to coral disease and bleaching outbreaks. An ecological baseline from the period before the 1980s is necessary in order to resolve the timing and causes of change in Caribbean coral communities.

We used paleontological sampling techniques to construct a timeline of ecological change in scleractinian coral and mollusk communities on reefs in western Caribbean Panama that extends back to the 19th century in lagoonal reef environments and to the post-1960 period in offshore reef environments. We collected coral, bivalve, and gastropod death assemblages at 5m water depth from reef sites in Bocas del Toro, Panama by excavating material down to 80cm below the modern reef from four 20cm-thick layers within a 60cm-diameter circular pit. The coral life assemblage was also assessed from 40m long point-intercept line transect surveys with sampling at 5cm increments. This procedure resulted in five time horizons total for corals (four death plus one life) and four death horizons for mollusks. Life and death assemblages were sampled from three circular pits from each of six reef sites. Three sites were from offshore reef environments with less exposure to terrestrial runoff and three were from semi-protected lagoonal environments with greater exposure to terrestrial runoff. Layers within pits were assumed to be in stratigraphic order because: (a) most coral skeletons were in life position when excavated and showed no evidence of biological or physical re-working, (b) the location of the study region well outside the Atlantic hurricane zone precluded the large-scale physical transport of rubble, and (c) clear and progressive species gradients were observed among adjacent layers.

The timing of change in coral and mollusk community parameters was assessed from radiocarbon dates of coral material from each death horizon in each pit. Due to the dramatic increase in bomb-produced surface water Δ14C values circa 1960 AD in the Caribbean (Kilbourne et al. 2007), it was possible to clearly distinguish between radiocarbon ages from the period before and after this year. Trends in coral and mollusk communities occurring before 1960 were assessed from the ten pits (1 offshore and 9 lagoonal) that contained more than one pre-bomb horizon, and trends occurring after 1960 were assessed from the eight pits (all offshore) that contained one or no pre-bomb horizons. Statistical significance of trends was determined from the Wilcoxon Signed-Ranks non-parametric paired t-test. Radiocarbon results were calibrated to calendar age ranges using coral (Kilbourne et al. 2007) and tree-ring reference datasets (Hughen et al. 2004, Reimer et al. 2004).

Coral communities were dominated by branching *Acropora cervicornis* and *Porites furcata* or foliaceous *Agaricia tenuifolia*. *A. cervicornis* was dominant or subdominant in older time horizons at offshore sites as well as at lagoonal sites characterized today by turbid waters (D'Croz et al. 2005). Molluscan communities were dominated by the herbivorous gastropod *Cerithium* spp. and by the epifaunal suspension feeding bivalves *Dendrostrea frons*, *Chama* spp., and *Barbatia cancellaria*. Dominance by epifaunal and suspension feeding mollusks indicated that throughout the pre- and post-1960 periods reefs had a high availability of live or dead coral substrates and relatively high amounts of planktonic productivity from nutrient inputs from river runoff.

Although coral and molluscan community composition were highly variable among pits, significant temporal changes were detected in community parameters. Pits that contained more than one pre-bomb horizon (primarily from lagoonal sites) displayed significant changes in coral community composition prior to 1960 and pits that contained one or no pre-bomb horizons (all from offshore sites) displayed significant changes after 1960. Calibrated radiocarbon age ranges for each pit and layer and estimates of sediment and rubble accumulation rates from lagoonal sites in Bocas del Toro (Hilbun 2009) and Belize (Aronson et al. 2004) indicated that the deepest pre-bomb horizons were from approximately 80-140 years old (Figure 4.1).

The relative abundance of the staghorn coral *A. cervicornis* declined significantly between the deepest and shallowest pre-1960 horizons, from 42-6% of the coral community on average ($V = 28$, $p < 0.05$; Figure 4.1). *A. cervicornis* continued to decline from the post-1960 period to the present in the same pits, from 6-0% of the coral community on average, although the relative abundance of this species was so low by 1960 that the later decline was not statistically significant. The relative abundance of the branching coral *P. furcata* increased significantly in pits that lost *A. cervicornis* (from 10-26% of the coral community on average, $V = 1$, $p = 0.05$), but did not change in pits where *A. cervicornis* was not present at any horizon. Because the total amount of coral material did not vary among horizons, the increase in *P. furcata* relative abundance represented a replacement of *A. cervicornis* by this species prior to 1960. A significant decline in the relative abundance of *A. cervicornis* also occurred in the offshore pits during the post-1960 period, declining from 33-7% of the community on average between the oldest post-1960 horizon and the modern reef ($V = 36$, $p < 0.01$, Figure 4.1). A qualitative assessment of coral species proportions across death and life horizons revealed a gradual and progressive two-phase successional sequence of dominance by branching *A. cervicornis* → branching *P. furcata* → foliose *A. tenuifolia* that occurred before 1960 at lagoonal sites and continued in the post-1960 period to the present at offshore sites (Figure 2.6).

