Molluscan subfossil assemblages reveal the long-term deterioration of coral reef environments in Caribbean Panama

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ABSTRACT

Caribbean reef corals have declined sharply since the 1980s, but the lack of prior baseline data has hindered identification of drivers of change. To assess anthropogenic change in reef environments over the past century, we tracked the composition of subfossil assemblages of bivalve and gastropod mollusks excavated from pits below lagoonal and offshore reefs in Bocas del Toro, Panama. The higher prevalence of (a) infaunal suspension-feeding bivalves and herbivorous and omnivorous gastropods in lagoons and (b) epifaunal and suspension-feeding bivalves and carnivorous and suspension-feeding gastropods offshore reflected the greater influence of land-based nutrients/sediments within lagoons. Temporal changes indicated deteriorating environmental conditions pre-1960 in lagoons and post-1960 offshore, with offshore communities becoming more similar to lagoonal ones since 1960. Relative abundances of dominant bivalve species tracked those of their coral hosts, revealing broader ecosystem effects of coral community change. The nature and timing of changes implicate land-based runoff in reef deterioration.

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1. Introduction

Caribbean coral reefs have undergone a dramatic transformation over historical time, beginning with a loss of coral reef megafauna centuries to millennia ago (Jackson et al., 2001; Pandolfi et al., 2003) that culminated with a ~50% loss of corals since the initiation of systematic ecological surveys in the 1970s (Jackson et al., 2014). These declines have been attributed to multiple anthropogenic stressors including fishing, land-based pollution, and global climate change as well as coral and urchin disease epidemics that began in the 1980s and whose drivers remain unresolved (Aronson and Precht, 2001; Hughes et al., 2003; Fabricius, 2005; Jackson et al., 2014). Because reef ecological survey data is restricted to the past few decades and multiple anthropogenic disturbances have been affecting reefs simultaneously, the relative importance of these stressors is debated (Hughes et al., 2003). Without an ecological baseline for Caribbean reef ecological

communities and environments that predates disease and bleaching epidemics, it is impossible to disentangle or mitigate the drivers responsible for recent catastrophic declines.

Coral reefs within the Bocas del Toro region ("Bocas") along the western Caribbean coast of Panama are no exception to the overall Caribbean trend. Benthic surveys have revealed an up to 10% decline in live coral cover from 1999–2002, the first four years of ongoing monitoring in this region (Guzmán, 2003). A recent reef coring program conducted at fringing reefs in Bocas' Almirante Bay found a general transition in coral dominance from *Porites furcata* to *Agarica tenuifolia* that occurred sometime after 1960 and was unprecedented over a millennial scale (Aronson et al., 2004, 2005). The analysis of subfossil coral assemblages excavated from large pits below modern reefs in Bocas confirmed that recent reef deterioration has deeper historical roots: the loss of the regionally co-dominant staghorn coral *Acropora cervicornis* occurred before 1960 and in some cases likely as far back as the early 1900s in lagoonal reefs, contemporaneous with the onset of land clearing for industrial agriculture (Cramer et al., 2012; Cramer, 2013). This change predated urchin and coral disease and coral bleaching events by at least two decades at lagoonal reefs, confirming the important role of local anthropogenic stressors.

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The majority of Caribbean coral reef monitoring has been restricted to surveys of corals, macroalgae, urchins, and fish (Jackson et al., 2014), with little effort devoted to tracking the status of other common reef organisms and virtually no attempts to track multi-year changes in reef environmental quality (e.g., water clarity, siltation, eutrophication; Jackson et al., 2014). Bivalve and gastropod mollusks are abundant and diverse components of Caribbean coral reefs with a variety of documented life habits, making them ideal indicators of reef environmental conditions (Todd, 2001; Oehlmann and Schulte-Oehlmann, 2002; Todd et al., 2002). Bivalve and gastropod community composition has been successfully utilized to infer environmental gradients in coral reef and seagrass habitats across space (Jackson, 1972, 1973; Heck, 1977; McClanahan, 1992, 2002a) and over geological (Allmon, 2001; Johnson et al., 2007; Leonard-Pingel et al., 2012) and ecological timescales (McClanahan, 2002b). Their usefulness as environmental proxies can therefore be leveraged to provide additional information about the timing and causes of recent reef deterioration.

To produce a pre-disease/bleaching baseline and timeline of change for coral reef environments in Bocas, we reconstructed gastropod and bivalve community composition from the past 50–150 years from subfossil assemblages excavated from large pits below modern reefs. These data were collected to provide ecological context for historical changes in coral communities observed on these same reefs (Cramer et al., 2012). First, we used the variability of the reef molluscan community across a known natural environmental gradient (lagoonal versus offshore reefs) to test the reliability of faunal differences as environmental proxies. Second, we assessed molluscan community change over the past 50–150 years to reconstruct a more detailed picture of the nature of reef environmental change during a period of increasing human disturbance. This study serves as the first complete description of modern or historical coral reef bivalve and gastropod communities from the southwestern Caribbean, and provides additional evidence that land-use changes associated with the growth of banana plantations in the coastal zone of Bocas during the first half of the 20th century were a driver of historical reef degradation in this region.

1.1. Mollusks as environmental indicators

The dominant feeding habits and substrate relationships exhibited by bivalves and gastropods can be used to assess various aspects of the reef environment including wave action, relative amount of planktonic/benthic productivity, the relative amount of hard/soft substrata, and stress (Table 1). The prevalence of suspension-feeding bivalves or gastropods indicates high current/wave action or lower amounts of suspended sediments (Levinton, 1991; Birkeland, 1987, 1988; Vermeij, 1990) while the prevalence of deposit feeders indicates low-flow conditions or higher amounts of organic debris (Sanders, 1958; Jackson, 1972; Arruda et al., 2003). Reef environments with higher relative planktonic productivity are likely to host more suspension feeders, while reef environments with high benthic algal productivity can support more herbivores (Russ, 2003). Dominance of epifaunal or boring bivalves is an indication of high (live or dead) coral cover (Hauser et al., 2007; Harries and Sorauf, 2010), while dominance of infaunal bivalves is an indication of high sediment and lower coral cover (Leonard-Pingel et al., 2012). Molluscan life habits may also indicate the amount of environmental stress in a reef environment, which can have a natural or anthropogenic source. Simplified, herbivore-dominated food webs are typically found in high stress environments (Odum, 1985; McClanahan, 1992). Likewise, higher relative amounts of infaunal forms may indicate the presence of stressful environmental conditions above the sediment–water interface, such as fluctuating oxygen concentrations,

temperature, and/or salinity (Jackson, 1972, 1973), while prevalence of chemosymbiotic forms indicate low oxygen conditions (Jackson, 1973; Ríos-Jara et al., 2008).

The size structure of bivalve and gastropod communities provides an additional reliable indicator of reef environmental condition. 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 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; Roy et al., 2003; O'Dea et al., 2014).

