UNIVERSITY OF CALIFORNIA SAN DIEGO

A 1200-year record of parrotfish teeth suggests centuries of overfishing in Belize.

A Thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Oceanography

by

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The Thesis of Wendy Tamiko Muraoka is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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Chair

University of California San Diego

2019

DEDICATION

For Mom and Dad.

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ABSTRACT OF THE THESIS

A 1200-year record of parrotfish teeth suggests centuries of overfishing in Belize.

by

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Humans have utilized the Mesoamerican Reef for millennia but the effects of prehistorical and historical fishing on this ecosystem remain understudied. To assess long-term trends in reef fish abundance in the central Belizean portion, we used three reef matrix cores from this region to construct a record of parrotfish (Labridae) tooth abundance relative to the total number of all fish tooth subfossils. Parrotfish positively affect reef accretion rates and play a pivotal role in maintaining reefs in a coral-dominated state. Our study examined a 1200-year record across three coral cays: Elbow and Lagoon Cays and Bakers Rendezvous. Despite initial increases of fish tooth abundance at all three cays, declines were observed well before modern reef degradation. At Elbow Cay, an initial decline, likely due to Pre-Columbian Maya fishing, appears to be halted near the time of Spanish arrival. A subsequent decline begins at Elbow and Lagoon Cays likely due to Spanish colonization. The religious practices of the Catholic Spanish and the arrival of English privateers and logwooders likely increased fishing pressure.

Bakers Rendezvous shows rapid accretion and parrotfish tooth accumulation as well as high tooth abundances, even as the other two cays show declines. Its sharper, more recent decline is likely the result of either the use of new, more southern fishing territories for Catholic Maya converts, the 1832 founding of Stann Creek Town by the Catholic Garifuna, or an interaction of the two. Our data suggest that the origins of reef degradation began hundreds of years before modern declines.

INTRODUCTION

Coral reefs face a myriad of threats, including climate change, physical damage, bleaching events, pollution, overfishing, and disease (1-3). The Mesoamerican Reef (MAR) is the Northern Hemisphere's largest reef, stretching over 1000 miles and across the coastlines of four countries (2). It contains the world's second largest barrier reef, the Belize Barrier Reef Complex (2). Like many others in the Caribbean, these reefs have struggled with modern threats, resulting in unprecedented changes (1, 2). In 1986 Belize's primary reef-building coral, *Acropora cervicornis*, experienced mass mortality due to an outbreak of the likely bacterial, white band disease (4, 5). These corals continue to show little recovery, resulting in a region-wide turnover to dominance of the lettuce coral, *Agaricia tenuifolia* (4, 6-8). This event was shown to be unique for at least the past 3800 years (4, 9). The 1983-84 Caribbean-wide mass dieoff of the urchin, *Diadema antillarum*, left Belize with reduced herbivore populations (10). Hurricane and bleaching events of the 1990s and 2000s substantially decreased coral cover while the now reduced herbivore populations allowed algal overgrowth of the reef (1, 11, 12). The 1998 mass coral die off from bleaching, the first event of its kind in the Caribbean, was unprecedented in Belize's central lagoon for at least the last 3000 years (12). The continued effects of agricultural pollution and runoff combined with these disturbances and low herbivore population has resulted in a phase shift in many areas of the Belize Barrier Reef from coral to algal dominance (1, 2, 13-15).

This change was seen earlier on other reefs in the Caribbean; disturbance has exposed the vulnerability of coral reef ecosystems and decreased recovery has been the result (1, 3, 16). However the historical roots of these vulnerabilities are poorly understood (17, 18). Belize has been continuously inhabited for at least the past 4000 years but the earliest systematic reef monitoring in the Caribbean did not begin until the 1970s, after many areas were already experiencing declines (1, 17-20). Shifting baselines—or baselines set after human impacts had already begun—thus represent a major problem for reef management (21, 22). Comparative studies have looked at remote reefs as models for pristine conditions, untouched by human interaction but it has been suggested that no reef area is entirely free of human influence (22-24). Over recent decades, climate change has increased bleaching events worldwide

and ocean acidification has changed the saturation state of calcium carbonate, integral to calcifying organisms and corals (25, 26).

Fossil records can provide insight into these questions of historical reef conditions. In Bocas Del Toro, archaeological investigations have shown prehistoric switching of mollusk resources and decreases in the trophic level of fish consumed, suggesting overexploitation of preferred resources (27). Fossil records from the area also show reef degradation began decades before the 1960s, likely by the 19th century (28). Fossil records from Barbados show that the last several hundred thousand years of coral community continuity have been interrupted by recent changes due to human activity (29). Archaeological records have also shown a decrease in the size of reef fishes across the Caribbean islands as a result of prehistoric human exploitation (30). Prehistoric and historical human fishing before 1800 heavily reduced Caribbean populations of large vertebrates, including turtles, manatee, and the now extinct Caribbean Monk Seal (31). Decreases in all marine species, worldwide, especially large carnivores and herbivores have also been shown (17). Sediment cores provide further insight into the past and represent a quantitative look into the fossil record. They provide continuous chronologies that can be dated and contain an abundance of fossil material across diverse taxa (18, 32-34). Sediment core records have shown unprecedented mass dieoffs and species turnovers, decreasing water quality, and the importance of parrotfish on reef accretion (4, 9, 18, 35, 36). Together, these fossil records show that reefs were degraded long before recent coral bleaching events began.

Herbivores have been shown to play a key role in reef ecosystem health, resilience after disturbance, and maintenance of high coral cover (16, 37-44). Parrotfish (family Labridae) scrape and excavate filamentous turf algae, endolithic algae, and reef substrate with their specialized tooth morphology and grinding jaws (1, 45-47). By consuming algal competitors, parrotfish promote coral recruitment and reef resilience, complexity and accretion (1, 38, 39, 41, 46, 48, 49). This has been shown to outweigh the negative effects of occasional parrotfish corallivory (50). However, parrotfish are frequently overfished; human reef fishing preferentially exploits the largest fish species but upon their depletion, fishing shifts focus to the exploitation of large parrotfish (40, 51-54). On heavily fished reefs,

small parrotfish, damselfish and juveniles of other species dominate the fish assemblage but are frequently incapable of controlling macroalgae (37, 40, 48, 51). By comparison, large parrotfish, directly affected by reef overfishing, have been shown to be a crucial piece to maintaining low macroalgal cover on coral reefs (37, 40, 51, 52).

