# MARKED ECOLOGICAL SHIFTS IN SEAGRASS AND REEF MOLLUSCAN COMMUNITIES SINCE THE MID-HOLOCENE IN THE SOUTHWESTERN CARIBBEAN

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## ABSTRACT

Caribbean coastal ecosystems have undergone severe degradation both historically and recently, primarily caused by the synergistic effects of overfishing, eutrophication, sedimentation, disease, and other factors associated with humans. Baseline conditions from pristine Caribbean reefs and seagrass beds are required to understand and quantify degradation. Only the fossil record can provide pre-human baselines. We present preliminary results from a recently discovered mid-Holocene (7.2–5.7 ka) fossil fringing reef and seagrass system in Bocas del Toro, Panama. Molluscan assemblages from the fossil reef and seagrass habitats were compared to death assemblages in corresponding modern habitats. The proportion of suspension-feeding molluscs more than doubled from fossil to the present day in the reef habitat, and the proportion of herbivores declined by a third, reflecting declines in coral cover and architecture, and increased eutrophy. Conversely, in seagrass beds, the proportion of different mollusc guilds was remarkably similar between fossil and modern day, suggesting that unlike reefs, seagrass beds are functionally similar today compared to a "pristine" baseline, although key community members were different. Our study reveals novel evidence that the health of molluscan communities on Caribbean reefs may have declined to the extent observed in corals and fish, and that the decline follows a trajectory predicted by known ecosystem degradation. Molluscs represent a biodiverse and functionally crucial component of reefs and must be considered in ecosystem-scale research on reef conservation. Revealing the structure of baseline communities using the fossil record represents one important step toward this aim.

Coral reef and coastal ecosystems across the Caribbean and worldwide are declining in extent and quality due to eutrophication, overfishing, physical damage, and disease (LaPointe 1997, Carpenter et al. 1998, Aronson and Precht 2001, Jackson et al. 2001, Gardner et al. 2003, Lotze et al. 2006), yet we have little knowledge of the changing states of most of the inhabitants of reefs. Sixty-three of the 287 described Caribbean scleractinian coral species (Miloslavich et al. 2010) have been assessed for threats by the International Union for the Conservation of Nature (IUCN 2012), but none of the more than 3000 known Caribbean molluscs (Miloslavich et al. 2010) have received the same attention.

The fossil record represents a valuable baseline that can help reveal the state and long-term stability of ecosystems and place current changes to ecosystems into historical context (Lotze et al. 2011, Harnik et al. 2012), but its use in this regard so far has generally been restricted to corals (e.g., Aronson and Precht 1997, Wapnick et al. 2004). This represents a serious omission because many crucial functional roles in reef ecosystems are performed by taxa other than corals. In the present study, we address this issue with a quantitative comparison of the entire molluscan (gastropod

and bivalve) community in a mid-Holocene reef complex and a comparable modern reef complex in the southwestern Caribbean (SWC).

The molluscan classes Gastropoda and Bivalvia dominate coastal ecosystems across the world. In the tropics they often represent the most diverse members of reef complexes: one intensive study of an Indo-Pacific coral reef and its associated habitats found 2738 species of marine molluscs in 295 km$^2$ (Bouchet et al. 2002). Detailed surveys of individual reef and seagrass systems frequently reveal 100 species or more (Greenway 1995), and comprehensive compilations reach thousands of species across regions such as the Caribbean (Jackson 1972, Hauser et al. 2007, Miloslavich et al. 2010). Life habits, feeding modes, reproduction, and life histories vary immensely among different bivalves and gastropods, and combine to form a wide array of functional modes performed by molluscs (Todd 2001, Leonard-Pingel et al. 2012). Because of their skeletal durability, fossil assemblages of molluscs have high fidelity to their original living community, both in terms of composition (Kidwell and Flessa 1995) and location (Miller 1988). Here, we use "molluscs" to refer only to the gastropod and bivalve molluscs, noting that other fossilizable taxa such as Polyplacophora and Scaphopoda were rare and consequently were not evaluated.

A number of studies have compared the ecological roles of molluscs between recent past and present marine communities. Historical data from fishing records, sailors' logs, and other sources can be used to track changes in marine molluscan communities over time. For example, historical records of oyster fishing in the United States chronicle the increase in fishing effort and subsequent population decline and eventual collapse of oyster beds (Kirby and Linares 2004). Cramer et al. (2012) observed a decline in the oyster *Dendostrea frons* (Linnaeus, 1758) and an increase in the ark clam *Barbatia cancellaria* (Lamarck, 1819) in three lagoonal and three offshore fossil reefs in the SWC, which the authors attributed to a steep decline in gorgonian and acroporid coral cover accompanied by an increase in coral rubble substrate. The shell characteristics of *Tawera gayi* (Hupé, 1854) have been used to reconstruct a 6000-yr record of environmental change in waters off Tierra del Fuego (Gordillo et al. 2011) and shifts in molluscan communities through cores in Florida have revealed shifts in environments in Florida Bay (Brewster-Wingard et al. 2001).

Despite its potential, the utility of the geologically recent fossil record to illuminate changes in molluscan communities and their critical roles in coastal ecosystems remains largely unexplored. We address this with an ecological comparison of mid-Holocene and modern molluscan assemblages from the same island in Caribbean Panama.

## Study System

### Bocas del Toro

Isla Colón is part of the Bocas del Toro Archipelago in Panama, SWC, that has a long geological history of coral reef growth (Coates et al. 2005, O'Dea et al. 2007, Klaus et al. 2012). Early archeological records in Panama date to about 9000 BC or before and are concentrated on the Pacific coast, although humans probably had reached Bocas del Toro as hunter gatherers around 5000 yrs ago (Ranere and Cooke 1991, Cooke 2005), and had settled and were actively fishing by around 500 AD (Wake et al. 2004, 2013) and almost certainly earlier. These

precontact communities subsisted largely on nearshore marine fauna, including large molluscs. An abundance of conch—*Strombus raninus* Linnaeus, 1758 and *Strombus pugilis* Linnaeus, 1758—in Pre-Columbian shell middens suggests that tangible effects of harvesting in the Caribbean began at least several centuries precontact, and in some cases perhaps much earlier (Linares 1980, Wake et al. 2013). Colonists arrived in Bocas del Toro in the 1500s, and probably continued to harvest megafauna in the Caribbean (Jackson 1997, McClenachan et al. 2010). Intensive agriculture began in the late 1800s, when banana plantations were established throughout Bocas del Toro, causing increased sedimentation and coastal eutrophication due to deforestation and fertilizer runoff (D'Croz et al. 2005, Stephens 2008, Cramer 2013).

