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CONCH FRITTERS THROUGH TIME: HUMAN PREDATION AND POPULATION DEMOGRAPHICS OF *LOBATUS GIGAS* ON SAN SALVADOR ISLAND, THE BAHAMAS

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ABSTRACT: ***Lobatus gigas*, the queen conch, is a central component of Caribbean cuisine but over-fishing of juveniles has threatened the stability of wild populations. Strombid gastropods, upon reaching sexual maturity, cease growing along the shell length axis and continue growing in width via a flared and thickened shell lip. This morphology serves as a useful indicator of an individual's sexual maturity. Here we examine temporal trends in population demographics, size, and morphology of harvested *L. gigas* individuals over the last $\sim$1 ky from San Salvador Island, the Bahamas to quantify the dynamics of human-induced stress on the local queen conch fishery. We collected 284 human-harvested individuals from shell middens at seven localities, measured seven morphological variables, and classified the specimens as either adult or juvenile. We randomly selected 64 of these shells for rapid AMS radiocarbon dating in order to establish three geochronological bins: Lucayan (Pre-European invasion, 1492 CE), Modern ($\sim 10^2$ y), and Global ($\sim 10^1$ y). The proportion of juveniles harvested increased significantly from 47% (Lucayan) to 61% (Modern) to 68% (Global) suggesting increasing pressure on the fishery through time. Patterns in body size and morphology diverge between adults and juveniles and are likely the result of an increase in the proportion of harvested juveniles, the selection of smaller juveniles through time, and possibly changes in fishing methods. This size selective predation did not result in the suppression of adult body size as found in other studies. Geohistorical data, such as these, are vital for providing long term ecological context for addressing anthropogenic ecological degradation and are central to the conservation paleobiology approach.***

INTRODUCTION

Lobatus gigas, the queen conch, is a large herbivorous marine gastropod in the Caribbean and western Atlantic, which ranges from Venezuela to Florida and the Bahamas. It is of commercial, nutritional, and cultural importance to peoples in the Caribbean. The flesh is used in many Caribbean dishes, such as conch fritters and conch salad. The shells are used in traditional ceremonies, as jewelry, and are often sold as tourist souvenirs. Queen conchs often occupy shallow depths, are slow moving, and aggregate during reproductive season, which makes them particularly prone to exploitation (Appeldoorn et al. 2011). Moreover, they are slow to mature, with an age of reproduction estimated at 3.5–4 years (Appeldoorn 1988).

Determining sexual maturity in gastropods from shell characters can be difficult as this typically requires the examination of soft tissues (Coe 1944). Shell growth along the length axis ceases near the onset of sexual maturity, however this length at maturity is also highly variable among individuals (Vermeij 1980). After reaching its maximum length, the growing shell margin of *L. gigas* flares outward and develops a lip that increases in thickness prior to and after the onset of maturity (Appeldoorn 1988; Stoner et al. 2012a). Lip thickness has been shown to be a more appropriate and reliable index of maturity than shell length for the queen conch (Vermeij 1980; Theile 2001, 2005; Aranda and Frankeil, 2007; Stoner et al. 2012c; Mueller and Stoner 2013; Foley and Takahashi 2017) even though the growth of lip thickness varies between geographic locations in the Caribbean and can be dependent on sex, depth, latitude, temperature, food availability, age class, and available shelter (Appeldoorn 1988; Stoner and Sandt 1992; Vermeij and Signor 1992; Posada et al. 1999; Posada et al. 2006; Appeldoorn and Baker 2013; Boman et al. 2018. As a rule of thumb, it is generally recommended in the literature to harvest only individuals with a shell lip thickness of 15 mm or greater (Thiele 2001; Stoner et al. 2012c; Foley and Takahasha 2017; Boman et al. 2018) as these are more likely to be sexually mature adults with thick well-formed shell lips.

San Salvador Island is perched atop an isolated carbonate platform on the eastern flank of the Bahamian archipelago (Fig. 1). Though the islands of origin and exact routes taken by the first aboriginal settlers of San Salvador are debated, the Bahamas were likely settled between 600 and 800 CE (Berman and Gnivecki 1995). Blick et al. (2011) analyzed the spatial distribution of 39 prehistoric archaeological sites on San Salvador and interpreted a preference for the Lucayan people to establish settlements in clusters associated with coastal environments. These initial inhabitants of the Bahamas practiced fishing, horticulture, and sea-faring trade, perhaps as far away as South and Central America (Blick 2007a; Berman and Pearsall 2000). The Lucayan people inhabited San Salvador for approximately 800 years prior to the arrival of Columbus in 1492 and the subsequent European invasion and colonization. Blick (2007a), in a zooarchaeological analysis of two sites on San Salvador (radiocarbon dates ranging between 963–1426 CE), analyzed the ecological influence of fishing/hunting of a relatively small population of Lucayans (estimated to be between 500–1000 people) during this time. He found, through time, a decrease in the richness and mean trophic level of marine animals consumed by people. Moreover, within individual taxa, Blick (2007a) revealed declines in weight and quantity of land crabs, weight of gastropod fragments, and body size of parrotfish.