Using three sediment cores taken from the Belize Barrier Reef, I inferred a record of local fishing pressures through the use of fish teeth as a proxy for fish abundance. Parrotfish have highly robust, abundant, and identifiable teeth, which were of particular focus. Cores were dated using high precision U/Th dating of corals, which provided errors of less than 13 years. This method has been used on sediment cores to great success—records show rapid, linear sedimentation rates for thousands of years (18, 32, 33). Combined, my data spans from 683 C.E., the middle of the Maya Classic Period (250-900 C.E.), and continues uninterrupted through the Maya Post Classic Period (900-1550), and European Colonial Period to the near present date of 1972. Using these three records and historical and archaeological information, I propose a timeline reflecting Belize's demographic changes that may provide answers as to the last several centuries of decline in fish populations in this area. I suggest that overfishing as a result of culture changes after European colonization, resulted in decreases in the abundance of parrotfish. I suggest that decreases in this key herbivore group weakened this ecosystem and contributed to the degradation we currently see two centuries later. This may allow for the extrapolation of historical baselines for reef fish populations. Centuries of interaction with neighboring humans chipped away at these ecosystems, creating the vulnerabilities necessary for present day Caribbean-wide reef degradation.

RESULTS

For all sites, the proportion of parrotfish teeth increases over time until an inflection point is reached and a subsequent decrease is observed in all core records (Fig 1a). The earliest decline is observed in the Lagoon Cay record, beginning in the year 1300 CE and continuing until 1550 when abundances begin to increase. This increase continues until 1650 when parrotfish tooth abundances begin

a precipitous decline to the present. By comparison, the Elbow Cay parrotfish tooth abundance record increases until 1528 at which time a slow, declining trend begins and continues to the present. A substantial two-century long delay separates the decline in the proportion of parrotfish teeth in the Bakers Rendezvous record in comparison to Elbow and Lagoon Cay sites. The proportion of parrotfish teeth in this record increases until 1850 when it begins a sharp decline to the present. For each core, the overall number of teeth decreases simultaneous to declines in the proportion of parrotfish teeth (Fig 1b).

Trends in parrotfish tooth accumulation rates (total teeth/number of years represented per sample) for all three cays mirror the increasing and decreasing trends seen in parrotfish tooth proportion (Fig 1c). The magnitude of these accumulation rates are roughly comparable for Elbow and Lagoon Cay data, however Bakers Rendezvous stands in stark contrast (Fig 2a). Its accumulation rates are substantially higher, with its median roughly 3 times that seen at Elbow Cay and more than 4.5 times that seen at Lagoon Cay (Fig 2a). These magnitude differences are echoed in the accretion rate data: the Bakers Rendezvous rate is nearly double that of Elbow Cay and 2.5 times that of Lagoon Cay (Fig 2b).

A small negative correlation was found between accretion rate and the proportion of parrotfish teeth ($p=0.02$; correlation $=-0.23$) across all sites combined, but no correlation was shown for each individual site. Accretion and accumulation rates showed a small negative correlation for Bakers Rendezvous ($p=0.032$; correlation $=-0.39987$) and a strong positive correlation for Elbow Cay ($p=4.06e-07$; correlation $=0.77$). No significant correlation was shown for Lagoon Cay.

Examination of symbiont bearing foraminifera abundances in the Elbow Cay record stands in contrast to the parrotfish tooth data. Symbiont bearing foraminifera increase throughout the record, with low initial abundances increasing to modern times (Fig. 1d).

U-Th dates range from 683.4±10 AD to 1972.5 ± 2.4, with errors (2σ) between 2.4 and 12.1 years (Fig 3, Table 1).