2. Materials and methods

2.1. Study region

Bivalve and gastropod subfossil assemblages were sampled from the Bocas region along the western coast of Caribbean Panama. The region 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 but is geographically closer to the current epicenter of banana production in the floodplain of the Changuinola River (Fig. 1). Outside and to the east of these lagoons, the coastline is generally more exposed to oceanic conditions. A steep coastal mountain chain extending up to 400 m in altitude runs approximately 1–3.5 km inland from the coast, resulting in short and fast-flowing rivers that produce a consistent flow of fresh water to the coastal zone year-round (Guzmán et al., 2005). The water from these rivers forms a freshwater lens that is approximately 0.5 m thick and rich in suspended organic material that flows into both lagoons (Guzmán et al., 2005). Both Almirante Bay and Chiriquí Lagoon have a higher concentration of nutrients, chlorophyll, and zooplankton biomass compared to environments with more exposure to the Caribbean Sea and less exposure to river runoff (D'Croz et al., 2005). The region has a long history of human exploitation of coastal environments extending back at least 1000 years (Roberts, 1827; Linares, 1980; Pandolfi et al., 2003; Wake et al., 2013), with large-scale coastal land clearing for banana agriculture beginning in the late 1800s in Chiriquí Lagoon and continuing today primarily in the northwest portion of Almirante Bay (Gordon, 1982; Guzmán, 2003; Cramer, 2013). The lower water clarity within the lagoons has been attributed in part to the input of sediments and pollutants from agriculture, mining, and oil transport and storage within the coastal region (Guzmán and Jimenez, 1992; Guzmán and Garcia, 2002; Guzmán, 2003).

2.2. Data collection

Molluscan subfossil assemblages were collected from six reef sites total. 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. Three reef sites (STRI Point, Punta Donato, Punta Laurel) were located in lagoonal environments and three (Bastimentos Island, North Popa Island, Tobobe) were located in semi-exposed offshore reef environments
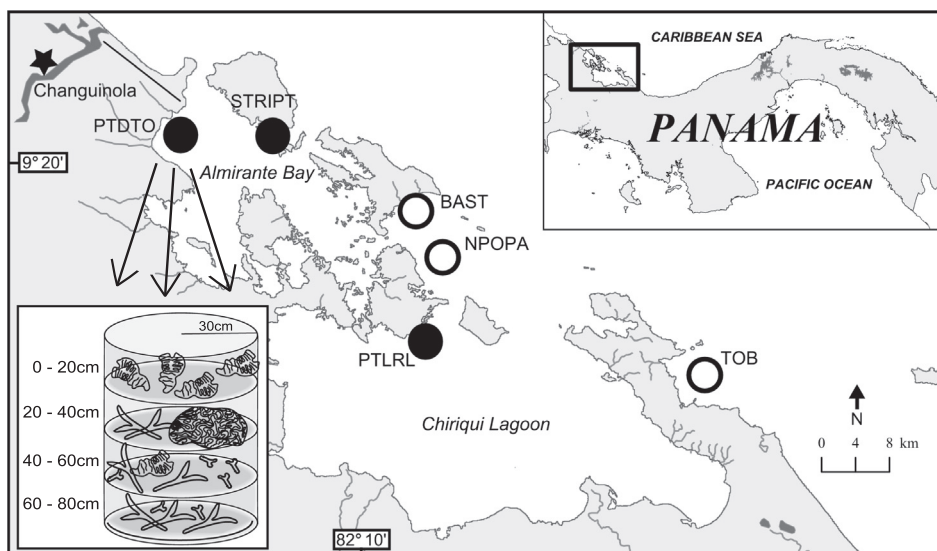
Fig. 1. Study sites and sampling scheme for molluscan subfossil assemblages from Bocas del Toro, Panama. Solid circles are lagoonal and open circles are offshore sites. Three replicate pits were sampled per site. PTDTO = Punta Donato, STRI PT = STRI Point, BAST = Bastimentos Island, NPOPA = North Popa Island, PTLRL = Punta Laurel, TOB = Tobobe.

(Fig. 1). Lagoonal sites are exposed to greater annual variability in salinity and water temperature than offshore sites (Heck, 1977; D'Croz et al., 2005). Although reef sites were separated into two distinct "lagoonal/offshore" environments, sites span a range of exposures to wind and wave action.

Bivalve and gastropod shells were obtained by excavating four 20 cm-thick layers from a 60 cm-diameter circular pit (Fig. 1). Pits were excavated at 5 m water depth from patches with little or no living coral but 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. Shells were extracted along with coral rubble using small gardening shovels and ice scoopers, and material was placed into bottomless buckets lined with 7 mm mesh netting that retained larger and more easily identifiable mollusk and coral remains >7 mm. Due to the dense packing of coral and mollusk material, however, many shells <7 mm were retained in the samples and included in the data presented here. Material was extracted from four distinct layers extending down to 80 cm below the reef surface: 0–20 cm, 20–40 cm, 40–60 cm, and 60–80 cm. Voucher specimens of bivalve and gastropod shells were deposited at the Smithsonian Tropical Research Institute and all remaining shells were deposited in the Geological Collections at Scripps Institution of Oceanography.

Reef environmental gradients related to differing hydrographic conditions and/or anthropogenic land clearing were assessed from analysis of carbonate and mud content of sediment from each sample, which indicate relative degree of autochthonous (marine) and allochthonous (land-based) inputs, respectively. Sediments from each layer within each pit were collected by inserting a 2.5″ diameter and 20 cm long PVC tube into the reef matrix before commencing excavation of that layer. Percent carbonate was determined by acid digestion (10% HCl) of the <2 mm sediment fraction, while the mud (<63 μm) fraction was determined by sieving dry sediments from the <2 mm fraction over a 63 μm sieve.

2.3. Radiocarbon dating

Age ranges for mollusk assemblages from each horizon and pit (i.e., sample) were estimated from radiocarbon dating of co-occurring coral fragments of *P. furcata* or *Agaricia tenuifolia*. Radiocarbon dates were produced for 93 coral fragments total, providing 1–2 dates for each sample. Radiocarbon analyses produced

"fraction modern" values that included background subtraction and $\delta^{13}C$ correction (Stuvier and Polach, 1977) which is equivalent to $F^{14}C$ (Reimer et al., 2004), as well as calendar years AD from the calibration of radiocarbon ages. Radiocarbon ages were converted to calendar years using one of two reference datasets. Fraction modern values <0.927 (corresponding to ages older than c. 1750 AD) were converted to calendar years using the Calib 6.0 program (Stuiver and Reimer, 1986) and the IntCal/MarineCal09 calibration dataset based on tree ring chronologies (Reimer et al., 2004), whereas values >0.927 were converted to calendar years using the Calibomb program (Reimer et al., 2004) and a surface water $F^{14}C$ reconstruction for the Caribbean from a *Montastraea faveolata* coral core from Puerto Rico (Kilbourne et al., 2007).

This calibration procedure produced conservative estimates of measurement uncertainty for all parameters, and provided calendar age probability distribution functions and ranges that included one standard deviation (Tables 1 and 2). 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, we could unambiguously distinguish samples from before and after circa 1960. Consequently, we labeled samples with calendar ages older than 1960 and 1960 or younger "pre-bomb" and "post-bomb" to analyze temporal trends within and between these periods. The few layers with two dated coral fragments that contained one pre- and one post-bomb age were assigned to the post-bomb category. Coral fragments with very high fraction modern values could definitively be assigned post-bomb calendar ages with very high precision (±5 years or less), while those with very low values could definitively be assigned pre-1900 calendar ages. Due to a large number of fluctuations in ocean surface water $F^{14}C$ 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. For a given coral fragment, all possible calendar age ranges were either pre-bomb or post-bomb.