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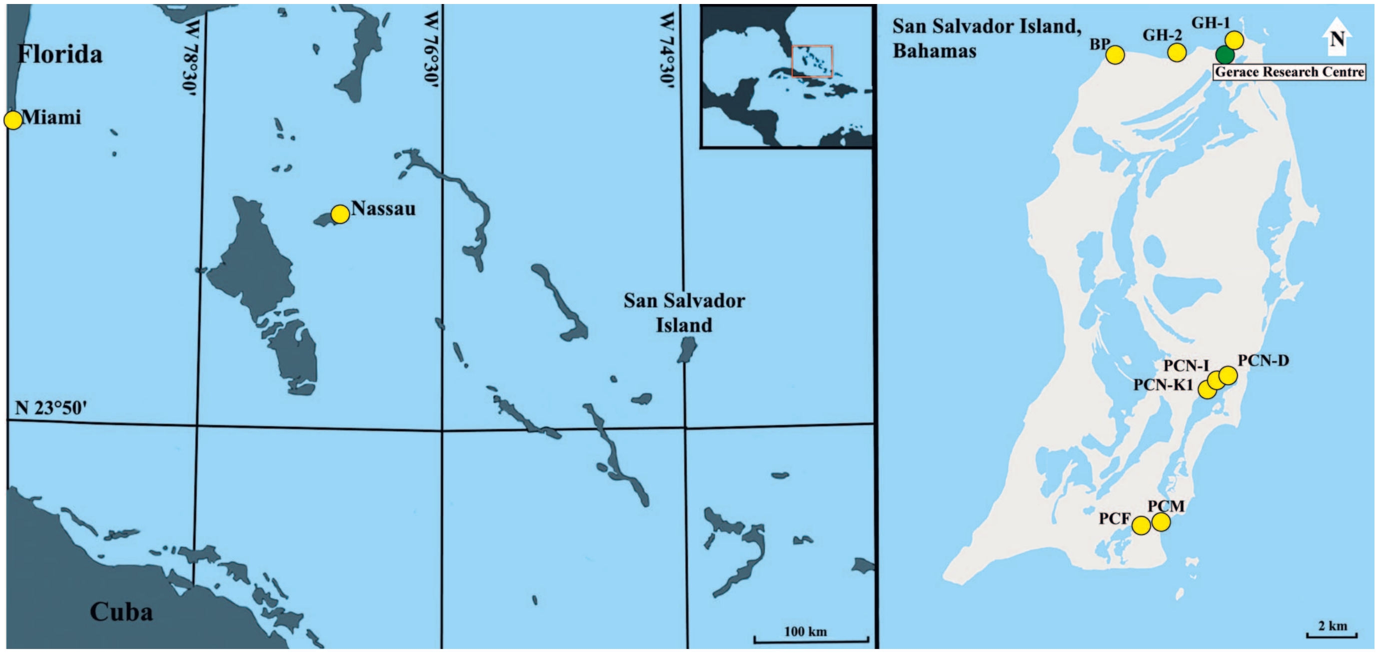

FIG. 1.—Map of eight sampling localities on San Salvador Island, The Bahamas. Collection localities are marked by yellow stars on the map: BP = Barker's Point; GH1 = Graham's Harbour 1; GH2 = Graham's Harbour 2; PCN-D = Pigeon Creek North Dock; PCN-I = Pigeon Creek North Island; PCN-K1 = Pigeon Creek North Kris 1 (includes surface and subsurface); PCM = Pigeon Creek Mouth; PCF = Pigeon Creek Fossil. Gerace Research Centre is marked by a green circle. (Map data modified from Google Maps 2018 and from Selly et al. 2018)

The Lucayan population in the Bahamas was destroyed by disease and kidnapping into slavery by the early 1500s CE; indeed, the human population of what is now the Bahamas declined from approximately 40,000 in 1492 to 4,000 in the 1780s (Buchan 2000). The human population increased around the time of the American Revolution as slave owners loyal to the British Crown relocated African slaves from the American south to the Caribbean to establish new plantations. These plantations were short lived as Great Britain outlawed the slave trade in 1807. The loyalists abandoned the newly freed former slaves who established their own new communities and their numbers swelled to 25,000 by the early 1840s. This number ebbed and flowed as people emigrated for employment opportunities during the 1920s and the population has steadily increased since the 1950s (Buchan 2000) to the current number of 395,000.

As a result of increasing demand with a growing population, *L. gigas* was heavily exploited during the late twentieth century throughout the Caribbean (Theile 2001, 2005), which resulted in many fisheries being on the verge of collapse as early as the beginning of the twenty-first century (Stoner et al. 2012c, 2018). Since 1992, the fishery has been subject to both international and local management measures (Acosta 2006). The Natural Resources Management Unit (NRMU) of the Organization of the Eastern Caribbean States (OECS), an organization of nine Caribbean member nations (Anguilla, Antigua and Barbuda, British Virgin Islands, Dominica, Grenada, Montserrat, Saint Kitts and Nevis, Saint Lucia, Saint Vincent and the Grenadines), is responsible for fishery management and provides legal policy and administrative framework for the establishment of regional marine environment management programs (Thiele 2001). As a response to overfishing, the NRMU recommended regulations including minimum size restrictions, allowing only the harvest of shells with a flared lip, fishing gear restrictions, and the establishment of closed seasons and marine protected areas (Thiele 2001; Acosta 2006; Aranda and Frenkiel 2007). These recommendations have been implemented by several Caribbean nations, but not by all, making awareness and enforcement of regulations from nation to nation problematic. Regulations in the Bahamas require the conch to possess a well-formed lip and limit catches to 10 conchs per person (Fisheries Resources 1986). Thus, it is illegal to harvest juvenile individuals as they do not have a "well-formed shell lip". This verbiage of "well-formed shell lip" is subjective and it is up to the interpretation of the fisher to determine the legality of their catch.

We hypothesize that size-selective fishing and increasing demand for conchs in the San Salvador fishery over the last ~1,000 years has resulted in the harvesting of proportionally more juveniles and that such pressures led to a concomitant decrease in body size of both adult individuals and all individuals harvested. Here we test these hypotheses through the examination of human-produced shell middens.

MATERIALS AND METHODS

Sampling Localities

Bulk samples of *L. gigas*, totaling 284 individuals, were collected from shell middens at eight localities on San Salvador Island, the Bahamas (Fig. 1, Table 1). Sampling localities were limited to on-shore or shallow nearshore (<4 m water depth) locations. Shells collected were from one of four midden types: (1) scattered nearshore middens: active dumping sites underwater in nearshore settings; (2) scattered onshore middens: dumping sites scattered along the shore; (3) mounded onshore middens: well-defined onshore mounds; and (4) an *in situ* deposit exposed in a channel side bank on Pigeon Creek below the living *Thalassia* rhizomes mat. Mounded onshore middens tended to be located further inland on the shore of Pigeon Creek, a shallow tidal creek. Collection localities are as follows: Barker's Point (BP), a scattered onshore midden; two sites at Graham's Harbour (GH1, GH2), nearshore locations; Pigeon Creek Mouth (PCM), an onshore mounded midden; multiple sites at North Pigeon Creek (PCN-K1, PCN-D, and PCN-I), all onshore mounded middens. At Site PCN-K1, we excavated a 1 m deep pit to sample a lower stratigraphic level within the midden. Shells from the top (surface) of the midden are labeled as "PCN-K1-S" and those collected from the bottom (sub-surface) are labeled as

TABLE 1.—*Summary table of Lobatus gigas individuals collected from each locality, temporal bin assignment, and ontogenetic stage.*