Coral reef decline in the Caribbean is well documented, and often ends in a regime shift after the combined impacts of overfishing, eutrophication, disease, and other factors overwhelm the resilience of the reef system (Hughes 1994, Jackson et al. 2001). A key reef-building coral genus, *Acropora*, has become rare or locally extinct in many reefs throughout the Caribbean due to white-band disease, which has a particularly adverse effect on already-compromised reefs (Aronson and Precht 2001, Cramer et al. 2012). Paleontological studies have found no precedent for this collapse in the Pleistocene (Aronson and Precht 1997, Greenstein et al. 1998). Reef cores starting approximately 3000 yrs ago show a continuous record of dominance by branching *Porites* species in Bocas del Toro and *Acropora* species off Belize, until those corals abruptly declined in the 1980s and both reef types transitioned to dominance of *Agaricia tenuifolia* (Dana, 1846), a lettuce coral (Aronson et al. 2004). However, *Porites* remains abundant around Bocas del Toro (Guzman and Guevara 1998), and records obtained from larger sampling pits suggest that *Acropora* was also once abundant in Bocas, and has been declining since at least the 19th century (Cramer et al. 2012).

Study Sites

Extensive geological uplift across the Caribbean region means many Pleistocene reefs are commonly exposed along Caribbean coasts. However, these reefs are not particularly useful for producing pre-human baselines of molluscan communities, because molluscs in such sediments tend to be poorly preserved and highly indurated, making collection and identification difficult. There is a well-founded argument against using pre-Holocene assemblages as baselines because of non-analogous environmental and evolutionary states. The exposure of a mid-Holocene (see later) fringing reef system in Bocas del Toro in the SWC revealing a rich suite of well-preserved mangrove, seagrass, and reef molluscan assemblages in non-lithified sediments, therefore provides the opportunity to reconstruct the pre-human molluscan community of the region from a time when sea levels and other environmental settings were comparable to the present day. The aim of this preliminary study was to compare mid-Holocene and present day molluscan assemblages from geographically-close locations.

The fossil site is located close to the old village of Lennond on the southwest coast of Isla Colón, Bocas del Toro, Panama, and approximately 500 m northwest of the Smithsonian's Bocas Research Station (Fig. 1). Originally a large mangrove tract, excavations of two approximately 1-km canals made by Sunset Point, Inc. from 2006 to 2008 exposed fossil-rich sediments underlying the mangrove. Sediments were
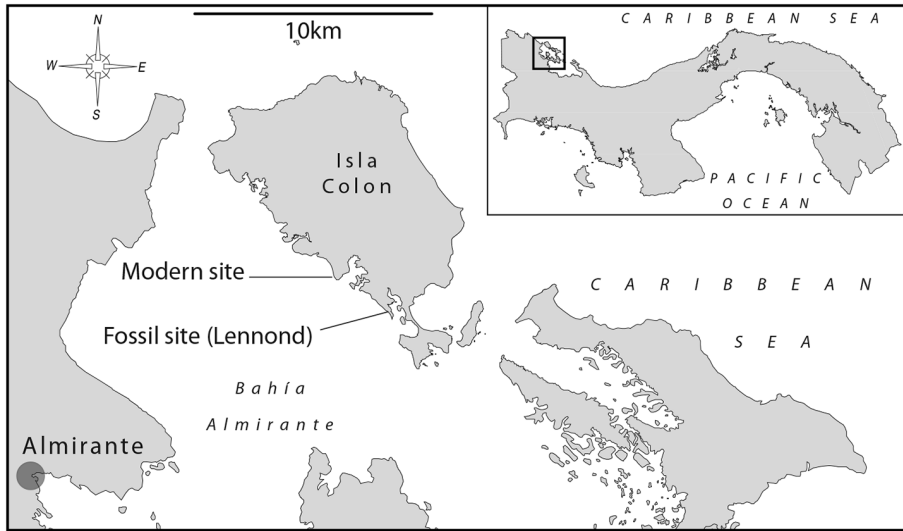
Figure 1. Bocas del Toro Archipelago fossil (9.35488°N, 82.26635°W) and modern (9.36322°N, 82.28375°W) sites.

dredged from about 3 to 5 m below present day sea level and deposited laterally and sub-aerially over approximately 30 m in 2–3 m thick banks parallel to the excavated canals. The exposed sediments are not in situ, but coarse reef zonation is maintained laterally along the exposed sediments because, although the sediments are mixed vertically, they retain their relative horizontal position to within a few meters, as dictated by the length of the arm of the mechanical dredge used. Thus, we first mapped the following clearly delineated zones following a north-south direction.

*Zone 1, Mangrove.*—Organic rich dark muds sit uncomfortably on top of an erosion surface of the Pliocene Old Bank Formation (Coates et al. 2005), which rises steeply and we consider to represent the ancient sea cliff. The molluscan fauna in this zone is dominated by the bivalves *Crassostrea* and *Nuculana* s.l., and the gastropod *Melongena*, all of which typically live associated with mangrove roots and sediments. However, we did not sample this zone given the general low abundance of molluscs and the difficulty in effectively sampling the modern molluscan mangrove death assemblage. Zone 1 at Lennond is best exposed from 9.36052°N, 82.26932°W to 9.36001°N, 82.26940°W.

*Zone 2, Seagrass.*—Carbonate-rich fine muds richly fossiliferous with an abundant bryozoan and mollusc fauna typical of seagrass beds including *Cerithium, Strombus,* and many infaunal lucinid bivalves of the genera *Parvilucina* and *Codakia*. Seagrass blades are occasionally found in the muds. Zone 2 is best exposed from 9.36001°N, 82.26940°W to 9.35985°N, 82.26950°W.