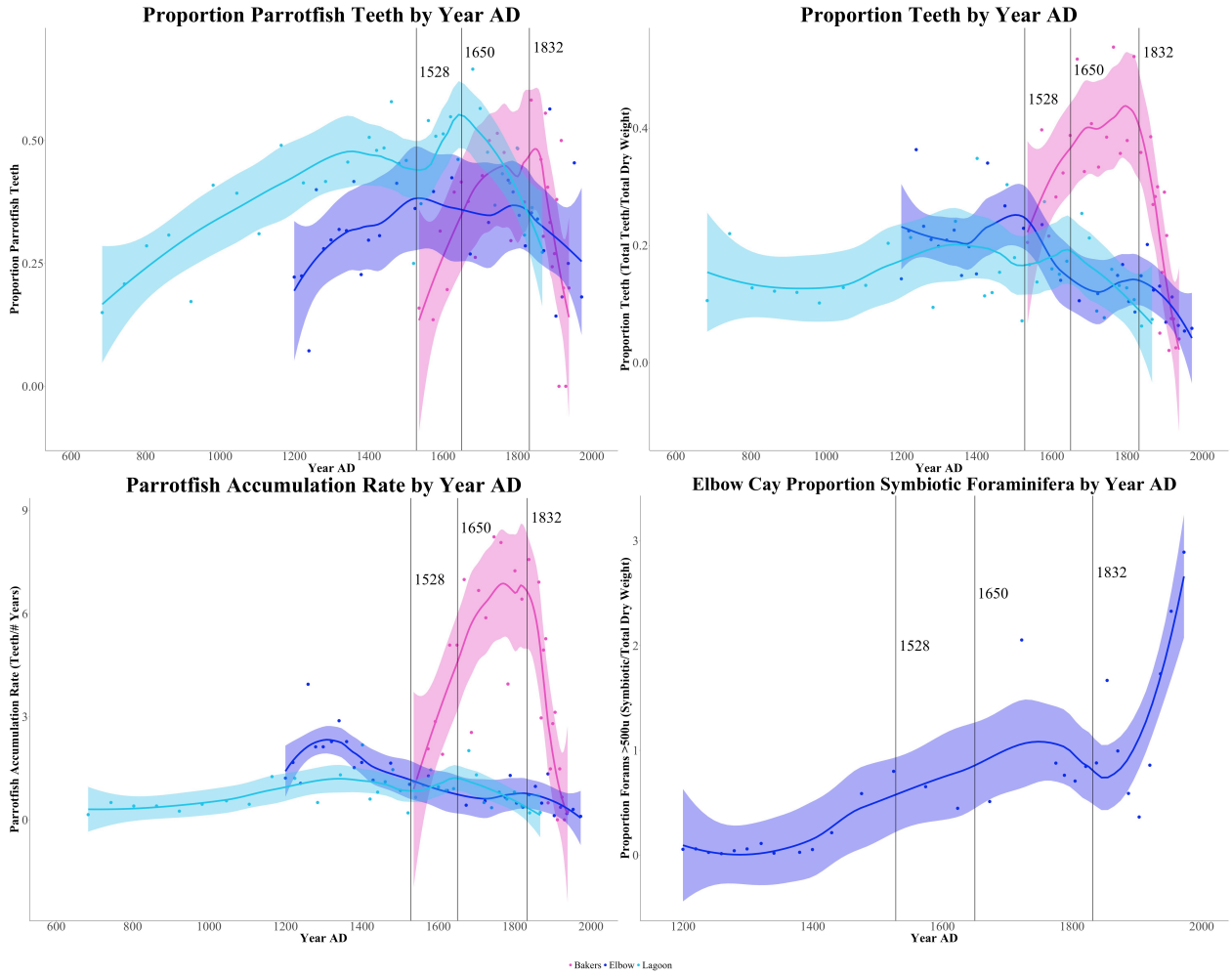

Figure 1. Trends in Parrotfish and Foraminifera Abundance and Accretion. A) Parrotfish abundance over time, represented by the proportion of parrotfish teeth to total teeth. B) Total fish abundance over time, represented by the total number of all teeth divided by the total dry weight of sediment samples. C) Parrotfish tooth accumulation rate through time, represented by the total number of parrotfish teeth in each sample, divided by the number of years represented by the sample. D) Elbow Cay symbiotic foraminifera abundances through time, represented by the total number of symbiotic foraminifera >500µm divided by the total dry weight of sediment samples. For all plots, lines are drawn at 1528 AD, 1650 AD, and 1832 AD. These mark initial Spanish entry into Belize, initial English presence in Belize and the founding of Stann Creek Town (now Dangriga), respectively. Loess lines were set to a smoothing of 0.5 for all plots to show trends.

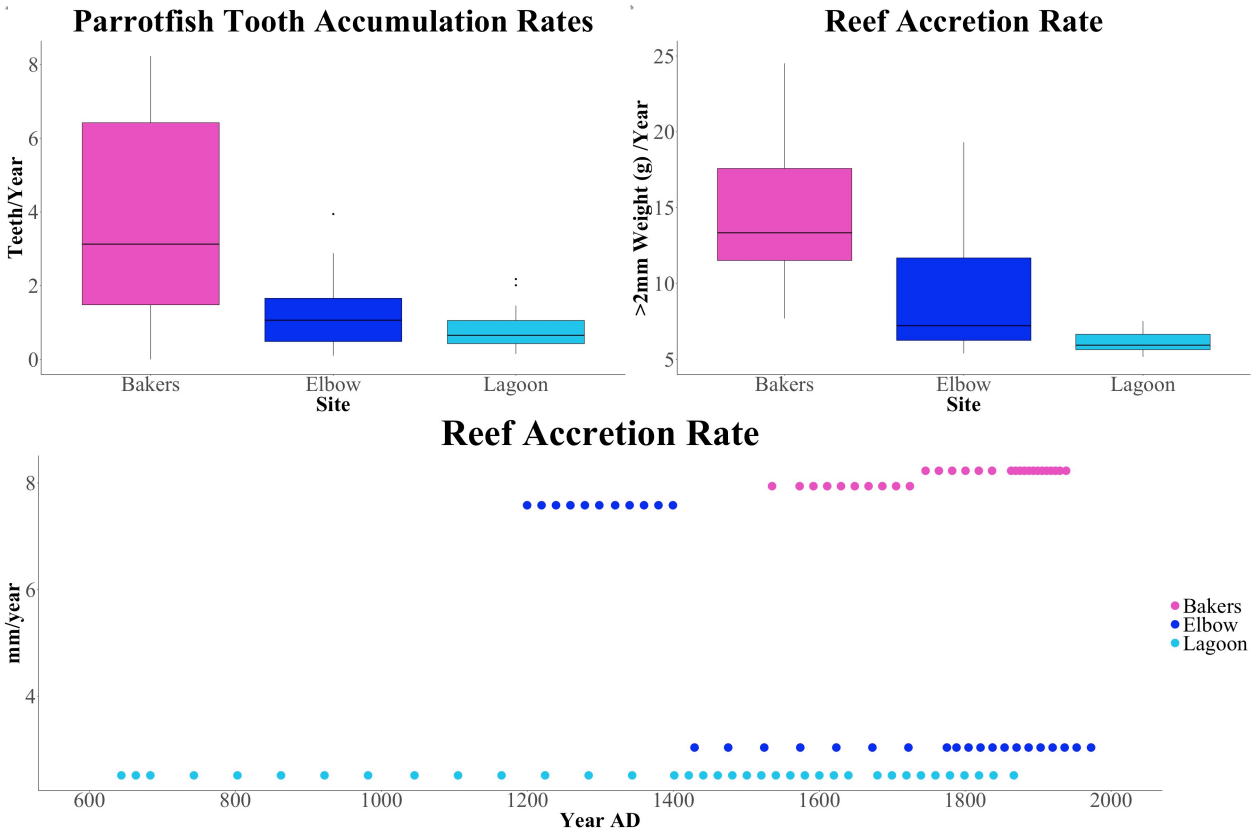

Figure 2. Accumulation and Accretion Rates. A) Parrotfish tooth accumulation rates by site, represented by the total number of parrotfish teeth found per year. B) Reef accretion rate by site, represented by the dry weight of sediment >2mm per year. C) Reef accretion through time, represented by the length (mm) of sediment deposited per year.