Locality	Time Bin	n	Adults	Juveniles	Unknown
Graham's Harbour 2 (GH2)	Global	57	14	43	–
Pigeon Creek Mouth (PCM)	Global	48	8	40	–
Pigeon Creek North Island (PCN-I)	Global	32	19	13	–
Pigeon Creek North Kris 1 Surface (PCN-K1-S)	Global	15	7	8	–
Pigeon Creek North Kris 2 Surface (PCN-K2-S)	Global	15	6	9	–
Graham's Harbour 1 (GH1)	Modern	32	8	24	–
Pigeon Creek North Dock (PCN-D)	Modern	18	12	6	–
Pigeon Creek North Kris 1 Sub-surface (PCN-K1-SS)	Modern	15	5	10	–
Pigeon Creek North Kris 2 Sub-surface (PCN-K2-SS)	Modern	15	6	9	–
Barker's Point (BP)	Lucayan	34	16	15	3
Pigeon Creek Fossil (PCF)	Lucayan	3	2	1	–

"PCN-K1-SS." Four specimens from the PCF location were collected in 2013 by DLM from an *in situ* deposit overlain by living *Thalassia* rhyzomes on the bank of Pigeon Creek.

Collection Methods

Shells at mounded midden sites were randomly sampled by tossing a 60 cm × 90 cm mesh bag onto the midden and collecting all the shells the bag was touching. The size of the shells and restricted access to the sites limited our ability to collect large numbers of shells at a time. All shells from the sea-floor at the Graham's Harbour shallow nearshore locations were collected from the sediment surface by hand via snorkeling. These were localities previously determined to be dumping sites as evidenced by shells dumped near the end of boat docks at these locations. At Barker's Point, shells were sparsely scattered along the beach and shoreline. Additionally, numerous shells are embedded in the lithified matrix at this archaeological site. The shells from the PCF location were excavated directly from the bank.

Laboratory Methods

Each shell was photographed from multiple perspectives and the following dimensions were measured in mm using calipers: shell length (the distance between the apex and the tip of the siphonal canal), shell width (the maximum distance perpendicular to length at the last body whorl where the lip is thickest, not including spines), siphon to penultimate whorl, siphon to final whorl, spire length, aperture length and width (along major and minor axis of aperture, respectively), and shell lip thickness (recorded from the outer lip in the mid-lateral region approximately 30 mm from the edge of the shell) (Fig. 2). The PCF shells were measured from a photograph using ImageJ freeware (v. 1.48) (Rasband 1997–2018). A fragment of shell was collected, at the approximate location where the shell lip thickness measurement was recorded, from a subset of shells (69 analyses of 67 shells) for radiocarbon dating.

Based upon radiocarbon dates and previous work documenting Barker's Point as a Pre-Columbus site (Blick 2007b, 2011; Blick and Bovee 2007; Blick and Dvoracek 2013), collection localities were assigned to one of three geochronological bins as modified from Lotze et al. (2011): Lucayan (Pre-1492 CE), Modern ($\sim 10^2$ years), and Global ($\sim 10^1$ years) (Table 1). A subset of 63 shells were selected from all sampling locations using random number generation in *R* (R Core Development Team 2016) and, along with the four specimens collected by DLM in 2013, were sent to the Amino Acid Geochronology lab at Northern Arizona University where they were prepared for the rapid AMS method as described by Bush et al. (2013). From there, samples were sent to the Keck Accelerator Mass Spectrometry (AMS) Laboratory at the University of California-Irvine for analysis. Sample preparation backgrounds were subtracted, based on measurements of ^{14}C-free marble and results were corrected for isotopic fractionation according to the conventions of Stuiver and Polach (1977) with δ^{13}C values measured on prepared graphite using the AMS spectrometer. Shells from localities which reported all modern radiocarbon dates (these samples contain excess C, likely due to mid-twentieth century atmospheric thermonuclear weapons testing) were assigned to the "Global" time bin. Shells from localities which reported a mix of older and modern radiocarbon dates shells were assigned to the "Modern" time bin. Shells from localities reporting radiocarbon dates >600 ^{14}C years before present were assigned to the "Lucayan" time bin (Fig. 3).

Quantitative Methods

Only whole shells with intact length and width axes were used for body size analysis. Shells were determined to be adults or juveniles based upon a flared 15 mm lip thickness threshold for maturity. Ninety-five percent confidence intervals were calculated for the proportion of juveniles in each time bin via the Agresti-Coull binomial method (Dorai-Raj 2014) and temporal trends in the proportion of juveniles hunted were assessed using the Cochran-Armitage trend test (Edelmann 2017). Temporal trends in $\log_{10}$-transformed shell length and shell width were analyzed using Tukey's *post-hoc* test and a Jonckheere-Terpstra trend test (Seshan 2018). A Principal Components Analysis (PCA) was performed on $\log_{10}$-transformed shell length, shell width, aperture length, aperture width, distance from siphon to final whorl, distance from siphon to penultimate whorl, and spire length for specimens with no missing observations for these variables (n=218). An $\alpha = 0.05$ is assumed unless otherwise stated. All analyses were conducted using R freeware (R v. 3.4.1) (R Core Development Team 2016) using the following packages: dplyr (Wickham et al. 2019), tidyr (Wickham and Henry 2017), binom (Doraj-Raj 2014), factoextra (Kassambara and Mundt 2017), ggplot2 (Wickham 2009), ggExtra (Attali 2017), ggridges (Wilke 2017), ggfortify (Horikoshi and Tang 2016), ggpubr (Kassambra 2017), CATTexact (Edelmann 2017), and clinfun (Seshan 2018). See Appendix for R code inputs.