*Zone 3, Backreef-Crest.*—Immediately adjacent to Zone 2 the branching coral *Porites furcata* (Lamarck, 1816) and the lettuce coral *Agaricia* sp. are abundant. These two corals dominate the reef crests of lagoonal fringing reefs in areas adjacent to seagrasses in Almirante Bay today (Guzman and Guevara 1998). We did not sample Zone 3 given its small geographic extent. Zone 3 is best exposed from 9.35985°N, 82.26950°W to 9.35969°N, 82.26957°W.

*Zone 4, Forereef-Crest.*—Moving south, *P. furcata* dominance yields to coral assemblages dominated by the shallow-water forereef-crest acroporids: *Acropora cervicornis* (Lamarck, 1816) and *Acropora palmata* (Lamarck, 1816), some of which are bio-eroded but most are well preserved and some almost pristine. The matrix in Zone 4 is typically slightly coarser grained than the sediments in Zones 1, 2, and 3, but always carbonate-rich. Skeletal remains of *Halimeda* are abundant whereas they were mostly absent in Zone 2. Molluscan assemblages in Zone 4 are locally well preserved in the carbonate sands and muds among the acroporid rubble. The section cuts laterally along the reef crest and so Zone 4 is exposed along much of the canal and is best exposed from 9.35907°N, 82.26954°W to 9.35511°N, 82.26606°W.

*Zone 5, Reef Slope.*—Zone 4 is occasionally interrupted by this distinct facies. Large massive faviids (mostly *Montastraea*) dominate, suggestive of a reef slope. We did not sample Zone 5 because of the lack of abundant molluscs. Zone 5 is best exposed around 9.35885°N, 82.26942°W.

This delineation of five zones in the fossil fringing reef found at Lennond closely resembles the structure of modern fringing reefs that exist along the southwestern coast of Isla Colón today (Fig. 1). The acroporids that dominated Zone 4 are all but absent in the living coral community, but frequently occur dead on the reef, where they presumably fell following their recent die-off (Aronson and Precht 2001, Cramer et al. 2012).

We selected the modern sampling location (Fig. 1) for comparison with the fossil reef based upon (1) its geographic proximity to the fossil reef complex, ensuring similar hydrological properties (Fig. 1), (2) the clear delineation of Zones 1–5 observed in the fossil reef with similar sedimentological conditions, (3) the apparently similar topography to the fossil reef complex as previously described, and (4) the presence of living coral rather than reefs that have almost no living coral cover such as the reef in front of the Smithsonian Tropical Research Institute (STRI) station that is geographically closest to the fossil reef.

Zone 1 (mangrove) in the modern reef complex is approximately 23 m in lateral extent and like Zone 1 in the fossil sits in front of a low cliff cut into the Old Bank Formation. Zone 2 (seagrass) in the modern day lies parallel to the cliff, is approximately 10 m wide and has *Thalassia* beds interspersed with bare carbonate muds and sands. Zone 3 (backreef-crest) has some living *P. furcata* and is roughly 2 m in lateral extent. Zone 4 (forereef-crest) in the present day is dominated by living *Millepora* and the sea floor has dead and bioeroded *Acropora* and *Porites* coral branches. Zone 5 (reef slope) has isolated stands of sponges and boulder and brain corals.

## Methodology and Approach

### Radioisotope Ages

Uranium-thorium radiometric analysis of fossil coral heads from Lennond was performed at Woods Hole Oceanographic Institution using 12 coral blocks collected from Zones 4 and 5 (forereef-crest and reef slope; see Study Sites). On slabbing and inspection, three of the samples were rejected due to visible recrystallization and/or staining, and were not processed further. The remaining samples had no detectable calcite using X-ray diffraction. Triplicate

discrete pieces of three samples were processed to assess age reproducibility. Approximately 8 g of each coral was dissolved in nitric acid and spiked with a 229Th-236U mixed spike. The mixed spike was calibrated with the Harwell uraninite standard HU-1, assuming secular equilibrium (Anderson et al. 2008). Uranium and thorium isotopes were measured at the WHOI Plasma Mass Spectrometry Facility on the Neptune multi-collector mass spectrometer. All isotopes were measured statically on Faraday detectors, resulting in isotope ratio precisions of better than 1‰.

Sampling Methods

In both fossil and modern sites, we sampled Zones 2 and 4 (seagrass and forereef-crest) separately, resulting in four total sampling locations. In each sample location we collected three replicate bulk samples that comprised approximately 25 kg (a bucketful) of sea floor sediment and skeletal material. Samples from the fossil site were collected from sub-aerially exposed sediments and modern samples were obtained by scuba by digging ≤10 cm into the sea floor over an area ≤2 m$^2$. Carbonate backreef lagoon sediments up to 125 cm deep are typically well mixed and do not include any depth-age correlation, although shallow sampling may omit deeply burrowed infaunal bivalves (Kidwell et al. 2005, Kosnik et al. 2007, 2009). In the modern site Zone 2 was approximately 2 m depth and Zone 4 was approximately 5 m depth. Replicates within sampling locations were spaced about 20 m at equivalent depth and midway between zonal boundaries to minimize faunal mixing.

Bulk samples were wet sieved to 10–2 mm. Molluscs comprised 7%–30% of forereef-crest bulk sample mass and 22%–69% of seagrass bulk sample mass, the remainder being almost entirely coral rubble. All bivalve and gastropod skeletal material in the 10 mm fraction was analyzed, whereas the 2 mm fraction was split into eighths using a halving machine. One eighth and the entire 10 mm fraction were analyzed further. For each fraction, every bivalve and gastropod was removed by hand and identified to genus if possible. We identified molluscs using Abbott (1974), with selected taxonomic updates, as no more recent taxonomic compendium exists for the region. Specimens were identified to a generic level for analyses as life habits between congeners, even in the widest sense, tend to be highly conserved (Roy et al. 1996 and references therein, Todd 2001). Genera whose classification has changed or been contested since the publication of Abbott (1974) are identified as either "s.l." (sensu lato), to indicate that the genus could refer to multiple genera now recognized to occur in the SWC and that have not been differentiated in our samples, or as s.l., to denote taxa where the genus is now standardly divided into two or more subgenera, both of which occur in the SWC. Specimens currently are stored in the Tropical Marine Historical Ecology lab at the STRI in Panama, and will ultimately be housed in the National Museum of Natural History in Washington, DC.