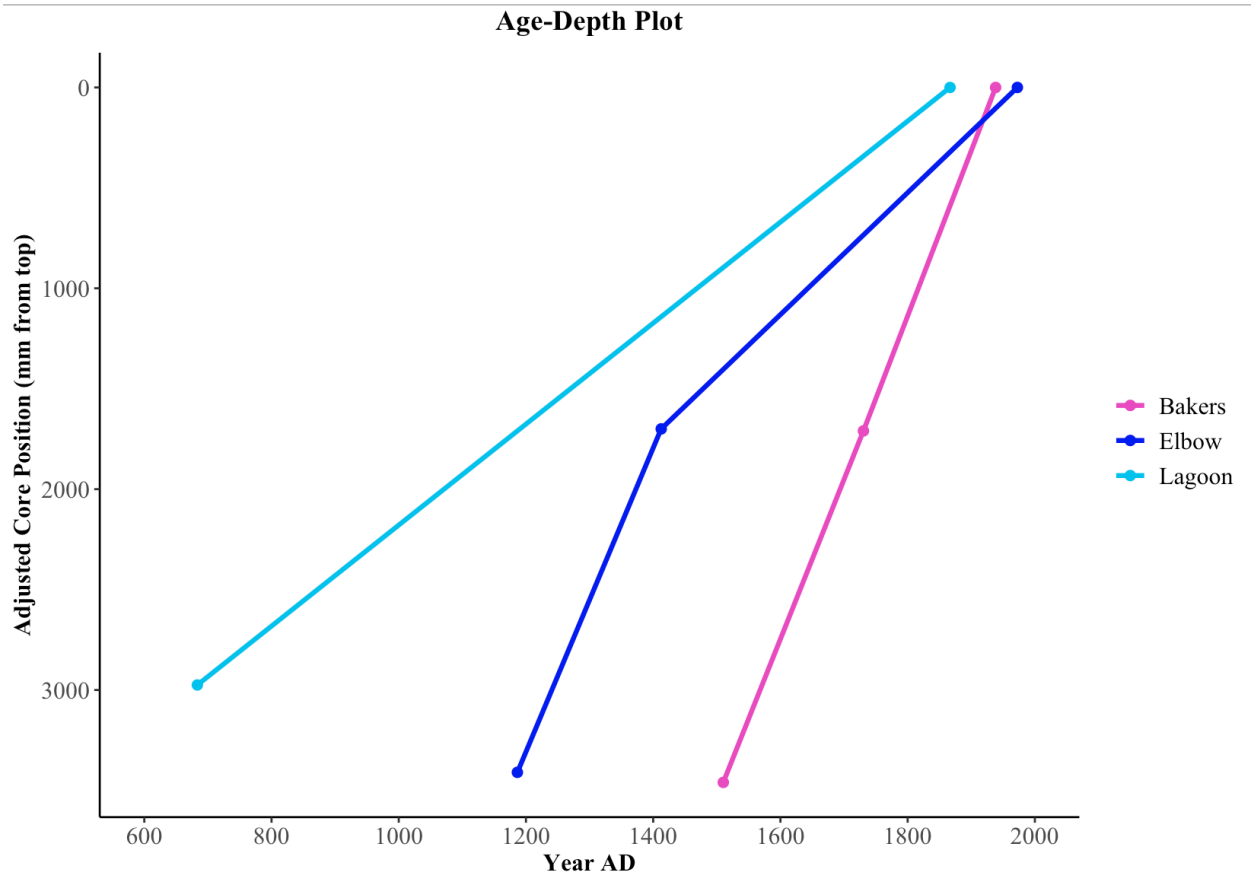

Figure 3. Age-Depth Plot. Trends in accretion rate through time using Uranium-Thorium dates.

Table 1. Uranium-Thorium Dates.

Location (Site)	Adjusted Core Position (mm from Top)	Year (AD)	±2sd (error)
Bakers Rendezvous	0	1938.3	4.1
Bakers Rendezvous	1710	1730.5	3.8
Bakers Rendezvous	3460	1510.2	3.4
Elbow Cay	0	1972.5	2.4
Elbow Cay	1700	1412.6	6
Elbow Cay	3410	1186.5	5.4
Lagoon Cay	0	1866.7	12.1
Lagoon Cay	2975	683.4	10

DISCUSSION

Potential timeline and causes

Classic Period Maya (AD 250-900) utilized marine resources, but both archaeological data and the timing of parrotfish declines suggest that Maya exploitation does not explain our findings (55). Maya fishermen used canoes for inland trade and to exploit marine resources well beyond the intertidal (56, 57). Fishing lines and harpoons, as well as floats for fishing nets, have been found from at least the Middle Classic Period (AD 400-600) (57-59). Coastal Maya settlements and specialized salt works were common and connected to cities in the interior by Belize's network of rivers (59-61). These salt works, located primarily in the south, likely preserved fish for shipping inland (58). Evidence of Maya use of marine resources has been found throughout the region and sites on or near the coast show the highest proportions of marine resources in their diet (55, 60). However, while fish were exploited, archaeological findings suggest that shellfish and manatee were heavily utilized at multiple coastal sites (55, 57). The fish tooth record at Lagoon Cay further suggests a growing proportion of parrotfish in the reef fish assemblage during the Classic Maya period, suggesting that any human exploitation of parrotfish was not noticeable in the tooth record. Moreover, though little archaeological work has been done in the Stann Creek area, coastal sites as well as the recently excavated, larger, inland, Late to Terminal Classic Period Alabama site (AD 700-900) show that Maya did inhabit the area (62). However, archaeological investigations at Alabama suggest minimal use of marine resources despite proximity to the coast (63-65). As the closest land area to the coral cays in which sediment cores were taken, these records from Stann Creek corroborate that fish were not widely used by Maya in the area.

The beginning of the Postclassic Period (AD 900-1550) is marked by the abandonment of inland Maya settlements and population movement to the coast (66, 67). Inland subsistence trade was replaced with the larger Circum-Yucatan Sea Trade that focused on luxury goods, particularly obsidian, but jade, copper, gold, and non-local pottery have also been found (60, 66, 68-70). This trade connected sites along the coastline from Xicalango in Campeche, to the North, to Honduras in the South (56). The effects of an increasing coastal population and reliance on parrotfish can be seen in the Lagoon Cay record and a small

decline begins in the mid1300s CE. However, the record of Elbow Cay, beginning in 1186 CE, shows increasing proportions of parrotfish teeth throughout this period, even as overall fish tooth abundances begin a slow decline. Evidently, any Maya take from this reef did not overexploit parrotfish and take was limited and localized to the nearby Lagoon Cay. Preference for manatee and shellfish continued throughout the Postclassic at many sites, though the Ambergris Cay settlement to the far north consumed higher proportions of fish than other Maya sites (70, 71). Maya coastal sites from this time commonly contain fish bones and consumption included estuarine species such as barracuda, grunts, groupers, and snapper, as well as reef species including triggerfish and parrotfish (61, 68). Our data show that small parrotfish tooth declines began during Maya periods. This is similar to other areas of the Caribbean where parrotfish populations and size were already decreasing as a result of indigenous fishing (30). However, records of tooth abundance at Lagoon and Elbow Cays suggest that fishing pressure was not as intense or substantial as other areas of the Caribbean; the Lagoon Cay parrotfish tooth record begins a slow decline even as Elbow Cay's continues to increase. Thus, Maya Postclassic Period take was likely limited, despite archaeological evidence for increases in coastal population and subsistence fishing

The arrival of Europeans resulted in a cultural shift and an increase in the exploitation of coastal marine resources across the New World (72). During this time, the first large scale declines in fish tooth abundances begin. However, Belize's reefs exhibited a high percentage of coral cover through modern times (1, 9, 12). Cross section images of all three sediment cores show that the three cays maintain a consistently high coral proportion throughout the record (Fig 4-6).

Figure 4. Elbow Cay Sediment Core Cross Sections. Time to the present increases from bottom to top, left to right.