RESULTS

Of the 284 shells sampled, 281 were assignable to a temporal bin, 272 had complete shell length preserved, 230 had complete shell width preserved, and 218 were suitable for the PCA with no missing values for the seven morphological variables under consideration. All specimens possessed a puncture hole on the spire, which is indicative of human butchering. Sixty-nine rapid AMS radiocarbon dates were calculated for 67 shells from eight sampling localities (Fig. 3) and assigned to either the Lucayan, Modern, or Global time bin. Barker's Point and Pigeon Creek fossil specimens were confirmed as belonging to the Lucayan time bin with ages of 555–1060 ^{14}C y BP and 520-715 ^{14}C y BP, respectively. Specimens

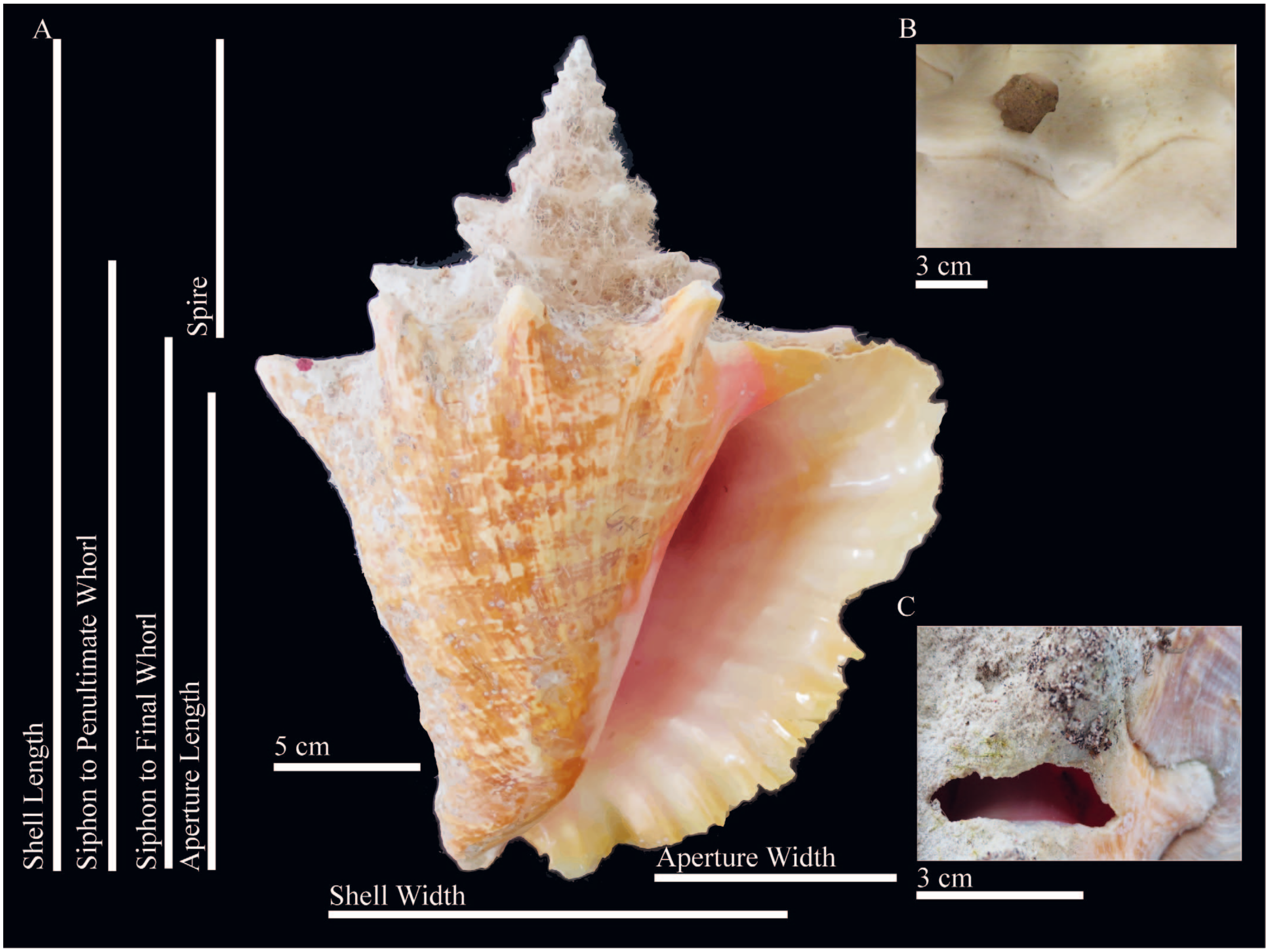

FIG. 2.—Morphometric measurements recorded for each shell. **A**) Shell length: distance between the apex and the tip of the siphonal canal; shell width: maximum distance perpendicular to length at the last body whorl where the lip is thickest, not including spines; siphon to penultimate whorl; siphon to final whorl; spire length; aperture length (parallel to long axis of aperture); aperture width (parallel to minor axis of aperture). **B**) Circular puncture hole typical of Lucayan-aged shells found at Barker's Point; likely made using the spire of another conch shell. **C**) Elongate puncture hole typical of Modern and Global aged shells; likely made using a hatchet or other tool.

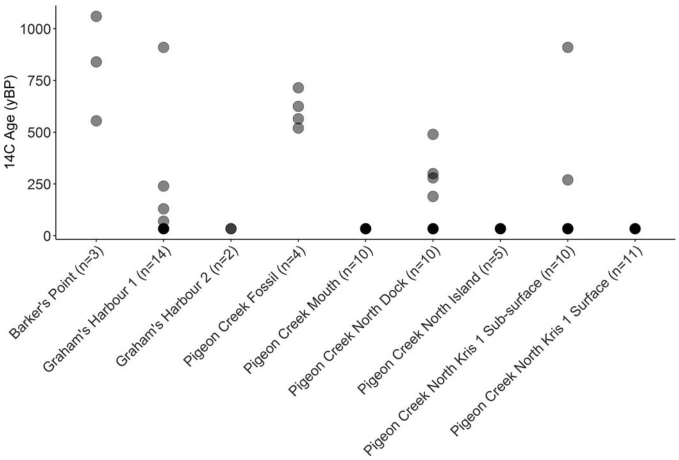

FIG. 3.—Results of rapid AMS radiocarbon dating of *Lobatus gigas* shells.

from Graham's Harbor 1, Pigeon Creek North Dock, and Pigeon Creek North Kris 1 Sub-surface were dated between 910 ^{14}C y BP and post-thermonuclear testing and were placed in the Modern time bin. The Pigeon Creek North Kris 2 Sub-surface sample was assigned to the Modern time bin given its close proximity to the Kris 1 Sub-subsurface sampling locality. Specimens from Graham's Harbor 2, Pigeon Creek Mouth, Pigeon Creek North Island, and Pigeon Creek North Kris 1 Surface resulted in solely post-thermonuclear testing dates and were assigned to the Global time bin. Similarly, the Pigeon Creek North Kris 2 Surface sample was assigned to the Global time bin.

The percentage of juveniles harvested on San Salvador Island increased through time from 47% (Lucayan) to 61% (Modern) to 68% (Global). This increase was statistically significant as determined by the *Cochran-Armitage* test for trend in binomial proportions ($p = 0.016$) (Table 3).