The total mass of skeletal material per genus was calculated. To obtain a sum mass for the sample, the results from the 10 mm fraction were divided by eight and added to the results from the 2 mm eighth fraction. Each genus was assigned a guild and a feeding mode based on Todd (2001) (Table 1). Molluscs that were too damaged to be identified with confidence were excluded from all analyses.

The use of skeletal mass of molluscan groups as an estimate of abundance works well in an ecological study of death assemblages (Kidwell and Flessa 1995), but is susceptible to bias. For example, the shells of epifaunal bivalves tend to be thicker than infaunal bivalves (Best and Kidwell 2000) and there likely is to be a phylogenetic component to shell thickness that we did not account for. We therefore stress that skeletal mass is not directly representative of living biomass. Nonetheless, we consider the approach of focusing only on changes in relative abundance to be the most effective when exploring relative ecological differences. Unlike counts of shells, relative skeletal mass reduces issues of missing data caused by post-mortem fragmentation, and lessens distortions due to over-emphasizing small taxa with comparatively little ecological impact relative to larger, potentially more important taxa.

Our study compared fossil death assemblages with modern death assemblages, allowing us to make direct comparisons in community structure across time without compensating

Table 1. Descriptions of 10 detailed feeding groups used to categorize bivalve and gastropod genera by life mode. Adapted from the Neogene Marine Biota of Tropical America database (Todd 2001).

| Name | Abbreviation | Description |
|---|---|---|
| Carnivores | | |
| Browsing carnivore | CB | Feed on sedentary, often clonal, animals (i.e., corals, sponges) without killing them; often parasitic. |
| Predatory carnivore | CP | Kill and feed on entire macro-organism (sedentary or mobile). |
| Herbivores | | |
| Herbivore on fine-grained substrate | HM | Herbivores living on sandy substrates with a variety of food preferences. |
| Omnivorous herbivore | HO | Browsing macroherbivores with unselective omnivory. |
| Herbivore on plant substrate | HP | Herbivores living on seagrass or macroalgae with a variety of food preferences. |
| Herbivore on rocky substrate | HR | Microalgivores on rock, rubble, or coral substrates. |
| Suspension feeders | | |
| Suspension feeder | SU | All taxa that feed mostly or entirely on suspended particles or microorganisms. |
| Deposit feeders | | |
| Chemosymbiotic deposit feeder | DC | Obtain nutrients from chemosymbiosis with oxidizing bacteria. |
| Surface deposit feeder | DS | Digest deposited material on or above the surface of the seabed. |
| Subsurface deposit feeder | DU | Digest deposited material below the surface of the seabed. |

for the effects of turnover that hinder the comparison of live and death assemblages (Kidwell 2013). However, our modern assemblages include time-averaged components (Kidwell et al. 2005, Kosnik et al. 2009) that could predate some environmental or ecological degradation, presumably offsetting any changes in community structure of our samples caused by very recent environmental or ecological changes.

### Analysis

The proportional skeletal mass of guilds within each sample location was normally distributed with equal variance. Differences in skeletal mass of guilds and genera between fossil and modern seagrass and forereef-crest locations were tested using a Student's $t$-test. Ranked skeletal mass of genera in each sample location was calculated using the mass from all replicates. Analyses were performed using the software package R (R Development Core Team 2011).

## Results

### Radioisotope Ages

Three of the 12 coral blocks were discarded due to recrystallization. Radiometric dates were consistently mid-Holocene, ranging from 7187 to 5711 yrs before present (Table 2). Three samples were analyzed in triplicate to assess reproducibility, with a 95% confidence interval of 5, 12, and 42 years for age estimates between replicates.

### Forereef-Crest Samples

In the forereef-crest samples, molluscan generic richness was considerably higher in the fossil (79) compared to the modern (59), although densities of genera per gram of sediment collected were roughly comparable, suggesting that greater richness in the fossil site may have been due to sampling, taphonomic artifacts, or greater time-averaging in the fossil samples (see Online Tables 1, 2). Forty-two of

Table 2. Age and 95% confidence interval of fossil coral samples analyzed using U-Th radioisotopes. * = mean from three measurements to assess reproducibility of results.

| Age (yrs) | 95% confidence interval (yrs) |
|---|---|
| 7187 | 8 |
| 6708 | 8 |
| 6702 | 42* |
| 6671 | 3 |
| 6021 | 3 |
| 5834 | 5* |
| 5818 | 7 |
| 5781 | 12* |
| 5711 | 3 |

the genera were shared between the fossil and modern samples. Fifty-one per cent of the 37 taxa that were unique to fossil samples were carnivores, each of which was small and rarely found in our samples. The remaining 18 fossil-specific genera comprised five deposit feeders, four herbivores, and nine suspension feeders. Curiously, among the genera found only in the mid-Holocene, several were highly ranked, including *Anodontia, Anomia, Codakia,* and *Plicatula* (Table 3). The 17 genera found only in the present day included seven carnivores, six suspension feeders, two herbivores, and two deposit feeders, and only *Gouldia* was highly ranked (Table 3).

Significant differences were found in the relative and rank abundances of taxa between fossil and modern forereef-crest samples, and only 50% of the top 10 most dominant taxa were shared among them (Table 3). *Cerithium,* an herbivorous gastropod, was the most dominant mollusc in both fossil and modern collections, although its relative skeletal abundance by weight was significantly greater in fossil (56.2%) compared to modern collections (30.1%; $t = 5.53$, $P < 0.01$, df = 2). Two other genera revealed significant differences in proportional abundance between fossil and modern forereef-crest samples. *Americardia*, a suspension-feeding bivalve, constituted only 0.1% of molluscs in fossil samples, but 9.2% in the present day, resulting in a shift in rank abundance from 41 to 3 ($t = -4.326$, $P < 0.05$, df = 2). The surface deposit feeder *Tellina* s.l. was significantly more

Table 3. The first 10 ranked genera found in fossil and modern forereef-crest samples, using the mean percentage of total mollusc biomass of three replicates. Feeding modes defined in Table 1.