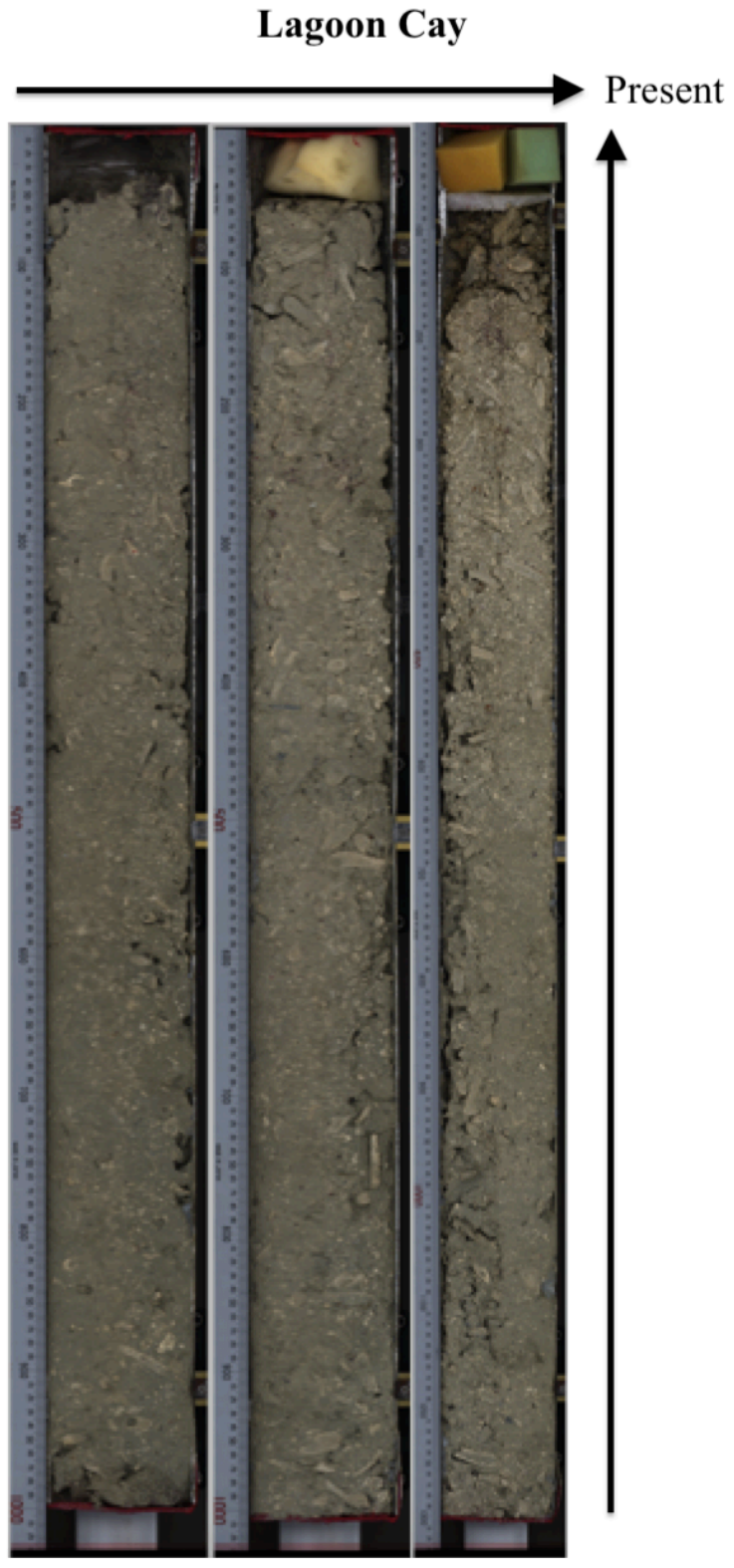

Figure 5. Lagoon Cay Sediment Core Cross Sections. Time to the present increases from bottom to top, left to right.

Figure 6. Bakers Rendezvous Sediment Core Cross Sections. Time to the present increases from bottom to top, left to right.

The symbiont bearing foraminifera record for Elbow Cay also increases throughout this time, suggesting increased water quality despite European colonization. Symbiont bearing foraminifera have been used as indicators for water quality because they require high water clarity to thrive. With the exception of declining fish tooth abundances, there is no evidence for a declining reef leading up to the modern period. Overfishing, not decreasing coral cover or water quality and loss of reef habitat is the likely cause of parrotfish declines.

A slow decline in the parrotfish tooth record of Elbow Cay begins by the early 1600s with Spanish contact (73). To contrast, the Lagoon Cay record experiences an increase in parrotfish teeth following Spanish arrival in Belize. This is similar to records in Jamaica which showed rebounds in reef fishes following the introduction of European disease and heavy indigenous population reduction (21). European epidemic disease, likely smallpox, was introduced to the Yucatan by 1517 resulting in an estimated 50 to 90 percent death rate of indigenous populations (73-75). The human population of the Yucatan Peninsula, alone, is conservatively speculated to have declined from at least 800,000 to 250,000 after Spanish contact (73). The Maya in Belize were no exception. The parrotfish tooth record from Lagoon Caye is decreasing at the time of Spanish arrival but Maya mortality reduced fishing pressure and parrotfish populations rebound at this location. Historical and archaeological records of heavy Maya mortality due to European disease coupled with Lagoon Cay's increase in parrotfish teeth following Spanish arrival suggest that native Maya in Belize are unlikely to be the initial cause of decreasing parrotfish populations.

In 1528, the Spanish arrived in Belize and successfully conquered areas of northern Belize by 1544 (73). The Spanish believed that maintaining a diet similar to that consumed in Spain directly affected their ability to conquer (76). As a result, they brought herds of European livestock to their settlements in the New World; in Hispaniola, European livestock dominated Spanish diets (77). However, the conditions in Hispaniola and the Caribbean islands were uncommon and cattle, goats, and sheep often adapted poorly to the New World (78). Spanish diets across the Caribbean changed in the mid 1500s as a result of the lack of success of their livestock, particularly cattle (77-79). The diet of Spanish settlers in

16th and 17th century tropical Florida was nearly 70% native fish because herds did poorly (79). Although inland Belize has areas of pastureland, the coast is primarily tropical mangrove, wetland and swamp (65, 80). The Spanish did have some success establishing herds but cattle theft was a common, profitable past time for English privateers and logwooders beginning with their arrival in the 1650s (81). Further, jaguars prey on cattle to this day, and vampire bats are a continual vector to spread rabies amongst cattle populations (82, 83). Vampire bat populations boomed following the introduction of Spanish cattle and populations remain high (83). Early Spanish accounts document vampire bat attacks and likely rabies deaths (84). In his 1530 book, De Orbe Novo, Peter Martyr D'Anghera describes vampire bats attacking humans, "During the night the men were tortured by bats, which bit them; and if one of these animals bit a man while he was asleep, he lost his blood, and was in danger of losing his life," (85). The primary prey of these vampire bats shifted with the introduction of cattle and modern attacks on humans are uncommon (83). The presence of native deer competing for pastureland would also likely have negatively impacted Spanish herds (80). Moreover, Belize was far enough from Spanish centers in the Yucatan to be considered frontier, resulting in lesser importation of Spanish goods (86). Combined, these factors would likely have forced a heavier Spanish reliance on marine resources.