The mean length of all harvested shells increased significantly between the Lucayan and Modern time bins and decreased with marginal statistical significance in the Global time bin. Similarly, the mean width of all harvested shells increased significantly between the Lucayan and Modern and exhibited stasis in the Global time bin (Fig. 5, Tables 2–4). Neither of

TABLE 2.—*Summary statistics of Lobatus gigas shell length (only specimens with complete shell length), shell width (only specimens with complete shell width), PC1 score, and PC2 score by age.*

	n	Mean length (mm)	n	Mean width (mm)	n	Mean PC1	Mean PC2
Global							
All	164	213.9	141	155.3	137	-0.186	-0.012
Adults	53	223.6	53	166.6	52	0.631	0.437
Juveniles	111	209.3	88	148.6	85	-0.686	-0.287
Modern							
All	78	222.4	67	163.8	65	0.708	-0.129
Adults	30	224.3	31	167.5	30	0.916	0.205
Juveniles	48	221.2	36	160.6	35	0.529	-0.415
Lucayan							
All	30	193.8	22	152.2	16	-1.280	0.629
Adults	16	198.8	14	157.3	10	-0.908	0.558
Juveniles	14	188.1	8	143.4	6	-1.899	0.749

these overall temporal trends were statistically significant as tested by the Jonckheere-Terpstra test (Table 4).

Considering only adult shells, length increased significantly between the Lucayan and Modern time bins and exhibited stasis in the Global time bin (Tables 2, 5). The temporal trend of increasing length was statistically significant (Table 4). Similarly, shell width of adults increased significantly between the Lucayan and Modern and maintained stasis in the Global, however the temporal trend was not statistically significant (Tables 2, 4, 5).

Shell length of juveniles increased significantly between the Lucayan and Modern and decreased significantly from the Modern to the Global (Table 5). The temporal trend of shell width among juveniles was not statistically significant. There was no significant change in juvenile shell width through time, neither in pairwise comparisons nor in the overall temporal trend (Tables 2, 4, 5).

The first principal component explains 75.2% of the variation among the seven morphological characters analyzed (Fig. 6). All variables are strongly positively correlated with PC1 values, which is a proxy for body size. PC2 explains 11.5% of the variation, is moderately positively correlated with shell width and aperture length and width, and is moderately negatively correlated with the four measures related to shell length. PC1 and PC2 account for a combined 86.7% of the variation in the data set and the scree plot reveals an inflection point at PC2, therefore subsequent principal components are not further considered.

Mean PC1 scores for all specimens increased significantly between the Lucayan and Modern time bins and decreased significantly into the Global time bin (Tables 2, 6). Mean PC1 scores for adult specimens increased significantly between the Lucayan and Modern, but exhibited stasis into the Global. Mean PC1 scores for juveniles increased significantly between the Lucayan and Modern and decreased significantly between the Modern to Global time bins (Tables 2, 6). Mean PC2 scores for all specimens decreased significantly between the Lucayan and Modern and maintained stasis into the Global. Adult and juvenile specimens considered separately exhibited stasis in mean PC2 values between all bins.

TABLE 3.—*Proportion of hunted Lobatus gigas individuals that were juveniles and Cochran-Armitage test results.*

	Lucayan	Modern	Global
Juveniles	16	49	113
Total	34	80	167
Proportion	0.47	0.61	0.68

Cochran-Armitage test for trend in binomial proportions: -2.25, $p = 0.016$

DISCUSSION

All shells in this study were harvested by humans as indicated by a puncture hole in the top of the shell near the spire. All specimens from the Barker's Point locality (Lucayan) possessed an ovoid puncture hole near the spire, likely made with a stone tool or the spire of another conch (Blick 2007b) (Fig. 2). This puncture hole gives access to the retractor muscle, which, when cut, releases the snail from the shell. This is still common practice throughout the Caribbean today but the oblong puncture hole in Modern and Global aged shells is made with modern tools, such as a hatchet or screwdriver, and can be easily distinguished from the sub-circular puncture on most Lucayan shells (Fig. 2).

Demographics of Harvested Individuals through Time

As predicted, the proportion of juveniles harvested steadily and significantly increased through the studied time interval (Fig. 4), as a result of increased human population. This finding is consistent with other studies demonstrating heavy exploitation of the queen conch throughout much of its natural range (Stoner 1997; Acosta 2002; Stoner et al. 2018). These results are consistent with those of Blick (2007a) and reveal that even a small human population, perhaps as small as 500–1000 people, over-fished marine taxa prior to European colonization. Over-fishing of *L. gigas* has worsened in the post-colonial Caribbean. Increasing demand

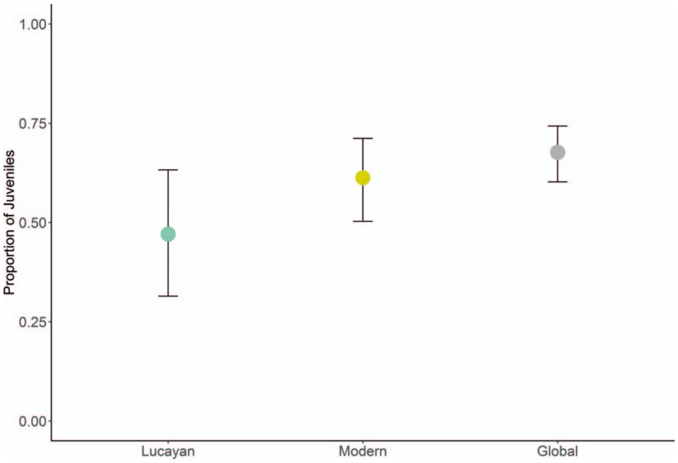

FIG. 4.—Proportions of juvenile *Lobatus gigas* harvested in each time bin. 95% confidence intervals calculated using the Agresti-Coull method.