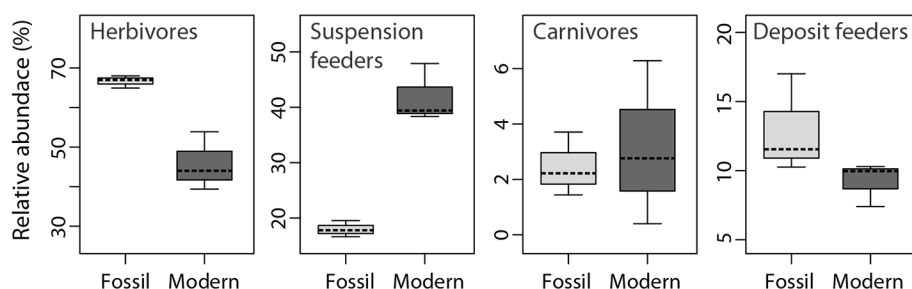| Rank | Fossil forereef-crest | | | Modern forereef-crest | | |
|---|---|---|---|---|---|---|
| | Genus | Feeding mode | Percentage | Genus | Feeding mode | Percentage |
| 1 | *Cerithium* | HM/HR | 56.2 | *Cerithium* | HM/HR | 30.1 |
| 2 | *Modulus* | HR/HP | 6.0 | *Pitar* | SU | 10.3 |
| 3 | *Chama* | SU | 5.8 | *Americardia* | SU | 9.2 |
| 4 | *Anodontia* | DC | 4.9 | *Chama* | SU | 7.7 |
| 5 | *Parvilucina* | DC | 4.0 | *Modulus* | HR/HP | 5.8 |
| 6 | *Anomia* | SU | 3.6 | *Parvilucina* | DC | 4.4 |
| 7 | *Codakia* | DC | 2.3 | *Gouldia* | SU | 3.6 |
| 8 | *Strombus* | HO | 1.9 | *Arca* | SU | 2.9 |
| 9 | *Arca* | SU | 1.6 | *Lucina* | DC | 2.7 |
| 10 | *Plicatula* | SU | 1.5 | *Tegula* | HR | 2.0 |

Figure 2. Relative abundance by skeletal weight of major mollusc guilds between fossil and modern forereef-crest samples. Box-and-whisker plots show median (heavy line), first quartile (lower edge of box), third quartile (upper edge of box), minimum (bottom whisker), and maximum (top whisker). Each comparison is a Student's $t$-test (df = 2, $n$ = 3). (A) $t$ = 4.781, $P$ = 0.008. (B) $t$ = −7.607, $P$ = 0.001. (C) $t$ = −0.377, $P$ = 0.725. (D) $t$ = 1.643, $P$ = 0.175.

abundant in modern coral samples (1.7%) compared to fossil samples (0.1%; $t$ = −4.693, $P$ < 0.05, df = 2).

Although no carnivorous genera were significantly more or less dominant between fossil and modern samples, several revealed interesting patterns. *Anachis* contributed 0.5% of total skeletal biomass in the present day, yet only 0.2% of fossil biomass. *Coralliophila*, a corallivorous carnivore (Rotjan and Lewis 2008), was found only in fossil samples where it constituted 0.33% of molluscan skeletal mass.

When skeletal masses were pooled by gross trophic group, herbivorous molluscs accounted for 66.6% of mollusc skeletal biomass in the fossil, but only about 45.8% in the present day (Fig. 2), a significant difference ($t$ = 4.781, $P$ < 0.01, df = 2). Even more strikingly, suspension feeders were 2.5 times more dominant in modern than in fossil forereef-crest samples (Fig. 2; 41.9% vs 18.0%; $t$ = −7.607, $P$ < 0.001, df = 2). The relative dominance of carnivorous and deposit feeding molluscs was not significantly different between fossil and modern collections (Fig. 2; $t$ = −0.377, $P$ = 0.725, df = 2; $t$ = 1.643, $P$ = 0.175, df = 2, respectively).

Seagrass Samples

Generic richness in fossil seagrass samples was substantially higher (48) than modern seagrass samples (38), although richness was similar between samples when standardized by sample mass (see Online Tables 1, 2). Only 22 genera were present in both fossil and modern samples. Of the 26 genera found only in the fossil, 2 were deposit feeders, 14 were suspension feeders, 3 were herbivores, and 7 were carnivores. *Nuculana* s.l.*, Strombus, Anomia,* and *Chione* were among the fossil-specific taxa with high ranks (Table 4). The 5 herbivores, 5 suspension feeders, 3 deposit feeders, and 3 carnivores that occurred only in the present day included the bivalves *Codakia, Arcopsis, Arcopagia,* and *Semele* (Table 4).