Significant changes in molluscan community composition and size structure occurred during the pre- and post-1960 intervals (Table 4.1). Change in bivalve taxonomic composition prior to 1960 and primarily at lagoonal sites included a significant decline in the previously dominant oyster *D. frons* (from 40-18% on average;

V=42, $p < 0.05$) and a significant increase in the mussel *B. cancellaria* (from 6-18%; V=0, $p < 0.05$). A significant decline in *D. frons* also occurred after 1960 at offshore sites (from 27-12% on average, V = 32, p = 0.05). *D. frons* attaches to and lives primarily on branching plexaurid and gorgoniid octocorals and secondarily on *A. cervicornis* (Forbes 1971), while *B. cancellaria* attaches onto coral heads and coral rubble (Kobluk and Lysenko 1986, Cerridwen and Jones 1991). The changes in relative abundance of these two species was not related to human exploitation because neither bivalve was harvested in the past (Wake, Linares 1980) and they are not harvested today (Carpenter 2002).

The decline in *D. frons* prior to 1960 is a strong indication of an historical decline in abundance of its gorgonian and/or scleractinian branching coral hosts. Disease epidemics decimated Caribbean gorgonian populations in the 1980s and 1990s (Guzmán and Cortés 1984, Nagelkerken et al. 2007), but primarily affected species not commonly associated with *D. frons*. The decline of this oyster before modern ecological surveys in the 1980s signifies a mass mortality of gorgonians in Bocas del Toro that preceded the first reported disease outbreaks. The relative abundance of *A. cervicornis* and *D. frons* were highly positively correlated (Spearman $\rho = 0.66$ for offshore and 0.84 for lagoonal sites, $p < 0.001$) and this oyster was virtually absent from pits and horizons that did not contain *A. cervicornis*, strongly suggesting a causal link between the species declines.

Significant changes in bivalve size structure occurred prior to 1960 primarily at lagoonal sites and after 1960 at offshore sites. Average individual bivalve shell weight (a proxy for size) was halved before 1960 primarily at lagoonal sites (V=47, $p < 0.05$), and was also halved after 1960 at offshore sites (V = 36, $p < 0.01$). The decline occurred only in epifaunal bivalves (pre-1960: V=47, p=0.06; post-1960: V = 33, $p < 0.05$) but not in infaunal bivalves. Change in gastropod trophic structure occurred after 1960 and at offshore sites only. The proportion of carnivorous gastropods declined during the 1960 interval ($V = 35$, $p < 0.05$), resulting in a level of dominance at offshore sites by herbivores similar to that at lagoonal sites (Table 4.1). As with the changes in bivalve species composition, changes in size and trophic structure were not related to human exploitation because the affected species and ecological guilds were not harvested in the past (Linares 1980, Wake) and are not harvested today (Carpenter 2002).

The temporal patterns in the taxonomic, size, and trophic structure of the coral and molluscan communities observed in the life and death assemblages show that reefs in Bocas del Toro were experiencing large-scale ecological change before 1960 that likely were underway during 19th century. A decline in the relative abundance of the previously dominant branching coral *A. cervicornis*, oyster *D. frons*, and gorgonian sea whips as well as a 50% decline in the individual size of bivalves had already occurred prior to 1960 at lagoonal sites and at one offshore pit, decades before modern episodes of coral disease and bleaching. The timing of these changes implicates historical anthropogenic disturbances such as fishing and land-clearing as ultimate causes.

The observed changes in molluscan size and trophic structure signal the deterioration of reef environmental conditions over time in Bocas del Toro. Reef mollusk communities dominated by small individuals and low trophic levels indicate high environmental stress from terrestrial runoff and restricted water flow (Jackson 1972, McClanahan 1992) that disproportionately affect larger and higher trophic level species. The shift in trophic structure of gastropod communities at offshore sites towards that of higher-turbidity and higher-nutrient lagoonal sites indicates that these reef environments may be becoming more similar because degraded conditions are expanding to offshore environments. Overall, changes were greater at lagoonal sites, but the pits from this environment also extended further back in time.