2.4. Mollusk community data

Gastropod and bivalve shells were identified to species, subgenus, or genus level, resulting in a total of 88 gastropod and 78

Table 1
Calibrated radiocarbon ages obtained for each pit and layer at lagoonal sites, represented by midpoint value and ± one standard deviation. Maximum span of years encompassed within each pit computed from subtracting youngest possible age from 0–20 cm layer from oldest possible age from 60–80 cm layer. One age reversal indicated by *.

	PTDTO			PTLRL			STRIPT		
	A	B	C	A	B	C	A	B	C
0–20 cm	1900 ± 56	1907 ± 48	1925 ± 32	1975 ± 1	1930 ± 28	1985 ± 19	1964 ± 0	1930 ± 27	1901 ± 56
20–40 cm	1935 ± 24	1899 ± 56	1926 ± 31	1934 ± 25, 1936 ± 23	*1609 ± 50, 1935 ± 25	1926 ± 33	1618 ± 50, 1618 ± 50	1904 ± 45, 1908 ± 48	1914 ± 9
40–60 cm	1866 ± 27	1885 ± 70	1853 ± 39	1930 ± 28	1898 ± 57, 1930 ± 28	1935 ± 24	1626 ± 50	1549 ± 49, 1569 ± 53	1925 ± 31, 1926 ± 31
60–80 cm	1829 ± 61, 1935 ± 24	1885 ± 70	1832 ± 59, 1839 ± 62	1926 ± 31, 1958 ± 1	1822 ± 60, 1895 ± 52	1900 ± 54	1577 ± 52	1290 ± 35, 1470 ± 31	1925 ± 32
Max. year span	188	140	184	81	196	158	439	702	64

Table 2
Calibrated radiocarbon ages obtained for each pit and layer at offshore sites, represented by midpoint value and ± one standard deviation. Maximum span of years encompassed within each pit computed from subtracting youngest possible age from 0 to 20 cm layer from oldest possible age from 60–80 cm layer. One age reversal indicated by *.

	BAST			NPOPA			TOB		
	A	B	C	A	B	C	A	B	C
0–20 cm	1992 ± 4	1981 ± 15	1974 ± 6	1978 ± 10	2000 ± 3	1981 ± 15	1999 ± 2	1983 ± 5	1975 ± 5
20–40 cm	1968 ± 1, 1968 ± 1	1975 ± 2, 1975 ± 2	1975 ± 1	1954 ± 4	1974 ± 6	1981 ± 15	1981 ± 4	1975 ± 1	1969 ± 2
40–60 cm	1974 ± 3	1921 ± 28, 1925 ± 31	1958 ± 1, 1958 ± 1	*1978 ± 8	1977 ± 9	1981 ± 15	1975 ± 1	1963 ± 0	1930 ± 28
60–80 cm	1975 ± 1, 1975 ± 6	1935 ± 24	1958 ± 1, 1975 ± 1	1935 ± 25, 1962 ± 1	1900 ± 55	1981 ± 15	1968 ± 0, 1978 ± 10	1936 ± 23	1958 ± 1, 1974 ± 3
Max. year span	27	85	23	78	158	30	33	75	23

bivalve taxonomic groupings. Of these groupings, hereafter called species, 32% were identified to species level for gastropods and 49% were identified to species level for bivalves. The abundance of gastropod and bivalve species was calculated by shell weight and by number of individual shells. Weight was computed from all shell pieces that could be positively identified to genus level or higher. The minimum 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 (Gilinsky and Bennington, 1994; Kidwell, 2013). Because varying sedimentation rates could influence total shell abundance and proportional abundances of living molluscan communities are generally faithfully represented in subfossil assemblages (Kidwell, 2013), we used proportional data. Species proportions were computed from the fraction total weight and fraction total individuals. Both approaches yielded similar results; we present those from the latter. The average weight of an individual shell was computed for each sample by dividing the total weight of all individuals by the total number of individuals.

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 bivalves, species were divided into three diet categories (suspension feeder, deposit feeder, chemosymbiotic deposit feeder) and the two most common substrate relationship categories (epifaunal or infaunal). For gastropods, species were grouped into four diet categories: herbivore, carnivore, omnivore, or suspension feeder. For species and functional group proportions, relative abundances were compared between time horizons and reef environments.

2.5. 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 sample unit was a single time horizon within a single replicate or pit, resulting in 6 sites × 3 pits × 4 time horizons = 72 samples total.

Changes in molluscan communities before 1960 were assessed from 10 pits (nine lagoonal and one offshore) containing more than one pre-bomb horizon, and changes after 1960 were assessed from 9 pits (all offshore) with one or no pre-bomb horizons. Within each of the two time periods, the oldest (deepest) and youngest (shallowest) layers were compared. All molluscan taxonomic groups which comprised on average 5% or more of their respective ecological communities ("common" taxa) in the pre-1960 or post-1960 periods were included in analyses of temporal change. Statistical significance of temporal changes in molluscan taxonomic and functional group composition was determined using the two-tailed version of the Wilcoxon signed-ranks nonparametric paired t-test, with changes tracked within individual pits. Statistical differences between reef environments (lagoonal v offshore) were assessed using a bootstrapping procedure for each community parameter which sampled pit layers from each environment with replacement 1000 times to produce a distribution of differences in mean values. Distributions were deemed statistically different between environments if 95% confidence intervals of the difference between mean values did not include zero; p-values were determined by permuting data 1000 times and computing the proportion of permuted differences in mean values that were greater than observed mean differences (Efron and Tibshirani, 1986). All p-values were adjusted to control for the false discovery rate associated with multiple statistical comparisons (Benjamini and Hochberg, 1995). Differences in species composition between 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 p-value for R was

computed by permuting the data 1000 times. A comparison of the spatial versus temporal component of community variation was performed by computing the Bray-Curtis dissimilarity and then using the bootstrapping procedure to test for a significant difference between community dissimilarity over space (among pits at a given time period) versus time (between time periods within a given pit).

To determine if molluscan communities at offshore and lagoonal reefs have become more similar over time, community dissimilarity and Principal Components Analysis (PCA) were assessed for two data pairings: (1) oldest (60–80 cm) horizon from offshore pits and youngest (0–20 cm) horizon from lagoonal pits, and (2) youngest (0–20 cm) horizon from offshore and lagoonal pits. Between-environment dissimilarity was determined by computing Euclidean distances (chosen for straightforward comparison with PCA results) between relative abundance matrices from each environment. Significant change in the average between-environment dissimilarity was determined using the bootstrapping procedure. Separate analyses were performed for relative abundance matrices of species and functional group composition. To visually assess temporal changes in similarity between offshore and lagoonal communities, separate PCAs were performed for species and functional group datasets for each data pairing. For all analyses, statistical significance was determined at the $p = 0.05$ level. All analyses were conducted using the R software package (R Core Team 2013).