Striking differences were observed in the composition and abundances of constituent taxa between fossil and modern seagrass samples (Table 4). Only three of the 10 most abundant genera were shared in fossil and modern samples. The most conspicuous differences include a significant shift in rank (14 to 2) and relative abundance (0.7% to 26.6%) of *Parvilucina*, a chemosymbiotic deposit feeder ($t$ = −7.634, $P$ < 0.05, df = 2). The suspension-feeding bivalve *Pitar* was found to be 100

Table 4. The first 10 ranked genera found in fossil and modern seagrass samples, using the mean percentage of total mollusc biomass of three replicates. Feeding modes are defined in Table 1.

| | Fossil seagrass | | | Modern seagrass | | |
|---|---|---|---|---|---|---|
| Rank | Genus | Feeding mode | Percentage | Genus | Feeding mode | Percentage |
| 1 | *Cerithium* | HM/HR | 32.3 | *Cerithium* | HM/HR | 39.9 |
| 2 | *Nuculana* s.l. | DU | 11.6 | *Parvilucina* | DC | 26.6 |
| 3 | *Strombus* | HO | 10.5 | *Pitar* | SU | 15.3 |
| 4 | *Anodontia* | DC | 10.4 | *Codakia* | DC | 3.5 |
| 5 | *Bulla* | HP | 6.9 | *Modulus* | HR/HP | 2.7 |
| 6 | *Tellina* (s.l.) | DS | 6.5 | *Lucina* | DC | 2.5 |
| 7 | *Chama* | SU | 6.2 | *Tellina* (s.l.) | DS | 2.0 |
| 8 | *Modulus* | HR/HP | 1.9 | *Arcopsis* | SU | 1.2 |
| 9 | *Anomia* | SU | 1.8 | *Arcopagia* | DS | 1.1 |
| 10 | *Chione* | SU | 1.3 | *Semele* | DS | 0.9 |

times more abundant in modern samples compared to fossil (0.2% vs 15.3%; $t = -9.354$, $P < 0.05$, df = 2). The herbivorous gastropod *Bulla* was significantly more abundant in fossil vs modern samples (6.9% vs 0.8%; $t = 4.273$, $P < 0.05$, df = 2), and the subsurface deposit feeder *Nuculana* s.l. comprised 11.6% of fossil seagrass samples whereas it was entirely absent in the modern samples ($t = 7.102$, $P < 0.05$, df = 2).

No significant differences were observed in the relative abundances of gross molluscan trophic groups between fossil and modern seagrass samples, although a greater proportion of herbivores and carnivores were found in fossil samples while more suspension and deposit feeders were found in modern samples (Fig. 3).

## Discussion

### Age and Depositional Environment of the Fossil Site at Lennond

Excavations made by Sunset Point, Inc. in Bocas del Toro exposed the fossil coral and seagrass sediments used in the present study. Sediments were vertically mixed during excavation and not in situ. It is therefore somewhat surprising that the amount of variation in estimated ages among the nine coral samples dated radiometrically was as low as about 1.5 ka (Table 2).

The dominant corals in the fossil site are *A. cervicornis*, *Montastraea "annularis"* (Ellis and Solander, 1786), and *P. furcata*, all of which grow from 0 to 15 m deep (Mesolella 1967, Aronson et al. 2004). *Acropora cervicornis* usually inhabits slightly deeper waters, often occurring up to 25 m deep, except in protected areas such as a backreef or lagoonal setting where it can grow in depths as shallow as 5 m (Rützler and Macintyre 1982, Aronson and Precht 2001) such as the one that must have existed at Lennond, which sits on the leeward side of Isla Colón (Fig. 1). The molluscan community in the seagrass sediments is indicative of deposition in shallow (<5 m) depths.

Genera from the modern forereef-crest and seagrass sites provide information regarding the sedimentary conditions in those habitats. *Americardia* and *Tellina* s.l., both common in the modern forereef-crest samples, are typically found in sandy subtidal areas (Stanley 1970). *Tellina* s.l. burrows deeply, indicating substantial sand depth beneath the modern reef (Stanley 1970). The modern seagrass samples also contained *Arcopagia*, which burrows deeply in grass-covered sand just beneath low tide level (Stanley 1970). We did not find clear signals of
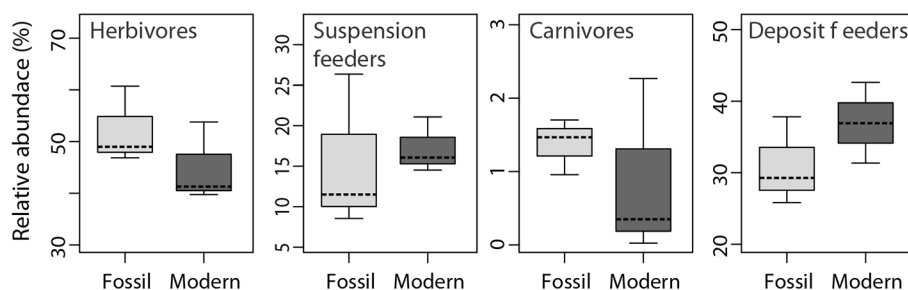
Figure 3. Relative abundance by skeletal weight of major mollusc guilds between fossil and modern seagrass samples. See Figure 2 for details. Each comparison is a Student's $t$-test (df = 2, $n$ = 3). (A) $t$ = 1.171, $P$ = 0.307. (B) $t$ = −0.298, $P$ = 0.780. (C) $t$ = 0.675, $P$ = 0.537. (D) $t$ = −1.243, $P$ = 0.282.

sedimentary conditions from the most common genera at the fossil site. The fossil forereef-crest site had abundant *Anodontia* and *Codakia*, which typically burrow deeply in grassy intertidal areas, suggesting either that the mid-Holocene reef was very heterogeneous in habitat or that some molluscs were transported to the reef postmortem (Stanley 1970).

Ecological Shifts in Forereef-Crest

The molluscan community of the forereef-crest habitat flanking the southwestern coast of Isla Colón, Bocas del Toro, appears to have undergone dramatic shifts in both its taxonomic composition and its ecological structure since the mid-Holocene. The modern reef has a significantly higher proportion of suspension feeding molluscs compared to its paired mid-Holocene reef and the proportion of herbivorous molluscs is significantly less in the modern reef.

These patterns can be best understood when placed into the local historical context of the Bocas del Toro archipelago and the regional historical context of the Caribbean. In the past century, overfishing of large herbivores that began in pre-Columbian times accelerated in the Caribbean (Jackson et al. 2001, Cramer 2013). *Diadema antillarum* (Philippi, 1845) masked this effect by filling the functional role of grazers on coral reefs, until a mass mortality of *Diadema* in 1983–1984 led to a collapse in the reef's ecological structure (Lessios 1988, Hughes 1994). Simultaneously, *A. cervicornis* and *A. palmata*—which first appeared in the Bocas del Toro fossil record approximately 5 Ma and have dominated Caribbean coral reefs for at least the past 2.2 My (Klaus et al. 2012)—also began to decline before the mid-1960s in lagoonal reefs in Bocas del Toro (Cramer et al. 2012). These species abruptly became rare throughout most of the Caribbean in the 1980s due to white-band disease (Aronson and Precht 1997, Greenstein et al. 1998, Aronson and Precht 2001). Finally, population growth and eutrophication in the Bocas del Toro area have caused increased eutrophication over the past century (Stephens 2008, Cramer 2013).