In 1503, the Spanish Crown created the *repartimiento* or *encomienda* system (77, 87). This was the forced labor of indigenous people, in this case the remaining Maya left after the spread of European diseases, at Spanish settlements in exchange for instruction in Catholicism (77, 87). Conversion to Catholicism of indigenous people was a primary mandate of the Spanish in the New World (88). A change in food practices would likely accompany conversion to Catholicism. Under this system Maya towns were occupied, churches were built, and friars sent across the country (86, 87, 89). At this time, to be nominally considered Catholic, one was required to fast on Lent, holy days and on Fridays (90). Fasting meant that red meat could not be consumed but fish were acceptable (90). One example of the widespread nature of this practice is reflected in the English cod fishery; by 1620, 90% of fish caught went to Catholics in Spain and the Mediterranean (90-92). As a result, King James I refused to declare profitable wars with Spain because closure of the Spanish market would jeopardize this important, highly

lucrative fishery (91). In 1624, the English Captain John Smith described the lucrative nature of New World fishing and the Spanish market to his countrymen, explaining, "let not the meannesse of the word fish distaste you, for it will afford as good gold as the mines of Guiana or Potassic, with lesse hazard and charge, and more certainty and facility," (93). The Spanish brought this religious practice to Belize. The midden record at two important Maya settlements occupied by the Spanish, shows a preference for large mammals by Postclassic Maya and an increase in fish during the Spanish Colonial Period (94). Manatee was also still highly prized as a substitute to the usual fish (55). Father Joseph de Acosta explains in his 1590 work, *Natural and Moral History of the Indies*, "it lives continually in the water, and therefore they eate it as fish; yet when I did eate of it at Santo Domingo on a friday, I hadde some scruple, not for that which is spoken, but for that in colour and taste it was like unto morselles of veale, so is it greene, and like unto a cowe on the hinder partes," (95). Still, less pious Catholics heavily exploited manatee for fast days, when other meats were not allowed, and are credited with its depletion in many areas (96). Clearly, manatee complimented the use of fish. Moreover, small human populations with low effort and artisanal fishing gear have been shown to effect significant declines in fish populations (21, 48, 97, 98). The slower parrotfish declines at Elbow Cay could easily have been caused by limited Spanish take, despite European populations likely never exceeding 100 before 1787 (99). As a result, Spanish settlers to Belize are likely responsible for increasing fishing pressure on the reef and the subsequent early declines seen in the parrotfish tooth record of Elbow Cay.

From the mid-1600s, coastal Belize supported growing communities of privateers and pirates and this group likely contributed to continued parrotfish declines at Elbow Cay (81, 91, 100). A decline in the parrotfish tooth record at Lagoon Cay also begins simultaneous to English settlement. The English and other European powers would hide in Belize's cays and lagoons and utilized marine resources as they harassed the Spanish off the coast (87, 91). Miskito Indians from Honduras were employed as experts for catching manatee, turtles, and fish (81, 100). The English treated them with respect both for their skill and because they hunted for the entire crew (81, 100). By the 1650s the English established coastal settlements (87). In Belize, manatee and turtle were likely the prime English meat sources with fish as

secondary (55). English privateers brought live sea turtles on voyages to be eaten when needed (101). The English naturalist and privateer William Dampier explains in his 1697 work, *A New Voyage Around the World*, "when we careen our ships we choose commonly such places where there is plenty of turtle or manatee for these Moskito men to strike," (100). Buccaneers were also present on the Belize coast from the time of English settlement, selling smoked turtle and manatee meat to English logwooders and privateers (102). Turtle has been suggested as the most important fishing resource for the English in Belize from the 17th to 19th century (102). In Jamaica, turtles were also heavily utilized as a meat source for the English through their depletion in the late 1700s (21). Though Dampier makes little mention of fish species in Belize, parrotfish tooth declines in the Lagoon Cay record correspond well with English arrival suggesting English take (100). The English are also documented to have consumed other fish species on Dampier's voyages, including snook, catfish, and grouper, suggesting that manatee was simply the most notable prey which he chose to highlight in Belize (100).

By 1641, Maya in northern Belize were in open rebellion and the Spanish lost control of their strongholds at Lamanai and Tipu, failing to regain control until 1695 (73, 86). They described the Maya they left as apostate (86). Even so, many Maya still practiced Catholic rituals syncretized with Maya religious practices (86, 87). Declines in parrotfish teeth in the Elbow and Lagoon Cay records were not halted by the departure of the Spanish, suggesting continued exploitation of parrotfish populations by the Maya and English. This is likely the result of Maya adoption of Catholic practices coupled with English fishing. The English are unlikely to be the sole cause of reef overfishing; the Anglican, Protestant English were not required to engage in fast days and showed little preference for fish when compared to other marine and terrestrial meat sources (90). Even in his argument that the English should engage in large scale New World fishing, Captain John Smith still describes fish as "a meane and base Commoditie," and emphasizes the wealth gleaned by the Dutch through "this contemptible Trade of Fish," (93).