Human population and deforestation have increased substantially over the past century in Bocas del Toro, increasing sediments, nutrients, and pollutants to adjacent coral reef environments (Guzmán 2003) that negatively impact corals (Fabricius 2005) and mollusks (Donohue and Irvine 2003, McIntyre et al. 2003, Salanki et al. 2003). Large-scale land clearing in the region began at the turn of the 20th century for intensive banana production (Stephens 2008) and has rapidly increased for tourism since the 1980s (Guzmán 2003). The paleontological data collected here reveal that during this time land clearing dramatically transformed lagoonal reefs in Bocas del Toro from communities that contained a historically high abundance of *A.. cervicornis*, *D. frons*, and gorgonian sea whips to communities dominated today by *A.. tenuifolia* and characterized by turbid waters that are unsuitable for *A.. cervicornis*. These same changes have occurred more recently on offshore reefs in Bocas del Toro within the past 50 years, and threaten to degrade reefs in this region that contain the last remaining large stands of *A.. cervicornis* (Guzmán and Guevara 1998). The historical changes that occurred in this region before the reported appearance of coral disease and bleaching suggest that recent disturbances may be symptoms of deeper-rooted change.

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Table 4.1. Temporal trends in coral and mollusk communities.

Species or ecological guild	**Parameter of interest**	**Pre-1960 trend (lagoonal sites primarily)**	**Significant trend during period before 1960?**	**Post-1960 trend (corals = lagoonal and offshore sites, mollusks = offshore sites only)**	**Significant trend during period after 1960?**
Acropora cervicornis	species proportion	decline	yes	decline	yes - lagoonal sites only
Porites furcata	species proportion	decline	yes	decline	no
Agaricia tenuifolia	species proportion	increase	no	increase	no
Dendostrea frons	species proportion	decline	yes	decline	yes
bivalves	average individual size	decline	yes	decline	yes
carnivorous gastropods	guild proportion	decline	no	decline	yes

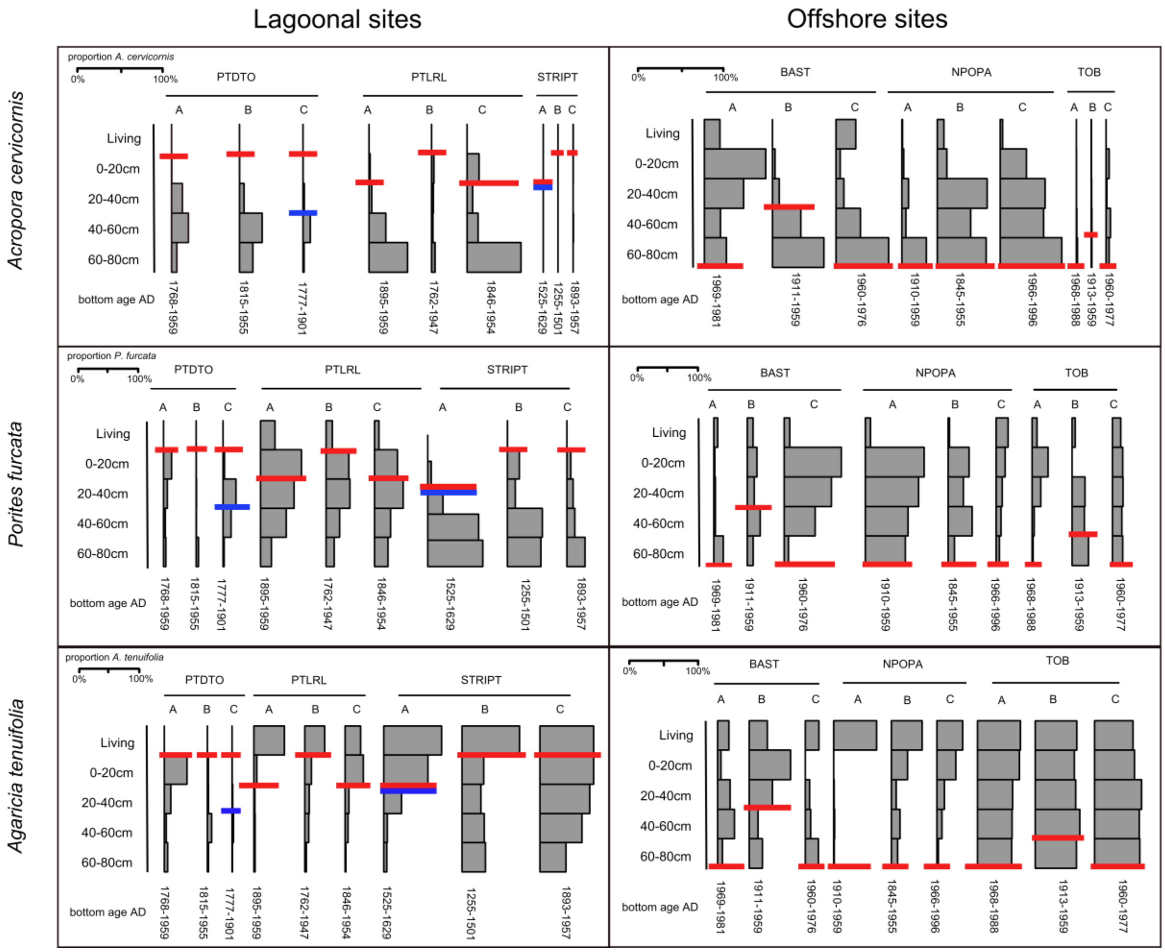

Figure 4.1. Proportion of dominant coral taxa by individual pit and time horizon. Horizontal blue line indicates boundary between pre- and post-1900 AD, red line indicates boundary between pre- and post-1960 AD.