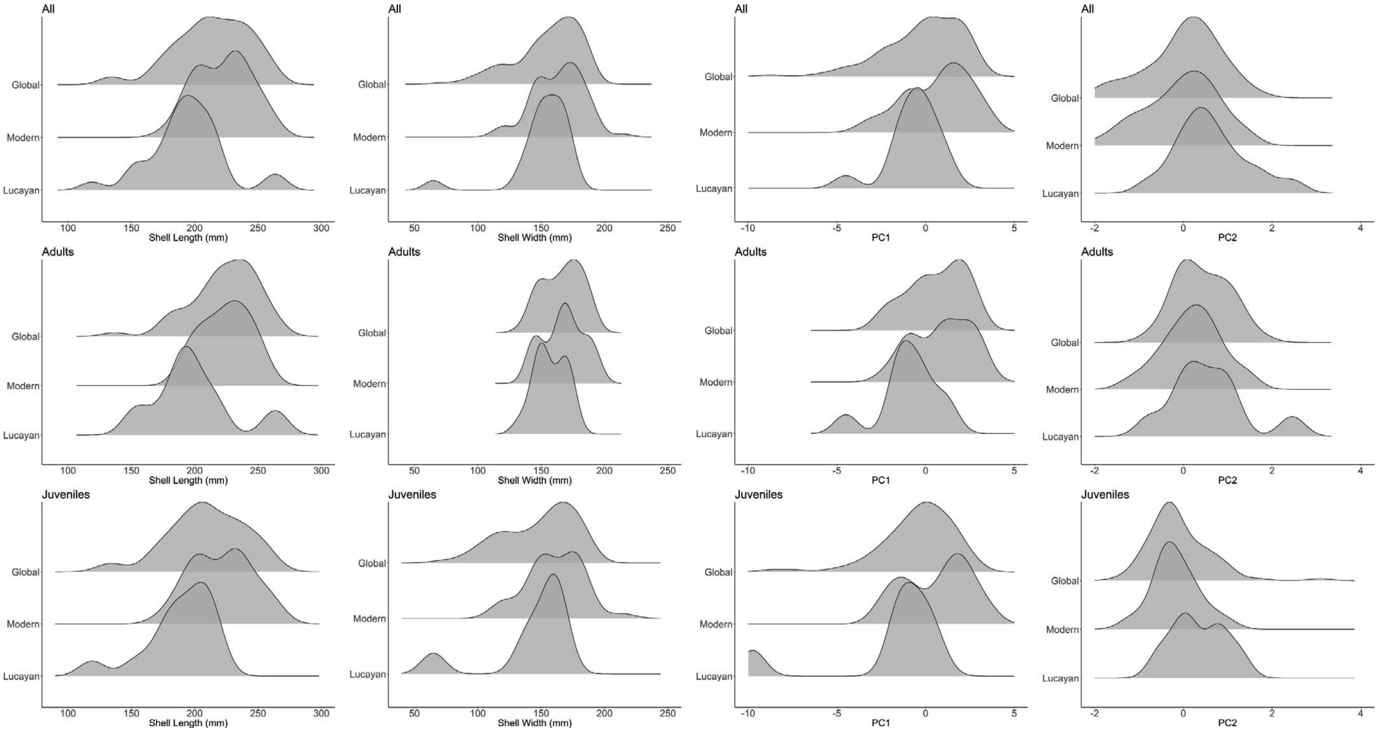

FIG. 5.—Density plots of shell length, shell width, PC1 scores, and PC2 scores of *Lobatus gigas* through time by all harvested specimens, adult specimens, and juvenile specimens.

escalated in the 1970s and overfishing led to decreases in conch population densities across the species' geographic range, though our geochronological bins did not have the resolution to detect such recent change (Acosta 2006; Stoner et al. 2012b; Stoner et al. 2014; Baker et al. 2016).

It should be noted that the sample size for the Lucayan time bin is small (n=37). Thus, ecological interpretations of statistically significant increases in the proportion of harvested juveniles from Lucayan to Modern bins should be considered with caution. Additional sampling of Lucayan-aged sites would aid in our understanding of the proportion of harvested juveniles on San Salvador Island prior to the arrival of Europeans. Further refinement of dates from the Modern time bin are needed to gain a higher-resolution image of how the proportions of harvested juveniles differed post-Columbus. The modern time bin is both a mix of older shells (>600 yrs) and newer post-thermonuclear weapons testing aged shells, while the Lucayan time bin is unquestionably Pre-Columbus in age and the Global is decidedly all post-atomic weapons testing. This time averaging, or temporal smearing, of the Modern time bin would likely serve to dampen secular trends, however there is a consistent and significant increase in the proportion of harvested juveniles indicating increased fishing pressure on the queen conch populations of San Salvador Island through time.

TABLE 4.—*Results (p-values) of Jonckheere-Terpstra trend tests for shell length, shell width, PC1 scores, and PC2 scores. Key: ns = non-significant.*

	Shell length	Shell width	PC1	PC2
All specimens	ns	ns	ns	ns
Adults	0.01	ns	ns	ns
Juveniles	ns	ns	ns	ns

Size of Harvested Individuals through Time

Given the complex growth patterns of this taxon, wherein the relationship between length and width differs dramatically before and after the onset of sexual maturity, single morphological variables are not reliable indicators of overall body size (Fig. 5). The scores on the first principal component axis (PC1) are positively correlated with all morphometric variables and are, therefore, interpreted as a proxy for body size. PC2 scores are interpreted as a size-free proxy for shape with positive scores indicating relatively wider shells and negative scores indicating relatively longer shells for a given size.

Overall, harvested shells increased in size and became relatively narrower between the Lucayan and Modern time bins and, as before, we interpret this increase with caution due to a limited Lucayan sample size. Harvested shell body size decreased from the Modern to Global time bins, consistent with increasing pressure on the fishery, however, the shells became relatively wider between the latter time bins. It is instructive to consider temporal trends in adult and juvenile body size and shape separately when estimating the impact of human predation on queen conch populations through time, especially when their proportion among the harvest so drastically changes. The mean body size of harvested adult shells increased from the Lucayan to Modern and are indistinguishable between the Modern and Global time bins. The relative shape of harvested adults, as indicated by the decrease in PC2 scores, did not appreciably change among the time bins. Harvested juveniles, in concert with being harvested at a higher proportion between the Modern and the Global time bins, decreased in body size, though there was no significant change in their relative shape. These results are consistent with increasing pressure on the fishery as humans harvested not only a higher proportion of juvenile gastropods through time but also collected smaller juveniles through time.

Previous studies have documented a decrease in adult body size of *Lobatus* with increasing fishing pressure (Schapira et al. 2009; Stoner et al.