In this historical context, the shifts observed in molluscan communities between the fossil and modern forereef-crests in Bocas are expected. *Cerithium, Modulus, Strombus,* and other herbivores that we found in abundance feed on microalgae and filamentous turf algae (Houbrick 1980, Steneck and Watling 1982), which require space and low water turbidity to flourish (Hay and Fenical 1988).

This contrasts with the eutrophication of waters in Bocas del Toro that favors macroalgal growth, which out-compete turf algae to the detriment of these herbivorous molluscs (Rasher et al. 2012). Likewise, increased eutrophication is beneficial to suspension-feeding molluscs due to increased plankton in the water column (Fisher et al. 1992, Ayukai 1995), thus explaining the proportional increase in suspension feeding molluscs from the fossil to the present day.

The proportion of deposit feeders is similar between fossil and modern coral samples. Deposit feeders include molluscs with both epifaunal and infaunal life habits, and molluscs with chemosymbiosis and those without, each of which are likely to respond differently to the known environmental changes that have occurred in the region. Therefore, given the wide functional roles of deposit feeders, it is likely that an analysis using finer functional groupings would reveal more easily interpretable patterns. However, our data do show that although deposit feeders without chemosymbiosis were generally scarce across all of our samples, the 13-fold increase in *Tellina* s.l. skeletal biomass in the modern relative to the fossil suggests that non-chemosymbiotic deposit feeders may have become relatively more abundant in Bocas del Toro because of an increase in detritus compared to the mid-Holocene.

No significant difference was observed in the proportion of carnivorous molluscs between fossil and modern forereef-crest samples. One obstacle to interpretation is the dearth of studies on the life histories and precise feeding habits of tropical carnivorous gastropods, making predictions difficult. Nonetheless we explore possible explanations for two intriguing, though non-significant, trends in carnivorous genera. (1) The predatory gastropod *Coralliophila* was present in our fossil samples but entirely absent from our modern forereef-crest samples. *Coralliophila* predates upon hermatypic corals (Rotjan and Lewis 2008) and its absence in the present day may reflect the overwhelming decline in extent and structure of Caribbean reef corals since the mid-Holocene (Aronson and Precht 2001, Gardner et al. 2003). (2) Some species of *Anachis,* an uncommon gastropod in all our samples but more prevalent in the modern day, are known to consume recently settled juvenile ascidians (Osman and Whitlatch 2004). Ascidians outcompeted and completely overgrew corals in the 1980s on a reef in Curaçao (Bak et al. 1996); ascidians often expand quickly into areas where they are non-native or rare (Lambert 2002) and are observed in abundance in Bocas del Toro today (Rocha et al. 2005). We speculate that the greater abundance of *Anachis* in the modern compared to the fossil could have been driven by a substantial increase in ascidian density on the reefs, which in turn may have been initiated by declining coastal ecosystem health. However, we must caution that prey specificity within *Anachis* and among closely related columbellid genera remains poorly understood and greater taxonomic resolution is required to support this interpretation.

The general trends seen in the guilds of herbivores and suspension feeders in the forereef-crest (Fig. 2) were corroborated by shifts between fossil and modern proportions of individual genera (Table 3). *Cerithium,* an herbivore that dominated every sample in this study, accounted for twice the proportion of skeletal biomass in the fossil than in the Recent. By contrast, several suspension feeders, including *Americardia* and *Pitar,* were present in greater proportions and higher ranks in the modern than in the fossil collections. These genus-specific results strengthen our conclusion that predominantly human-driven environmental change in the

region has made suspension feeding a more advantageous strategy, and herbivory less so, today.

Gastropod death assemblages recovered from discrete horizons in 80 cm-deep pits excavated in reefs in Bocas del Toro showed no significant change in the proportion of carnivores, herbivores, omnivores or suspension feeders between pre- and post-1960 horizons (Cramer 2011, p. 135). The study did, however, reveal a decline in herbivore shell weights over time, attributed principally to historical exploitation of edible conch species (Cramer 2011, p. 135). Declining weights of individual conch (*Strombus* or *Lobatus*) over time, driven by long-term artisanal harvesting pressure, have been documented in several regions around the world (Posada et al. 2007). There is evidence that several species of conch were being heavily exploited in Bocas in pre-Colombian times (Wake et al. 2013). This may help explain our finding of reduced relative abundance of herbivore skeletal mass in the present day. Indeed, we found that the skeletal weight contributed by *Strombus* was considerably higher in fossil than modern sediments in both seagrass and forereef-crest samples (Tables 3, 4).

Perhaps the most conspicuous change to have occurred on Caribbean coral reefs is the widespread loss of the reef-building corals *A. cervicornis* and *A. palmata.* This transformation is strikingly clear when the dominance of acroporids in the fossil site at Lennond is compared to their rarity in Bocas del Toro, particularly along the western coast of Isla Colón. This dramatic shift appears to have begun historically (Cramer et al. 2012) and accelerated in the 1980s due to whiteband disease (Hughes 1994, Aronson and Precht 2001). The end result is a shift to dominance by *Porites* and *Agaricia* corals, reducing the overall three-dimensional structure of Caribbean reefs (Aronson and Precht 2001). Macroalgal overgrowth due to historical removal of herbivorous fish, the widespread loss of *Diadema* in the 1980s, and long-term eutrophication is a key suspect of this collapse in reef structure (Hughes 1994, McCook et al. 2001, Fabricius 2005), but the potential role of molluscs in mediating this process has so far been overlooked.