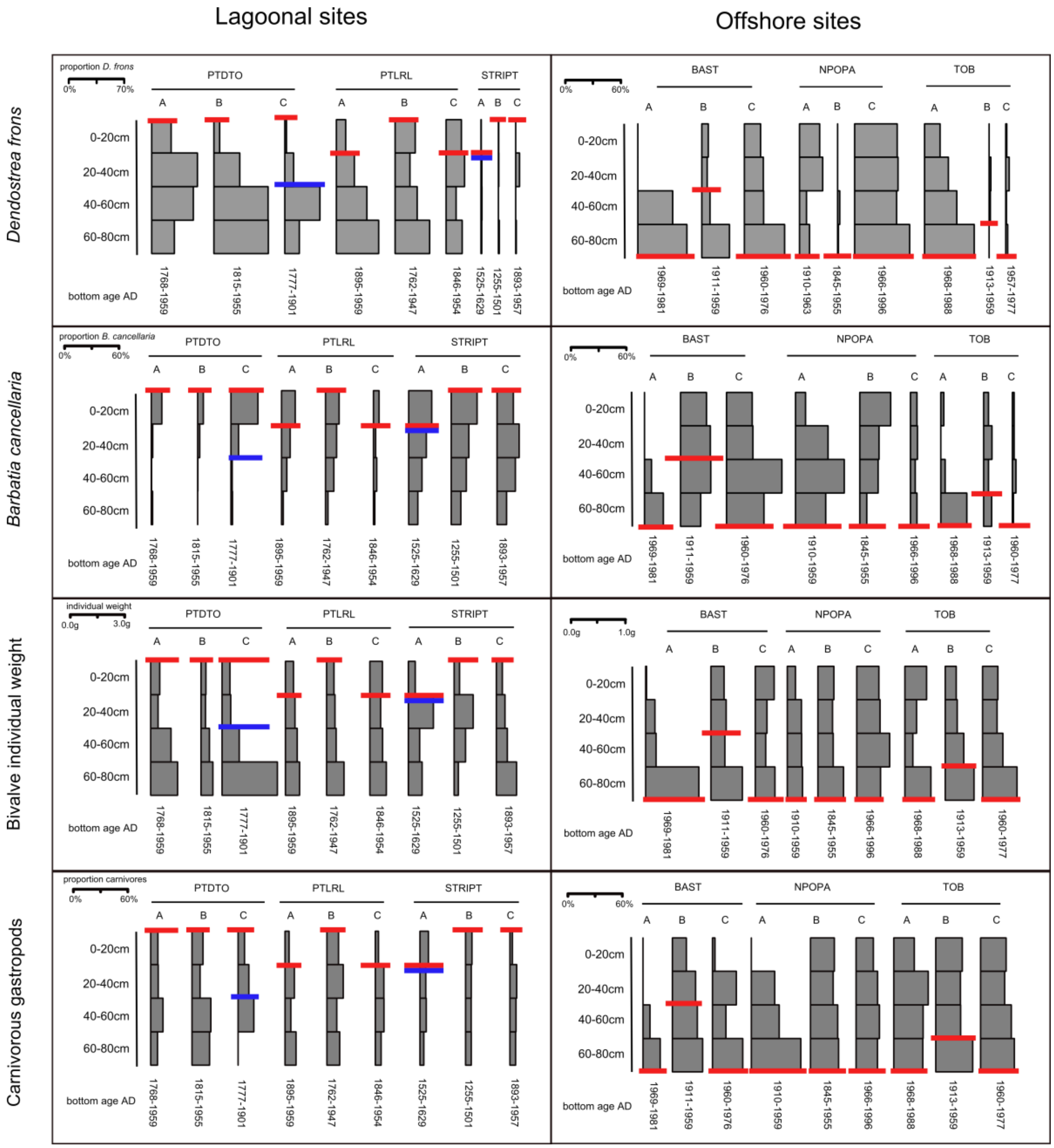

Figure 4.2. Mollusk community parameters by individual pit and time horizon. Horizontal blue line indicates boundary between pre- and post-1900 AD, red line indicates boundary between pre- and post-1960 AD.