Ultimately, parrotfish are not the preferred Caribbean food fish. Though they were consumed at the near coastal Late to Terminal Classic Maya site of Lubantuun, shark, mackerel, snook, grouper, jack, and tuna were also consumed--parrotfish were not the sole fish on which they relied (55, 103). In

addition, Classic and Postclassic Maya also ate grunts, barracuda, and triggerfish (55, 61). As populations of larger, preferred species are exploited and depleted, parrotfish become the next best choice (51). The high proportion of parrotfish teeth in these records might suggest that other reef fish were already heavily utilized by the Maya, elevating parrotfish tooth abundances in the data. Even so, fish bones rarely make up a high proportion of coastal Maya Classic and Post Classic middens, which are dominated by manatee and shellfish. At the Middle Classic Period site of Moho Caye (400-700 AD), fish represented only 0.3% of the total midden bone weight and less than 1% of the total consumed meat weight; it is estimated that manatee made up 89% of the consumed meat at this site with conch as a secondary source at 6.8% (57). At the Classic through Postclassic trading port settlement, Ambergris Caye, more than 50,000 conch were used to build Maya structures and fill in the mangrove swamp, suggesting heavy shellfish take (70). Maya at the Classic to Postclassic settlement, Wild Cane Caye, ate a higher proportion of reef fishes (PERCENTAGES TBD) but also exploited turtles and estuarine fishes amongst other meat sources. Situated near rivers and with close connectivity to the coast, the midden record at the inland settlement, Lubaantun, was 39% marine vertebrates, a far higher percentage than other inland sites (55). Maya exploitation may eventually have caused a shift in usage to parrotfish as these preferred food choices became scarce, but at the time of European arrival, manatee, turtle, and shellfish were still relatively abundant (55, 100). Thus, the decreases in parrotfish concurrent with European settlement represent a shift in resource use as a result of colonization.

In contrast to declining fish abundances at Lagoon and Elbow Cays, parrotfish teeth continue to increase in the Bakers Rendezvous record following European occupation. At Bakers Rendezvous, the decline begins in the early 1800s and though it is over a shorter period of time, it is more severe than the declines at Lagoon and Elbow Cays. Increased Maya fishing and the founding of Stann Creek Town by the Garifuna represent the two most likely causes for this decrease. After depleting the waters surrounding their settlements, it is likely that Maya fishing would expand into new territory, as is common with coastal subsistence fishing populations. In this case, depletion of Lagoon and Elbow Cays would lead to expansion south and further out to sea, to Bakers Rendezvous. As Maya populations rebounded and

converted to Catholicism, an increase in fishing pressure would be likely. Catholicism was the dominant religion by the 1861 census (99). Maya and Mestizos were almost entirely Catholic and Northern Belize was 89% Catholic at the time (99). Increased fishing to sustain this increasingly Catholic population would be likely.

Stann Creek Town, now Dangriga, was founded by 1832 by Garifuna settlers and is the closest large city to the cays from which these cores were taken. The Garifuna originated on the island of St. Vincent, were deported by the British government to Honduras in the 1790s, then fled to Belize in 1802, eventually founding Stann Creek Town (87, 99, 104). This group primarily practices Roman Catholic rituals syncretized with spiritual beliefs, though some converted to Protestantism (87, 104). Southern Belize as a whole, which at the time of the 1861 census included the Stann Creek area, was 80% Catholic primarily because of the Garifuna (99). Traditionally, this group pursued fishing and agriculture but the British Belize government initially placed restrictions on these vocations in an effort to force the Garifuna to work in mahogany camps (87, 99, 104). Nonetheless, the Garifuna settled on the coast in the Stann Creek area and relied almost entirely on marine resources for meat, specifically fish and manatee (104). The Garifuna population was unlikely to have numbered more than 300 through the early 1800s but by 1861 there were more than 2000 primarily in the Stann Creek area (99). Despite small populations, their exploitation of Bakers Rendezvous fish populations would likely be high and a precipitous decline is seen in the fish tooth record from this area.

Alternative Theories

Overfishing is the most likely cause of decreasing proportions of parrotfish teeth and decreasing overall fish tooth abundances in the data. At present, overfishing is the prime threat to parrotfish populations worldwide (53). Though sedimentation is a common cause of reef degradation, it is unlikely to cause fish decreases without concurrent decreases in coral quality (1, 105). The Late to Terminal Classic Maya pulse of runoff documented in lake and swamp records does not appear to have affected parrotfish populations as they increase in the Lagoon Cay record during this time (106, 107). These records also suggest that forests increased by the time of European colonization and high levels of runoff

do not begin again until modern times (80, 106, 108). Corals are highly sensitive to runoff and burial by sediments and are unlikely to exhibit growth and recruitment if water quality is poor (105, 109). Until the outbreak of white band disease in the 1980s, Belize's reefs were considered healthy and coral cover was high (1, 4, 7).

Even so, the Elbow Cay symbiont bearing foraminifera record clearly shows runoff entering the marine ecosystem. Beginning in 1186, well into the Maya Postclassic Period, the foraminifera assemblage shows a low abundance of symbiont bearing species which require high water clarity to thrive. With the arrival of the Spanish in the 16th century, the abundance of these species in the record increases, indicating increased water quality in this area. This suggests that some Maya practice hindered reef growth through sedimentation but likely ended with the 50 to 90 percent dieoff of indigenous people as a result of colonization and disease. Symbiont bearing foraminifera abundance continues to increase to the Elbow Cay record's end in 1972, suggesting increased water quality to modern times. This occurs even as parrotfish proportions show a simultaneous decrease. As a result, sedimentation is unlikely to have caused the decreases in the fish tooth record as the timing is incorrect.

Water depth could also be a cause for the initially low populations of parrotfish and would account for their population growth as sea-level decreased. Parrotfish inhabit shallow reef areas between xxx and xxx meters depth. However, in Belize, sea levels have been increasing slowly for the last several thousand years (8, 110). Further, over 100 Classic and Postclassic period coastal Maya sites have been found that cannot currently be accessed because they are below current sea level (61). Coastal Maya abandoned these sites as sea-level increased and Belize's coast naturally subsided over the last 1000 years (60, 110). This suggests that initial low densities of parrotfish are not a result of Elbow Cay, Lagoon Cay, and Bakers Rendezvous reefs existing below parrotfish preferred depth range.

Coastal mangrove deforestation represents another alternate hypothesis to explain fish declines. Mangroves are an important nursery ground for many species of parrotfish (111, 112). Destruction of nursery habitats has been shown to negatively impact parrotfish populations and reef resilience (38). Removal of mangrove areas could thus have caused the early declines seen in the Elbow and Lagoon Cay

parrotfish tooth records. However, the Spanish are unlikely to have removed extensive areas of mangroves because they primarily settled in pre-existing Maya settlements, the most widely documented being the inland sites at Lamanai and Tipu (86). The English worked extensively on the coast harvesting logwood (*Haematoxylon campechianum*) and mahogany (*Swietenia macrophylla*) but these trades did not begin until the late 1660s, after parrotfish were already in decline at these two sites (91, 99, 113). Logwood and mahogany grow near rivers and the English used boats to bring these resources to the coast (113). Roads were not built and there would have been little reason for mangrove destruction (113). Logwood and mahogany also do not grow closely together in forests but are spread throughout the landscape, suggesting that their removal would have little effect on runoff (113). This trade occurred simultaneous to the decline in the Bakers Rendezvous record, but was located further north in Belize, in the Bay of Honduras, and moving inland, making mahogany and logwood exploitation an unlikely factor in reef decline at any of our sites (113). If the founding of Stann Creek Town resulted in mangrove removal, parrotfish losses would also be expected. Mangroves are invaluable nursery grounds to many parrotfish species and their destruction would jeopardize parrotfish recruitment and reef populations (111, 112). At present, Belize's mangroves are still largely intact, further suggesting that historical destruction was not extensive and was unlikely to have caused the decreases seen in the fish tooth records.