3. Results

3.1. Radiocarbon dates

Radiocarbon dates represented calendar ages ranging from 1290 AD ± 25 to 2003 AD ± 3 (Tables 1 and 2). The overwhelming majority of all layers from lagoonal pits were from the pre-1960 period, with bottom layers from three lagoonal pits (from two reef sites) confirmed to be older than 1900 AD (Fig. 3). In contrast, the majority of offshore pit layers were from the post-1960 period, although two pits had bottom layers older than 1960 AD (Fig. 3). The calibrated radiocarbon ages of the deepest pre-bomb horizons varied greatly, from c. 50–750 years BP, although the majority of pits had maximum ages that extended back to the late 1700s or 1800s (Tables 1 and 2 and Fig. 3). The large age range is due to variation in sedimentation rates among pits and inherent limits and uncertainties associated with the calibration of radiocarbon ages from young fossil material (Guilderson et al., 2005). The large standard errors of many of the calibrated radiocarbon ages from the pre-bomb period made it difficult to measure and compare sedimentation rates within and between individual pits. However, comparison within each pit of the oldest possible age from the 60–80 cm layer with the youngest possible age of the 0–20 cm layer produced an estimate of the maximum possible number of years encompassed by an individual pit: 239 years and 59 years on average for lagoonal and offshore pits respectively (Tables 1 and 2). By comparison, coral rubble accumulation rates measured from lagoonal sites in Bocas and Belize predict a possible age span of 80–140 years for lagoonal pits (Aronson et al., 2004; Hilbun, 2009).

3.2. Reef environment

Although sediments from both reef environments were predominantly carbonate, the carbonate fraction was significantly higher at offshore than lagoonal sites (mean percent carbonate = 94% and 91%, respectively; Table 1). Conversely, although the mud content of sediments was very low in both environments, percent mud was significantly higher at lagoonal sites (offshore mean = 1%, lagoonal mean = 2%). No significant temporal trends were detected in the percent carbonate or mud within the pre- or post-1960 periods.

3.3. Community differences between reef environments

3.3.1. Bivalves

The pit excavations produced a total of 23,658 bivalve individuals weighing 11.0 kg. A total of 73 bivalve species were sampled, with 68 and 50 species occurring at lagoonal and offshore sites, respectively (Table 1). Bivalve abundance was significantly higher at lagoonal than offshore sites, with an average of 585 and 75 individuals per sample at each environment, respectively. Although both environments were dominated by suspension feeding bivalves, their percentage was significantly higher at offshore (93% of individuals) than lagoonal sites (90% of individuals; Fig. S1), reflecting greater water motion and/or planktonic productivity and lower amounts of fine suspended sediments on these reefs. Although both reef environments were dominated by epifaunal bivalves living on hard substrates, offshore sites had a significantly higher proportion of epifaunal individuals (91%) compared to lagoonal sites (85%). This pattern indicated a higher availability of live or dead coral at offshore sites and/or higher sediment or algal cover at lagoonal sites. All three feeding modes of infaunal bivalves were more prevalent on lagoonal reefs, but only the proportion of infaunal suspension feeders was significantly higher (Table 1).

Bivalve species composition was significantly distinct between offshore and lagoonal sites (ANOSIM R = 0.31; $p < 0.001$). Within each environment, species composition varied significantly more over space (among pits at a given time period) than over time (between time periods within a given pit), with average Bray-Curtis dissimilarity values of 0.47 and 0.27, respectively. Bivalve communities were composed of a small number of dominant species and a larger number of rare species (Table S1 and Fig. 2). Assemblages from both reef environments were dominated by the epifaunal suspension feeders *Dendostrea frons*, *Chama congregata*, and *Barbatia cancellaria* at one or both time periods. Together, these species comprised an average of 47% and 54% of individuals at offshore and lagoonal sites, respectively. The dominance of epifaunal suspension feeding bivalves in both environments is indicative of high-productivity coral reef environments dominated by hard substrates and influenced by terrigenous nutrients from river runoff (Birkeland, 1987; Todd et al., 2002). The prevalence of *D. frons* is a clear indication of the presence of branching colonies of the plexaurid and gorgoniid corals and staghorn coral *A. cervicornis* that are the primary hosts on which this oyster lives (Forbes, 1971; Cramer et al., 2012). The prevalence of dominant *Chama congregata* and subdominant *C. macerophylla*, typically found cemented to (dead) coral or other limestone debris (Jackson, 1972; Harries and Sorauf, 2010), indicates high availability of (live or dead) coral substrate.

Notable but non-significant differences in the relative abundance of dominant (at least 10% of community in either pre-or post-1960 time period) and subdominant (5–10% of community in either time period) bivalve species provided more insight into the differing environmental conditions at lagoonal and offshore reefs (Fig. 2). Although dominant in both environments, the dead coral rubble-associated epifaunal suspension feeder *C. congregata* was more abundant in lagoons, while branching *Porites* coral-associated epifaunal suspension feeder *B. cancellaria* (Stanley, 1970) was more abundant offshore. The epifaunal suspension feeder *Ctenoides* was dominant at lagoonal but only subdominant at offshore sites. This bysally-attached species has previously been recorded primarily in high energy environments (Hauser et al., 2007). Other subdominant species included
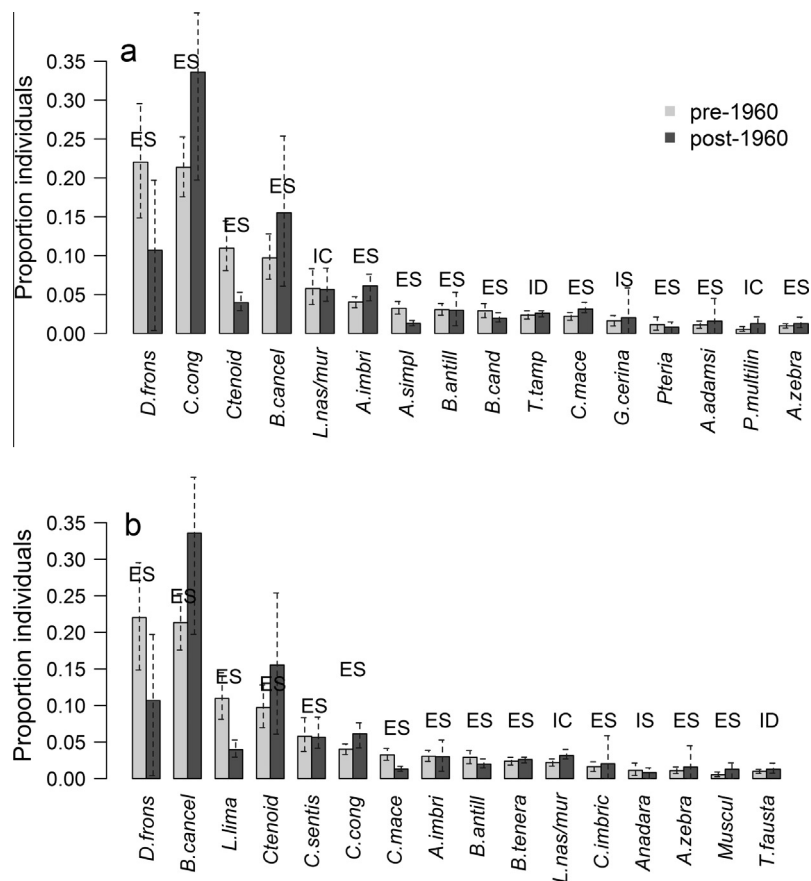
Fig. 2. Common bivalve species (comprising at least 1% of community) from a = lagoonal and b = offshore reefs. ES = epifaunal suspension feeders, IS = infaunal suspension feeders, ID = infaunal deposit feeders, IC = infaunal chemosymbiotic deposit feeding bivalves. Dotted lines are 95% bootstrapped confidence intervals. See Table S1 for full species names.

epifaunal suspension feeders *Lima lima*, *Caribachlamys imbricata*, and *C. sentis* offshore, and *Arca imbricata* at lagoons, highlighting the prevalence of hard substrata and relatively high plankton productivity in both environments. However, the greater importance at lagoonal sites of the infaunal chemosymbiotic deposit feeder *Lucinisca nassula/muricata* – which can tolerate high temperature, low salinity, high suspended sediments, and stagnant conditions – indicates that lagoonal environments are more stressful in terms of these factors (Jackson, 1972; Hauser et al., 2007).