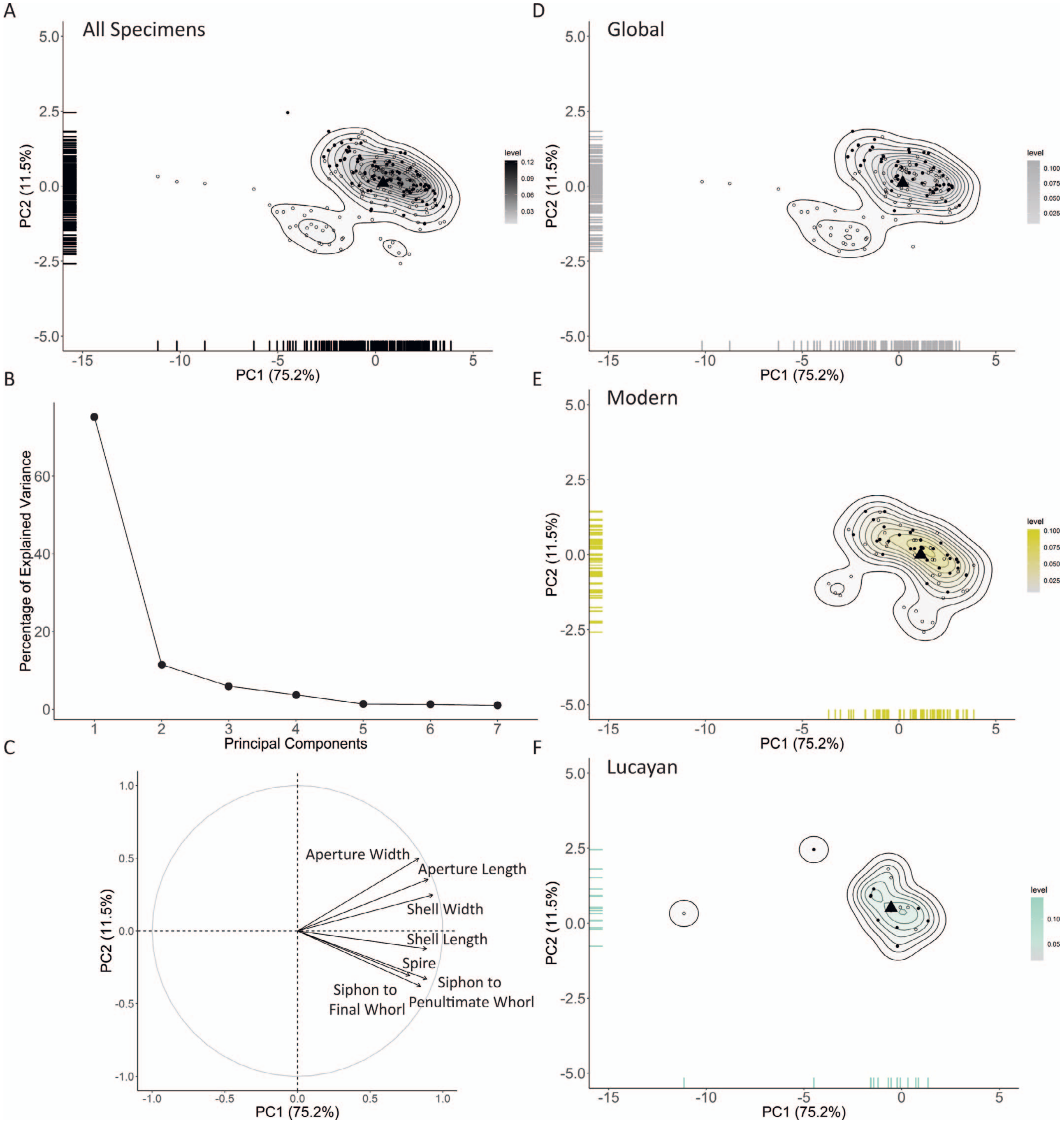

FIG. 6.—Principal components analysis of *Lobatus gigas*. **A**) PC1 versus PC2 of all specimens. **B**) Scree plot. **C**) Loadings plot displaying correlation coefficient values between individual variables and PC scores. **D**) PC1 versus PC2 of Global specimens. **E**) PC1 versus PC2 of Modern specimens. **F**) PC1 versus PC2 of Lucayan specimens. Key: solid circles = adult specimens, hollow circles = juvenile specimens.

2012a, 2012b; O'Dea et al. 2014). Schapira et al. (2009) examined 27 middens from Los Roques in Venezuela and documented a substantial increase in the proportion of juveniles harvested from 11% prior to the arrival of Columbus (1160–1540 CE) to 48%–67% juveniles among modern middens. This trend was accompanied by a significant decrease in the shell length of harvested adult individuals. O'Dea et al. (2014) demonstrated that size at sexual maturity of *Lobatus pugilis* declined from pre-human samples (7 ka) to pre-historic middens (∼1 ka) to present day in the Bocas del Toro archipelago of Panama. They concluded that size-selection introduced by subsistence farming was enough to drive a decrease in adult size. Encouragingly, O'Dea et al. (2014) noted an increase in body size in protected habitats, suggesting that the influence of

TABLE 5.—*Tukey's post-hoc test results comparing shell length and shell width by time bin and life stage of Lobatus gigas (p-values). Key: ns = non-significant.*

	Shell length			Shell width		
	All	Adults	Juveniles	All	Adults	Juveniles
Modern-Lucayan	4.50×10^{-6}	2.20×10^{-3}	4.51×10^{-4}	ns	ns	ns
Global-Lucayan	7.80×10^{-4}	1.67×10^{-3}	0.02	ns	ns	ns
Global-Modern	0.05	ns	0.04	0.04	ns	ns

these selective regimes can be reversed over short time scales. Why did we not find a similar pattern in San Salvador? Perhaps the activities of the small human population on San Salvador have not been adequate to induce such size selection, however this would be counter to O'Dea et al.'s (2014) suggestion that even artisanal or subsistence farming is enough to drive down body size. If adult body size has decreased during the most recent centuries, perhaps its record has been obscured by the temporal smearing in the Modern time bin.

Potential Caveats

Alcolado (1976) demonstrated that water depth during development was intimately related with growth rate and subsequent body shape of *L. gigas*. Gastropods that grew in shallow water (less than 2 m depth) tended to grow at a higher rate, which resulted in shells that were relatively lighter (presumably thinner), with shorter spines, and narrower shell width. Comparatively, individuals that grew in deeper water grew more slowly, developing thicker, wider shells with longer spines (Alcolado 1976). It is possible that the significant narrowing in shape seen during the Modern time bin and subsequent increase in relative width during the Global was related to an expansion of fishing into greater depths associated with diving.