Taphonomy and preservation biases could be responsible for falsely low parrotfish tooth abundances, making populations appear to decrease to the modern era. If core collection resulted in compaction of the top section of the core, parrotfish teeth and sediments may have been pushed down, falsely depressing modern abundances. However, visual inspection of core cross-section photos shows that any compaction at the top of the core ends well before fish tooth declines begin. In all three cores, compaction ends within the top 30 to 50 cm, whereas fish tooth declines begin at least 20 to 70 centimeters prior. The declining parrotfish tooth abundances begin early. While the zero values seen in the Bakers Rendezvous record may be an artifact of taphonomy, all three cores were already showing declines, suggesting that these trends are reflective of actual abundances.

Why the lag?

Though a 15-25% decrease in parrotfish tooth proportion is shown at all sites, likely as a result of fishing pressure, Belize's reefs were considered healthy through the 1970s and early 1980s. Even so, the effects of parrotfish on the reef can be examined through the use of tooth accumulation rates and core accretion rates. When compared to the records of Lagoon and Elbow Cays, the Bakers Rendezvous record has the highest accumulation rate of parrotfish teeth as well as the highest reef accretion rate. These trends support the positive effect of parrotfish in promoting reef growth (1, 39, 48). As key herbivores, parrotfish have been shown to have a positive effect on reef accretion (39). Bakers Rendezvous has comparatively high accumulation and accretion rates when compared to accumulation and accretion rates at Elbow and Lagoon Cays, suggesting that increased parrotfish abundance is responsible for increased reef accretion.

Continued reef quality despite parrotfish population declines at these sites can be explained by functional redundancies (114-116). *Diadema antillarum* urchins directly compete for food with parrotfish (115). Before the Caribbean-wide die-off of urchins in 1983-84, *Diadema* populations were inversely proportional to parrotfish populations in reef ecosystems (1). Removal of parrotfish through overfishing would have proportionally increased *Diadema* importance on the reef as they were granted increased access to algal resources (117). Urchin competitors could thus compensate for the lack of parrotfish on the reef, promoting coral cover by limiting algal overgrowth (40, 115, 118, 119). However, the overfishing and removal of parrotfish set the stage for later reef degradation upon *Diadema* dieoff in the 1980s (116). Top down control by herbivores is believed to have kept Caribbean reefs in a healthy state until overfished reef fish populations coupled with the diadema die off resulted in algal takeover (42, 116). On less fished reefs, herbivorous fish populations were more likely to control algal growth following urchin die-off (48). High biodiversity resulting in functional redundancies has been considered one of the most important reasons for the lag between overfishing and negative ecosystem response across multiple ecosystems (40, 116).

In Belize, the removal of parrotfish due to overfishing and the loss of functional redundancy as a result of the Caribbean-wide dieoff of *Diadema* likely increased the vulnerability of corals. Small

populations of parrotfish are capable of maintaining reefs when coral proportion is high (44). This is because grazing intensity is also high; a patch of algae is quickly eaten because food is scarce (44). However, when reefs are damaged, algae is faster to return than coral (44). Increasingly high proportions of algae require correspondingly high populations of diverse herbivores to return this ecosystem to coral dominance (44, 51, 120). Increasing disturbance further requires a higher proportion and diversity of herbivores (39, 120). Multiple bleaching events coupled with hurricane damage in the 1990s and 2000s devastated Belize's reefs and coral cover remains reduced (1). Corals were likely outcompeted by fast growing algae that could not be controlled by reduced herbivore populations. This effect has been seen on reefs across the Caribbean (1, 16). Large parrotfish have also been shown to have a greater importance in ensuring high coral cover and overall reef health as they are more important for the removal of large macroalgae (37, 44). These large fish are the targets for fishing and their removal would further decrease the likelihood of reef recovery (16, 37). That Belize's reefs would show a lag between decreasing parrotfish abundance and reef collapse is common with ecosystem phase shifts; coral reef ecosystems show resilience to changes until a threshold is reached and the shift to macroalgal dominance occurs (121). The overfishing seen centuries prior to present day reef collapse thus allowed for these conditions seen in Belize at present.

CONCLUSION

This quantitative record is one of the first of its kind to use fish teeth as a proxy for historic fish populations and fishing pressure. Archaeological data is sparse from the neighboring Stann Creek area and my data may provide some insight into Maya interaction with the Belize Barrier Reef. Combined, my more than 1200 year record shows reef persistence alongside Classic Maya agriculture, inland trade and subsistence, Post Classic Maya coastal settlement and fishing increases, and finally declines in fish populations as a result of European settlement, colonization, and the culture shifts that followed. My sediment cores end in the 1970s, shortly before monitoring began and a decade before the collapse of many Caribbean reefs. They suggest that baselines set on reefs in the 1970s and 1980s were

underrepresenting the role of parrotfish in the community as a result of centuries of overfishing. Reef ecosystems, even in Belize, have clearly been stressed for at least the last 150 years. Fish tooth declines evident in all three records show the greatest change and European colonization was likely a multiple century antecedent to the bleaching events and collapse seen on modern Caribbean reefs.

MATERIALS AND METHODS

Sites were selected from those used by Aronson et al. (2002) (9). Sediment core collection and processing proceeded as described in Cramer et al. (2017), with three replicate cores taken at each site and 30-35 samples taken from each core used (18). To aid in tooth counting, samples smaller than 250μm were acidified in 5-10% acetic acid to remove carbonates. Samples between 63-104μm were dyed using an Alizarin Red S solution described in Sibert et al. (2017) (122). Teeth were counted and data was processed using R Studio.

In five samples from the Bakers Rendezvous core (two 250-500μm samples and two 104-250μm samples used initially to test the efficacy of the dye in that size fraction, and one 63-104μm sample), the Alizarin Red S dye reacted with aluminum shrapnel scraped from the interior of the core barrel during initial reef collection. The resultant, undissolvable precipitate made fish teeth in the sample impossible to count and the three core depths represented by these samples are omitted from the data. One depth count was omitted from the Lagoon Caye data as a 104-250μm sample was missing.

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