3.3.2. Gastropods

The pit excavations produced a total of 13,666 gastropod individuals weighing 5.67 kg. A total of 85 gastropod species categories were sampled, with 67 and 75 species sampled at lagoonal and offshore sites, respectively (Table S2). As with bivalves, gastropod abundance was significantly greater at lagoons, with an average of 299 and 80 individuals per pit layer, respectively. Although abundance was greater at lagoonal sites, individual shell weight was significantly greater at offshore sites (Table 3).

As with bivalves, gastropod trophic structure differed between offshore and lagoonal reefs. Although gastropod abundance was dominated by herbivores at both reef environments, a significantly higher proportion of carnivores were present at offshore (26% of individuals) compared to lagoonal sites (9% of individuals; Table 1). Offshore sites also had a significantly higher proportion suspension feeding individuals, while lagoonal sites had significantly higher proportion herbivorous and omnivorous individuals (Table 3). These differences confirm the higher benthic productivity, lower amount of water motion, greater degree of salinity

and/or temperature stress (McClanahan, 1992), and/or lower habitat complexity (Kohn and Leviten, 1976) at lagoonal sites.

Gastropod species composition differed significantly between reef environments (ANOSIM R = 0.53; p < 0.001). Within lagoonal and offshore reefs, composition varied significantly more over space than over time, with average Bray-Curtis dissimilarity values of 0.50 and 0.32; respectively. Gastropod communities were composed of a small number of dominant species and a large number of rare species, a pattern observed in coral reef gastropod communities from other areas of the Caribbean (McClanahan, 1992, 2002a) and the western Indian Ocean (McClanahan, 2002b). Offshore sites had greater evenness in species proportions, and contained a larger number of species comprising $\geqslant$1% of the community (28 species) compared to lagoonal sites (11 species). The greater dominance by a few gastropod species at lagoonal sites may be a reflection of greater environmental stress.

Gastropod communities in both reef environments were dominated by the herbivorous snail *Cerithium* spp. (primarily composed of *Cerithium litteratum* and *Cerithium eburneum*), comprising 30% and 54% of individuals at offshore and lagoonal sites, respectively (Table S2 and Fig. 4). This species is typical of backreef environments and surrounding coarse carbonate sediments (Ekdale, 1974; Cerridwen and Jones, 1991) and is common in Caribbean coral reef and seagrass habitats (Jackson, 1972; Heck, 1977; McClanahan, 1992; Cox, 1997). The remaining two species that comprised $\geqslant$5% of individuals at both reef environments were the herbivorous gastropods *Astraea tecta* and *Hemitoma octoradiata*. *A. tecta* is commonly found in biogenic habitats such as coral reefs and seagrass beds (McClanahan, 1992), while *H. octoradiata*
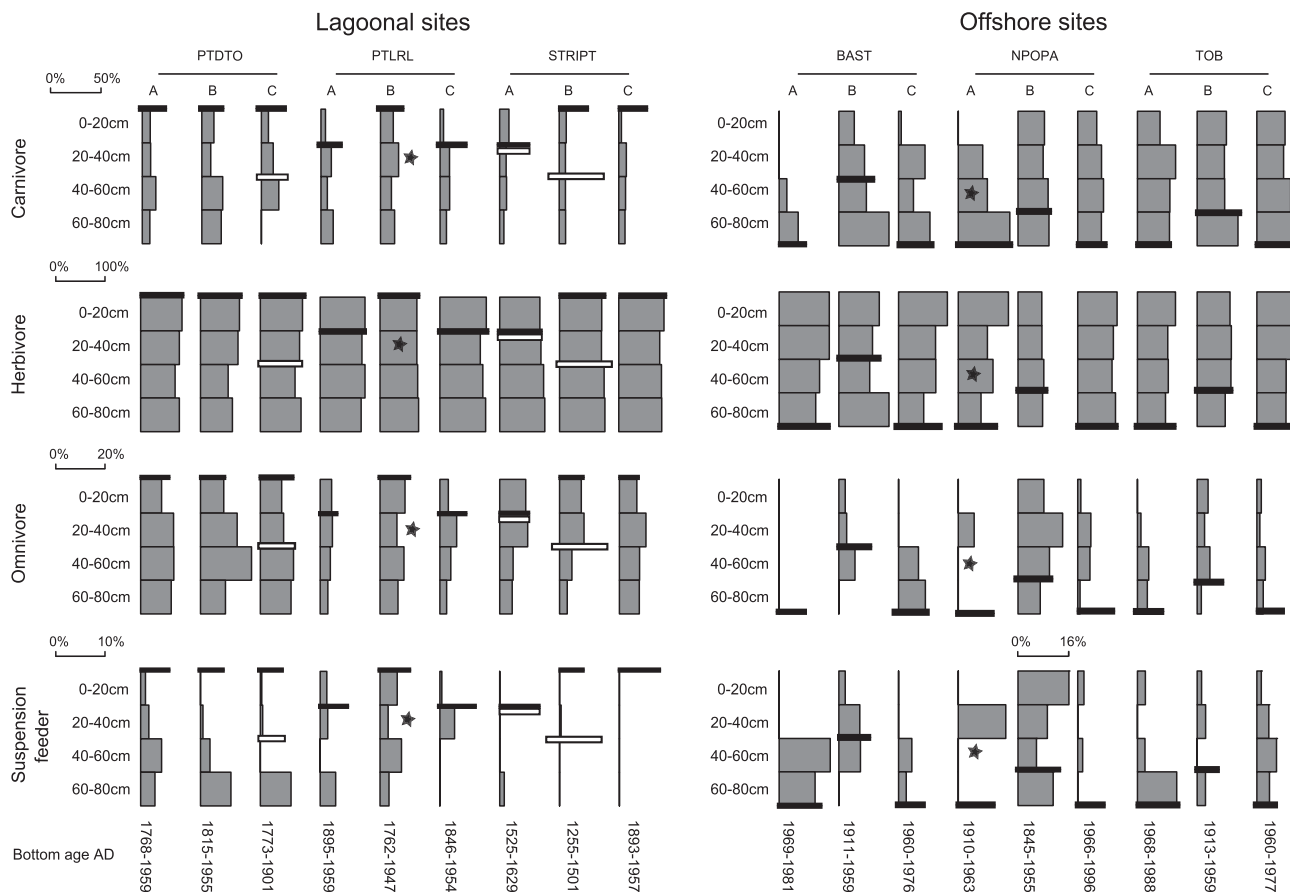
Fig. 3. Proportions of gastropod functional groups by individual pit and layer. White horizontal line indicates boundary between pre- and post-1900 AD, solid horizontal line indicates boundary between pre- and post-1960 AD, stars indicate layers with age reversals. Note different scale for suspension feeders for one pit.

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. prevalent at offshore sites and the herbivorous *Modulus modulus* and primarily herbivorous *Diodora* spp. prevalent at lagoonal sites. *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). The presence at offshore reefs of the subdominant corallivores *Coralliophila*, *Calliostoma* and *Cymatium* (Fig. 4) reflected the higher availability of hermatypic and gorgonian coral hosts at offshore reefs.