Massive declines in the relative abundance of herbivorous molluscs, as our data suggest, must have had important effects on the reef community, just as is commonly believed for the consequences of the removal of herbivorous fish from a reef. In order to explore such hypotheses, time-series data on molluscan assemblages need to be compiled from tropical reef communities, and their roles in reef function across space on living reefs explored.

Finally, given that our modern samples represent a time-averaged assemblage that may have components 100 yrs old or more (Kosnik et al. 2009, Kidwell 2013), all the shifts revealed by our data almost certainly underestimate the scale of ecological change that has occurred in Caribbean reef molluscan communities in the past decades.

## Ecological Shifts in Seagrass

At the guild level, this preliminary study found that molluscan communities in seagrass meadows on the western flank of Isla Colon in Bocas del Toro are functionally similar between the mid-Holocene and the present. No significant differences were found in the relative proportion of herbivores, suspension feeders, deposit feeders, or carnivores. Nonetheless, individual genera differed markedly between the two sites. *Pitar*, a suspension feeding gastropod, increased while the herbivorous *Bulla* (Malaquias et al. 2009) decreased in abundance in the present day, echoing our predictions.

*Parvilucina* contributed a quarter of total skeletal biomass in the modern seagrass samples, but was barely present in the fossil seagrass samples. *Parvilucina* is known to thrive in polluted and hypoxic environments, and to increase in both size and abundance near wastewater discharge sites in California. Consequently, *Parvilucina* may be a possible bioindicator of pollution (Word et al. 1977). In addition, as chemosymbiotic deposit feeders, the Lucinidae—including *Parvilucina*—maintain a codependent relationship with seagrass, reducing levels of sedimentary sulfide and receiving oxygen in return (van der Heide et al. 2012). However, a much larger lucinid, *Anodontia*, was barely present in the present day but accounted for >10% of fossil seagrass molluscan biomass. Individual genera of lucinids may respond differently to habitat change, and *Parvilucina* may have a distinct role in modern seagrass beds. Much more research is needed on the relationship between these genera and changes in their habitats, and our results could be due to a taphonomic effect that might erase small distinctions between optimal habitat of different genera.

Eutrophication is known to damage seagrass meadows by inducing macroalgal overgrowth and inhibiting photosynthesis (Lapointe 1997, Duarte 2002), but also potentially could enhance seagrass growth through fertilization (Lee and Dunton 2000, Ferdie and Fourqurean 2004). Increased growth of seagrass fronds may benefit herbivorous molluscs by providing greater surface area for turf and coralline algae to grow, particularly given that seagrass-dwelling *Strombus* and *Cerithium* heavily graze on periphyton (Klumpp et al. 1992). The harvesting of turtles and manatees releases seagrasses from grazing pressure and could enable more robust seagrass growth in the present day (Valentine and Duffy 2006). However, overfishing may also promote macroalgal overgrowth and lead to seagrass decline (Hauxwell et al. 2001). Since human activities lead to a wide range of ecological effects via many pathways, it would be surprising to find a simple and predictable response in seagrass meadows. Depending on local environmental conditions, the competing influences of eutrophication and reduced grazing could result in a "net zero" effect on the growth of seagrass, which may explain the lack of significant differences in guild structure between our fossil and modern seagrass samples.

Seagrasses and hence seagrass molluscan communities may be more resilient to environmental change than the molluscan communities in coral reefs, because anthropogenic drivers influencing the amount of ecosystem structure provided by the seagrass fronds and roots are not compounded. To our knowledge, human-driven regime shifts—which are common in coral reefs—have not been recorded in Caribbean seagrass meadows.

## The Ecological Roles of Molluscs and their Importance in Reef Conservation

Molluscs play an integral role in the biodiversity and structural integrity of Caribbean reef systems, and studies of reef degradation have failed to adequately include the function that molluscs play in reef ecosystems. Declining herbivory is considered to be a major driver of reef health decline, and the roles of herbivorous fish and echinoids have been extensively studied, yet the ecological importance of herbivorous molluscs remains overlooked. The popular paradigm is that a historic loss of herbivorous fish led to macroalgal overgrowth and eventual coral death, but this could be modified to include herbivorous molluscs (Scheibling 1994). Similarly,

although increased water turbidity is commonly perceived as a serious threat to corals and a boon to macroalgae, the ability of suspension-feeding molluscs to improve water quality has been poorly studied in tropical ecosystems, their historical abundances unknown and baselines lacking.

Reefs are much more than the corals that form them and the fish that inhabit them, and estimates of baseline conditions should incorporate into their assessments the important and diverse roles molluscs play. This is especially true given that the excellent preservation of ancient molluscan assemblages permits the rigorous and detailed reconstruction of baseline ecosystems. Likewise, conservation goals would be greatly enhanced if the structure of entire communities, molluscs included, were incorporated, rather than the few select species that are extensively researched.

## Summary

Reef and seagrass ecosystems in Bocas del Toro and the wider Caribbean have undergone extensive historical and modern shifts in their environments and ecological structure that included the collapse of acroporid corals, the near-extinction of *Diadema*, the selective removal of fish and macroinvertebrates, and the eutrophication of waters from pollution and runoff, all of which should be reflected in molluscan communities.

Excavations of adjacent and highly comparable mid-Holocene and modern forereef-crest and seagrass facies in Bocas del Toro have revealed a rich suite of molluscs that permit the description of changes in molluscan communities in these two habitats from before significant human interactions began to the modern day.

Modern molluscan communities on the reef crest have a greater biomass of suspension-feeding molluscs, as predicted by increased eutrophy in the present day, and significantly less herbivorous molluscs than the fossil reef. This finding parallels historical declines in herbivory in fish and echinoids, which may have been caused by the collapse in acroporid corals, or vice versa.

The functional structure of fossil and modern molluscan communities in seagrass beds is remarkably similar, although the taxonomic composition is quite dissimilar, demonstrating ecological but not taxonomic stability. A more thorough exploration at higher functional and taxonomic levels is required.

The role of molluscs in the ecology of reef ecosystems has long been appreciated by marine ecologists, but their importance in the integrity and diversity of the ecosystem has been overlooked, to the detriment of conservation science.

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