The energetic costs of processing the gastropods and meat preferences could have influenced the trends of juveniles harvested and body size and shape. Adult specimens with flared lips have, of course, thicker shells than juveniles. These thicker shells will require greater effort to puncture the spire and remove the meat. Moreover, as with many animals consumed by humans, meat from adult/senile specimens is often considered tougher and less desirable than that of ontogenetically younger quarry. The change in PC2 values between the Modern and Global time bins may indicate a shift to fishing in deeper waters in response to a depletion of juvenile specimens in shallow waters.

Species with large geographic distributions often exhibit differences in size at maturity along temperature gradients, the temperature-size rule (Atkinson 1994), with higher temperatures causing earlier maturation at a smaller size. This trend was observed in marine gastropods by Irie et al. (2013), however there is currently little evidence of this trend in the queen conch. Boman et al. (2018) recently found that temperature did not appear to be the sole driving factor behind variability in shell size. While they were not able to say whether the temperature-size rule applies to the queen conch, they did find that shell size does vary by geographic location, but that seems to be related to sexual dimorphism with females generally having larger shells and males generally having smaller shells. Other studies have also identified sexual dimorphism in queen conchs. Randall (1964) noted diminutive males relative to females from multiple localities in the Bahamas. Additionally, Boman et al. (2018) observed that females had a significantly greater lip thickness at maturity. We were unable to make distinctions between male and female individuals in our study as we only had the shells available and the gonads are needed for sex determination (though some populations do present with bimodal distributions (Fig. 5)).

Recommendations for Fisheries Management

The current fishing regulations for the Bahamas, a large exporter and consumer of the queen conch, currently states that harvested conchs must have a "well-formed shell lip." While it may be conservative, lip thickness of >15 mm is currently the simplest and most reliable proxy available for sexual maturity. The nation, however, currently does not have a closed season for queen conch reproduction. Though peak reproduction of conchs varies geographically (Appeldoorn and Baker 2013), the reproductive season occurs from May to September across the majority of the Caribbean (Boman et al. 2018). The implementation of an explicit 15 mm minimum lip thickness regulation and a closed season in the Bahamas and across the greater Caribbean would maximize protection of spawning sexually mature adults and perhaps help ease pressure on fisheries that have been present and increasing in the Caribbean over the last millennium (Berman and Gnivecki 1995; Berman and Pearsall 2000; Buchan 2000; Blick 2007a; Schapira et al. 2009; Blick et al. 2011; Stoner et al. 2012a, 2012b, 2012c; O'Dea et al. 2014; Stoner et al. 2018).

CONCLUSIONS

There has been an increase in fishing pressure on the queen conch fishery at San Salvador, the Bahamas, over the last 1,000 years. This is evidenced by a dramatic increase in the proportion of shells harvested by humans that were juveniles. Among all harvested shells, there was an increase in body size from the Lucayan to the Modern and a decrease from

TABLE 6.—*Tukey's post-hoc test results comparing PC1 scores and PC2 scores by time bin and life stage of Lobatus gigas (p-values). Key: ns = non-significant.*

	PC1			PC2		
	All	Adults	Juveniles	All	Adults	Juveniles
Modern-Lucayan	4.82×10^{-3}	7.36×10^{-3}	9.66×10^{-3}	6.49×10^{-3}	ns	ns
Global-Lucayan	ns	0.02	ns	0.02	ns	ns
Global-Modern	0.02	ns	0.03	ns	ns	ns

the Modern to the Global. The latter decrease in size was driven by the collection of more juveniles and smaller juveniles in the Global time bin. In contrast with other studies, we did not find evidence for the suppression of adult body size as a result of this size-selective hunting behavior. This is, perhaps, due to the relatively small human population on San Salvador.

Addressing the non-cohesive nature of fishing regulations across the Caribbean is vital to easing the pressure on living conch populations. The explicit implementation and enforcement of a minimum lip thickness of 15 mm and a closed season during reproduction (May to September) could relieve stress on living populations and help ensure their vitality in the future.

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APPENDIX

R-codes

Cochran-Armitage Test

```
#Conduct a Cochran-Armitage trend test to determine if there is a trend in the proportion of juveniles hunted from Lucayan to Modern to Global
doseratings <- c(1,2,3) #Numerical order of Time_Period
totals <- c(34,80,167) #Number of individuals per Time_Period in ConchsTimeAge
cases <- c(16,49,113) #Number of juvenile individuals per Time_Period in ConchsTimeAge
catt_exact(dose.ratings = doseratings, totals = totals, cases = cases)
```

Principal Components Analysis

```
#Create dataset with no missing values for morphometric variables and Time_Period and with Total_Length and Total_Width values equal to 1
conchsPCA <- dplyr::filter(conchs, Total_Length=="1” & Total_Width=="1” & !is.na(Time_Period) & !is.na(Shell_Length) & !is.na(Shell_Width) & !is.na(Spire) & !is.na(Aperture_Length) & !is.na(Aperture_Width) & !is.na(Siphon_to_final_whorl) & !is.na(Siphon_to_penultimate_whorl) & !is.na(Age_Class))
#Create object of PCA
PCAconchsPCA <- prcomp(scale(log10(conchsPCA[,c(14,15,17,18,19,20,21)])))
```

Jonckheere-Terpstra tests

```
LengthJonckheere <- jonckheere.test(ConchsTimeAgeLength$Shell_Length, ConchsTimeAgeLength$Time_Order, nperm = 10000)
WidthJonckheere <- jonckheere.test(ConchsTimeAgeWidth$Shell_Width, ConchsTimeAgeWidth$Time_Order, nperm = 10000)
attach(TotalPCAconchsPCA)
PC1Jonckheere <- jonckheere.test(TotalPCAconchsPCA$PC1, TotalPCAconchsPCA$Time_Order, nperm = 10000)
PC2Jonckheere <- jonckheere.test(TotalPCAconchsPCA$PC2, TotalPCAconchsPCA$Time_Order, nperm = 10000)
```

Tukey's post-hoc test

```
AdultLengthModel <- lm(log10(ConchsTimeAgeLengthAdult$Shell_Length) ~ ConchsTimeAgeLengthAdult$Time_Period)
AdultLengthANOVA <- aov(AdultLengthModel)
AdultLengthTUKEY <- TukeyHSD(x=AdultLengthANOVA, ’ConchsTimeAgeLengthAdult$Time_Period’, conf.level = 0.95)
```