3.4. Temporal trends

No significant trends were observed in bivalve or gastropod total abundance within pre- or post-1960 time periods. However, several significant temporal trends occurred in gastropod functional group and bivalve species group composition that were indicative of deteriorating reef environmental conditions. Those that were previously reported in Cramer et al., 2012 are briefly summarized here and in Table 4: prior to 1960 (mostly lagoonal sites), the relative abundance of the previously-dominant, staghorn and gorgonian coral-associated tree oyster *Dendostrea frons* declined while that of the branching *Porites* coral-associated clam *Barbatia cancellaria* increased. During this period, individual bivalve shell weight also declined for epifaunal but not infaunal species, suggesting more stressful environmental conditions above

the sediment–water interface in particular (Jackson, 1972; Stanley, 1970). This trend can also likely be attributed to the loss of the relatively heavier-shelled *D. frons*. After 1960 (offshore reefs), *D. frons* relative abundance and individual bivalve shell weight continued to decline. A decline in relative abundance of carnivorous and increase in herbivorous gastropods also occurred during this period.

The relative abundance of dominant bivalves closely tracked that of their preferred scleractinian coral hosts, with *D. frons* and *A. cervicornis* proportions positively correlated at pre- and post-1960 time periods (Spearman $\rho = 0.66$ and $= 0.84$, respectively; $P < 0.001$ in both cases and *B. cancellaria* and finger coral *P. furcata* positively correlated after 1960 ($\rho = 0.49$, $P < 0.01$; Fig. 5). Together, these trends reveal that bivalve species composition was greatly affected by the replacement of *A. cervicornis* with *P. furcata* that occurred in the older layers of nine out of 18 pits (Cramer et al., 2012). The loss of *D. frons* also suggests a decline in the branching plexaurid and gorgoniid corals to which it was commonly attached decades ago (Forbes, 1971).

Comparison of community dissimilarity and ordination results between the oldest offshore/youngest lagoonal and youngest offshore/youngest lagoonal horizons revealed that offshore molluscan communities have become more similar to lagoonal communities since 1960, with Euclidean distances declining significantly from 0.42–0.27 for the functional group analysis and from 0.66–0.52 for species group analysis ($P < 0.05$ in both cases). Ordinations visually confirmed the loss of distinctiveness between offshore and lagoonal communities during the post-1960 period, which was driven primarily by a reduction in carnivorous/increase in herbivorous gastropods and a loss of *D. frons* at offshore sites (Fig. 6).

Table 3
Significant differences in molluscan environmental and community parameters between lagoonal and offshore reef environments. Differences significant at $p = 0.05$ level (determined by bootstrapping procedure and multiple comparison correction described in Methods). Values are means (see Table S3 for 95% confidence intervals and *p*-values). Molluscan communities generally reflect higher benthic productivity, more suspended sediments, higher environmental stress, and lower coral cover at lagoonal reefs.

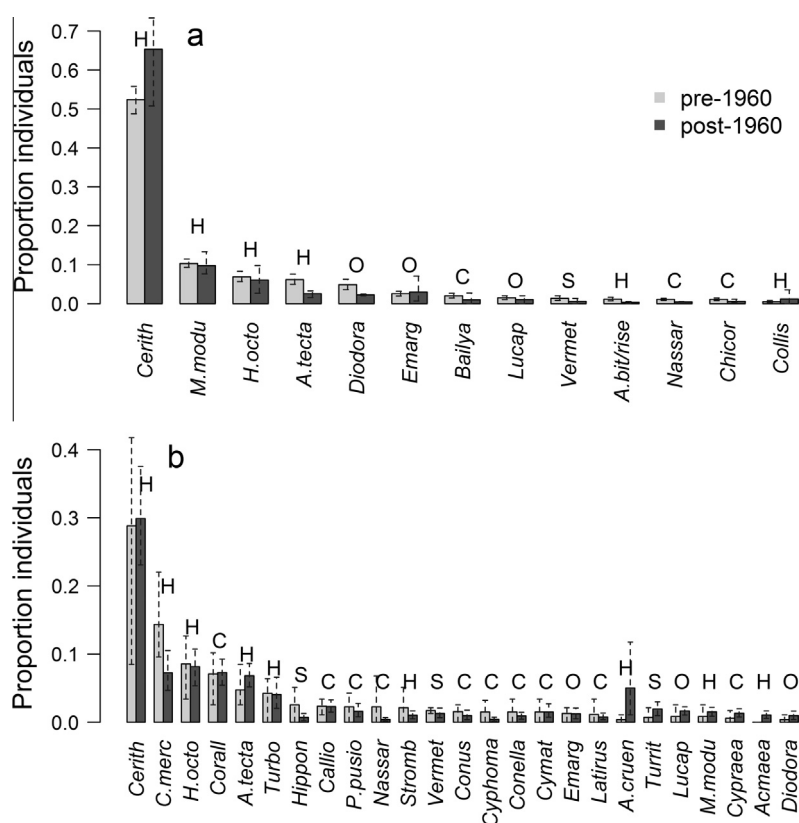|	Parameter	Lagoonal	Offshore	Inferred environmental signal (lagoonal reefs)
Environment	Carbonate	91%	94%	Higher terrigenous sedimentation
	Fine sediments (mud)	2%	1%	Higher terrigenous sedimentation
Bivalves	Abundance	585	75	Higher benthic productivity/greater time averaging
	Average shell weight	0.71 g	0.33 g	Higher benthic productivity
	Epifaunal	85%	91%	Lower coral cover
	Suspension feeders (all)	90%	93%	Lower water motion/more suspended sediments
	Infaunal suspension feeders	4%	2%	Lower coral cover/higher cover soft sediments
Gastropods	Abundance	299	80	Higher productivity/greater time averaging
	Average shell weight	0.37 g	0.64 g	Lower predation
	Carnivores	9%	26%	Higher productivity/higher environmental stress
	Herbivores	81%	69%	Higher benthic productivity
	Omnivores	9%	4%	Higher benthic productivity
	Suspension feeders	1%	3%	Lower water motion/more suspended sediments

Fig. 4. Common gastropod species (comprising at least 1% of community) from a = lagoonal and b = offshore reefs. C = carnivore, H = herbivore, O = omnivore, S = suspension feeder. Vertical lines are bootstrapped 95% confidence intervals. See Table S2 for full species names.

4. Discussion

4.1. Reliability and temporal resolution of the coral reef subfossil record

Several attributes of our subfossil data suggest they faithfully represent a chronological sequence of historical change: only two age reversals occurred out of 93 radiocarbon dates (Table 1), material was part of a tightly-packed matrix of coral rubble generally found in life position and with no signs of re-working, and clear continuous trends were found in coral and molluscan taxonomic and functional composition. Because our subfossil assemblages are undoubtedly time-averaged, we analyzed proportional data

which have been shown to faithfully represent the original living molluscan community (Kidwell, 2013).

Although time-averaging was greater within lagoonal than offshore pits, the degree of time-averaging was difficult to quantify within and among individual lagoonal pits because of the large uncertainties in pre-1960 calibrated radiocarbon ages in many layers. Compared to previous estimates of rubble accumulation rates from Almirante Bay of 1–1.75 cm yr^{-1} (Aronson et al., 2004; Hilbun, 2009) which predict a possible age range of 80–140 years for lagoonal pits, the average span of calibrated midpoint values from the top and bottom layers was 137 years (Table 1). Two lagoonal pits encompassed at least 400 years, and clearly had lower sedimentation rates (and higher degrees of

Table 4

Significant temporal changes in molluscan community parameters from Wilcoxon sign-ranks tests. N = number of pits, V = sum of ranks of paired difference resulting in a positive sign. Pre-1960 period is primarily lagoonal reefs; post-1960 is offshore reefs. False discovery rate multiple comparisons correction applied to p-values. (Note that this correction changed P values for average shell weight (all) pre-1960 and *D. frons* post-1960 from $P < 0.05$ to $P = 0.6$).

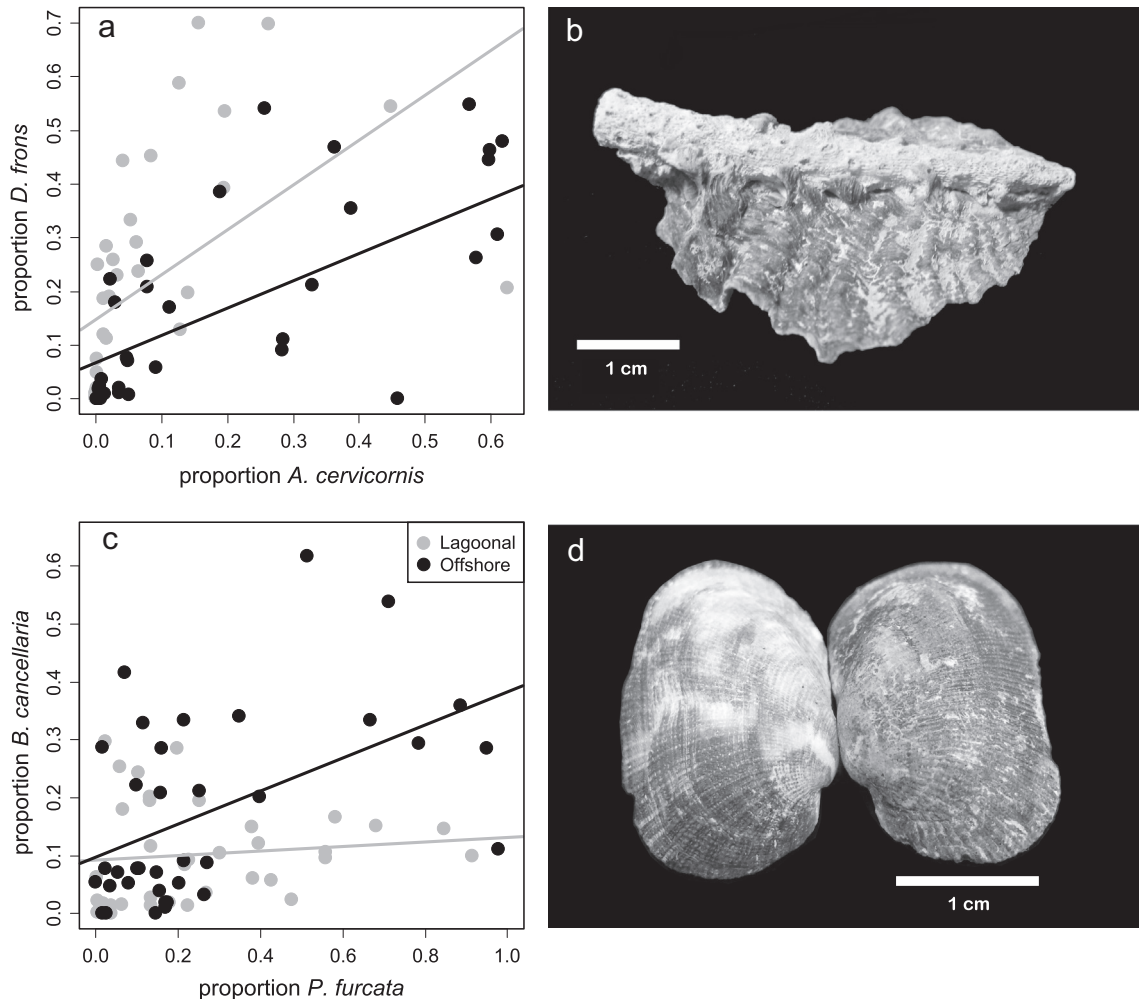|	Community parameter	Pre-1960	n	V	P	Post-1960	n	V	P
Bivalves	*Dendostrea frons*	40–18%	10	42	<0.05	27–12%	9	32	=0.06
	Barbatia cancellaria	6–18%	10	0	<0.05	–	–	–	–
	Average shell weight (all)	1.06–0.50 g	10	47	=0.06	0.50–0.26 g	9	36	<0.01
	Average shell weight (epifaunal)	0.90–0.43 g	10	46	=0.06	0.43–0.34 g	9	30	<0.05
Gastropods	Carnivores	–	–	–	–	32–16%	9	1	<0.05
	Herbivores	–	–	–	–	60–79%	9	3	<0.05

Fig. 5. Relative abundance of branching coral host species and their bivalve obligates in lagoonal and offshore reef environments. a = relative abundances of staghorn coral *A. cervicornis* and tree oyster *D. frons*, b = *D. frons* attached to *A. cervicornis*, c = relative abundances of finger coral *P. furcata* and clam *B. cancellari*a, d = *B. cancellaria*. All correlations significant except for *P. furcata* versus *B. cancellaria* at lagoonal sites.

time-averaging) than previously-published estimates. Therefore, it is very likely that all of the lagoonal pits span all or most of the entire 20th century.

4.2. Reef environmental gradients and molluscan community composition

Our molluscan subfossil data provide the first description of historical environmental conditions for reefs in Bocas and contribute valuable information about current reef environments, as no environmental data exists for these reefs before 2000 and current monitoring continues to be limited in spatial and environmental scope

(Collin et al., 2009; Seemann et al., 2014). The bivalve and gastropod communities in Bocas were typical of coral reefs with a high availability of hard substrates and relatively high productivity due to the influence of river runoff. Although common taxa were relatively consistent across sites and environments, variation in total mollusk abundance and functional group and species proportions revealed subtle and localized differences in natural and/or human-caused reef environmental conditions.

At lagoonal reefs, the higher prevalence of infaunal suspension feeding bivalves and herbivorous and omnivorous gastropods confirmed the greater nutrient availability, primary productivity, and soft substrates from terrigenous runoff in this environment. At

offshore reefs, the greater prevalence of epifaunal and suspension feeding bivalves and suspension feeding gastropods signaled a greater degree of water motion and availability of coral substrates, while the larger size of gastropods indicated favorable environmental conditions for this group. The greater numerical abundance of bivalves and gastropods within lagoons is likely in part due to greater time-averaging within these pits, although larger bivalve size suggests that these quieter, higher productivity environments are indeed more favorable for this group. These patterns illustrate the responses of coral reef mollusks to a complex suite of environmental stressors that include food availability, dislodgement, clogging of filtering mechanisms by suspended sediments, and variation in water temperature, salinity, and oxygen content.

Differences in reef sediment composition revealed similar but much subtler distinctions between reef environments compared to molluscan assemblages (Table 1). Despite the greater influence of terrigenous runoff in lagoonal reefs, differences in percent mud and non-carbonate (i.e., organic) content were less pronounced (although still significant) than were expected based on the observed differences in molluscan composition.

4.3. Historical change

Despite the large-scale clearing of coastal forests in Bocas in the early 1900s for banana agriculture (Stephens, 2008; Cramer, 2013), no temporal change in the abundance of mud or organic material was observed in reef sediments. This may be because terrestrial sediments are naturally introduced to lagoonal reef systems on a multi-decadal scale during periodic flooding events that characterize this region (Guzmán, 2003). In addition, the composition of molluscan functional groups was not related to sediment composition, likely because overall mud and organic contributions were consistently low at both reef environments.

In contrast, changes in molluscan community composition signaled deteriorating reef environmental conditions prior to 1960 primarily in lagoons and after 1960 offshore. The decline in average bivalve shell weight before and after 1960 and the decline in carnivorous/increase in herbivorous gastropods after 1960 further implicate stressful reef environmental conditions which result in short, simplified food chains (Odum, 1985; Birkeland, 1987).

The significant temporal changes we observed in bivalve taxonomic composition revealed the cryptic effects of reef habitat degradation on associated molluscan communities. Over the past 50–150 years, Bocas reefs were dominated by two epifaunal bivalve species which preferentially attach to a single scleractinian species. The relative abundance of the oyster D. frons closely tracked that of its preferred staghorn coral host A. cervicornis and the relative abundance of the clam B. cancellaria tracked that of its preferred finger coral host P. furcata. Changes in bivalve species composition demonstrated that the pre-1960 replacement of A. cervicornis by P. furcata at two of the three lagoonal reef sites (Cramer et al., 2012) precipitated a concomitant decline in the relative abundance of D. frons and increase in B. cancellaria. Coral communities underwent a more complex change at offshore sites after 1960 that entailed a two-step successional sequence of dominance by A. cervicornis → P. furcata → lettuce coral A. tenuifolia (Cramer et al., 2012). As a result, no unidirectional change occurred in either P. furcata or B. cancellaria, but relative abundances of these
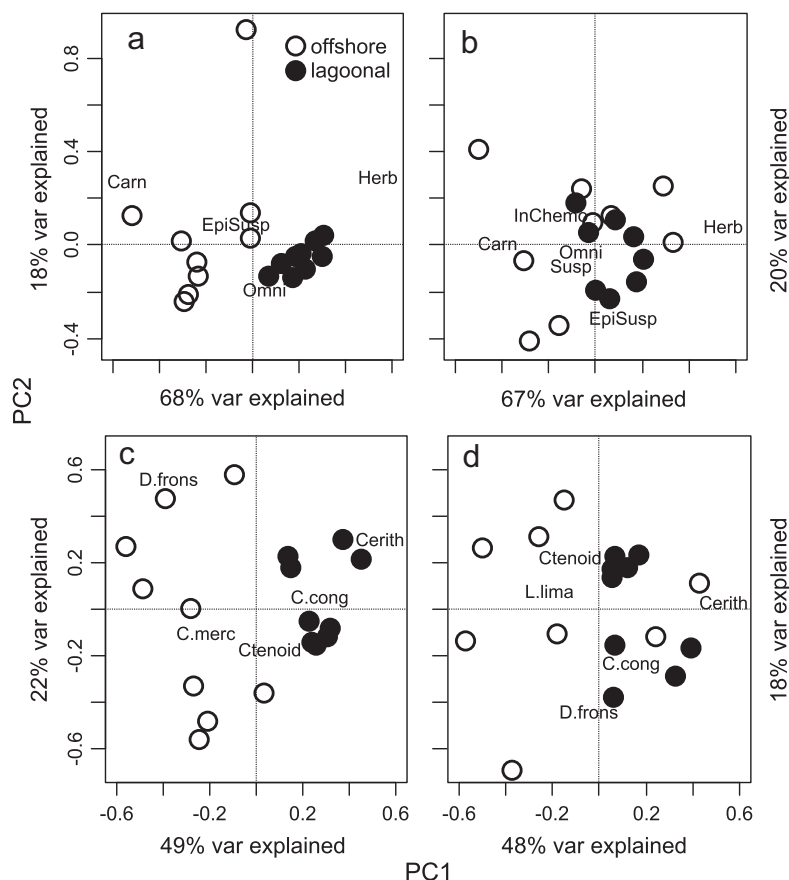

Fig. 6. Principal Components Analysis of relative abundances of molluscan functional (a and b) and species groups (c and d) from offshore and lagoonal pits. Plots (a and c) compare oldest (60–80 cm) horizon from offshore sites (open circle) and youngest (0–20 cm) horizon from lagoonal sites (solid circle), and plots (b and d) compare youngest (0–20 cm) horizons from both offshore and lagoonal sites. 0–20 cm layer from Bastimentos pit A excluded because contained only one gastropod. Functional and species groups labels located on origin are omitted.

species closely and significantly tracked each other (Fig. 5). Because the total abundance of bivalves did not vary within or between the pre- and post-1960 periods, we interpret these trends as changes in the absolute abundance of these two bivalve species. Moreover, because these bivalves are not harvested by humans, trends are a direct result of changes in coral host availability. This finding suggests that the recent dramatic loss of *A. cervicornis* across the Caribbean has likely had a profound but previously undetected effect on the abundance of the tree oyster *D. frons*. These results also reveal that mollusks can be used as a reliable proxy for coral community change.

4.4. Land-based runoff as driver of reef environmental change

The historical changes documented in reef bivalve and gastropod communities clearly indicate a marked deterioration of reef environments definitively occurring prior to 1960 at lagoonal sites. This timing is at least decades before outbreaks of coral and urchin disease and coral bleaching that are widely cited as the cause of the collapse of Caribbean coral communities. The nature and timing of molluscan community change implicates land-based agricultural activities as the main driver. At lagoonal reefs, the timing of change is likely contemporaneous with the onset of extensive coastal land clearing for banana agriculture in the first half of the 20th century, while at offshore reefs, changes are contemporaneous with the introduction of large quantities of synthetic agrochemicals toxic to marine life which were applied to plantations starting in the mid-20th century (Stephens, 2008; Cramer, 2013). Declining water quality due to land-based runoff since the mid-20th century has been documented for Almirante Bay from terrestrial plant biomarkers in reef sediments (Aronson et al., 2014) and from recent small-scale monitoring studies (Collin et al., 2009; Seemann et al., 2014), but the convergence of offshore and lagoonal molluscan communities since the 1960s documented here confirms that water quality has also substantially deteriorated offshore.

4.5. Recommendations

The analysis of subfossil reef bivalve and gastropod mollusks provides a valuable window into the structure and functioning of past reef environments and communities, providing a baseline state from which to judge future change. The lack of quantitative ecological data for reef communities pre-dating the 1980s and the overall dearth of environmental and water quality data for reefs in Bocas (and the Caribbean in general) have prevented an accurate description of ecological change, impeding the development of a mechanistic explanation of recent reef deterioration. The well-known and varied life habits and narrow environmental tolerances of bivalve and gastropod mollusks make these common reef organisms well-suited for assessing the environmental causes of past and present change. The historical environmental changes on reefs in Bocas del Toro uncovered by our paleoecological data emphasize the urgent need for reef environmental monitoring programs and improved land management practices to prevent further reef degradation and to promote resiliency in the face of impending climate change impacts.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.marpolbul.2015.05.031.

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