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Evidence of size-selective evolution in the fighting conch from prehistoric subsistence harvesting

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Intensive size-selective harvesting can drive evolution of sexual maturity at smaller body size. Conversely, prehistoric, low-intensity subsistence harvesting is not considered an effective agent of size-selective evolution. Uniting archaeological, palaeontological and contemporary material, we show that size at sexual maturity in the edible conch *Strombus pugilis* declined significantly from pre-human (approx. 7 ka) to prehistoric times (approx. 1 ka) and again to the present day. Size at maturity also fell from early- to late-prehistoric periods, synchronous with an increase in harvesting intensity as other resources became depleted. A consequence of declining size at maturity is that early prehistoric harvesters would have received two-thirds more meat per conch than contemporary harvesters. After exploring the potential effects of selection biases, demographic shifts, environmental change and habitat alteration, these observations collectively implicate prehistoric subsistence harvesting as an agent of size-selective evolution with long-term detrimental consequences. We observe that contemporary populations that are protected from harvesting are slightly larger at maturity, suggesting that halting or even reversing thousands of years of size-selective evolution may be possible.

1. Introduction

The persistent harvesting of the largest individuals from an ecosystem, whether for trophy, nutritional or economic gain, can impart strong directional selection for smaller size at reproduction [1–3] that is predicted to have significant negative effects on yield, population structure, fecundity and growth [4–6]. When harvesting is intensive, the evolutionary change to smaller size at maturity can be observed over decades [2,7] and under artificial experimental conditions can be forced to appear in just a few generations [8,9]. By contrast, low-intensity subsistence (artisanal) harvesting is widely presumed to lack sufficient directional selection to have an analogous significant evolutionary impact (cf. [10]), but does this assumption hold true if subsistence harvesting has persisted for a long time?

Archaeological middens the world over demonstrate that coastal shellfish have been harvested for hundreds of years to millennia [11–13] and have undergone marked changes to their ecological structure as a result [14–19]. Many (but not all) mollusc species that have a long history of subsistence harvesting have become smaller over time [14,16,20], suggestive of size-selective evolutionary change. It is impossible, however, to convincingly establish if the causal mechanism is selection to mature at a smaller size, as described above, or if it is simply because larger individuals become less common as they are preferentially harvested, thereby lowering mean size. One critical obstacle is that in order to demonstrate selection-driven evolution, measures of size at maturity are required and such data are not typically preserved in the skeletons of organisms. Here, we document changes in the size at maturity

of the West Indian fighting conch (*Strombus pugilis* Linnaeus 1758) in western Caribbean Panama over the past approximately 7000 years. The shift from juvenile to sexually mature is observable in the calcified shells of *S. pugilis*.

2. Setting

The Bocas del Toro archipelago in western Caribbean Panama (figure 1) is a series of Holocene-flooded basins forming islands with fringing reefs, thick mangroves and muddy lagoons. Major reef growth began with the Plio-Pleistocene closure of the Isthmus of Panama [21–23]. Almirante Bay (figure 1) was flooded sometime before 7.2 ka when modern fringing reefs began to develop [24]. Following the historical and more recent declines of the branching coral *Acropora cervicornis* [24,25], the fringing reefs of Bocas del Toro became dominated by a mixture of *Porites* and *Agaricia* [26].

Humans have modified the terrestrial landscapes on the Pacific slopes of lower Central America for over 11 kyr [27,28] and the less hospitable Caribbean slopes since about 6 ka [29], principally by land clearance and fire [28]. Likewise, coastal resources have been exploited for several thousand years on the Isthmus. The earliest evidence in the Bocas del Toro region is a coastal settlement at Black Creek, 9 km to the west of Bocas del Toro in Costa Rica, with radiocarbon dates ranging from 3440 to 2580 BP [30]. Shellfish were a resource at Black Creek, but which taxa and to what extent remains to be described publicly. Shell middens at Cerro Brujo on the Aguacate Peninsula dated AD 880–1250 and at Sitio Drago on Isla Colon dated AD 690–1410 (figure 1) reveal people were involved in regional trade, with a mixed farming–fishing–hunting subsistence that included the exploitation of fish, molluscs, terrestrial vertebrates, sea turtle and manatee [31,32] for at least 800 years until the arrival of Christopher Columbus on October the 5th, 1502 (see the electronic supplementary material for further information).

(a) Strombus pugilis

The West Indian fighting conch *S. pugilis* (Linnaeus 1758; family Strombidae; figure 2) is a grazing gastropod common in shallow water and sandy and muddy lagoons across the tropical western Atlantic from Brazil in the South to Florida in the North.

Strombus undergo marked shifts in mode of skeletal growth and behaviour between juvenile and adult. Juvenile skeletal growth adds body whorls resulting in increasing height and width of the shell (figure 2), often with the development of spines. As maturity approaches, whorl growth slows and stops, the shell begins to thicken, and the outer lip flares and thickens. In *Lobatus gigas* (formerly *S. gigas*), gonadal maturity, as observed in the development of sexual characters, histological examinations of the visceral mass and observations of behaviour and timing of egg-laying, is achieved only *after* the outer lip begins to flare and thicken [33–35]. The same pattern of lip thickening at maturity is also true for the Caribbean *L. costatus* [36] and the Indo-Pacific *S. luhuanus* [37] and *S. canarium* [38]. In *S. pugilis*, juveniles are cryptic, burying themselves in sediment, whereas adults are more aggressive, roaming the sea floor. This behavioural shift coincides with maturity, permitting mate competition and internal fertilization [39] and does not occur until the outer lip thickens for the protection it confers, presumably because

of the increase in predation risk as the animal moves to a less cryptic mode of life. Additionally, we observed that thin-lipped individuals of *S. pugilis* were frequently buried, implying immaturity and upon macroscopic investigation possessed sexually undifferentiated gonads. Conversely, thick-lipped individuals roamed the sea floor and possessed granulated and brown female gonads and light red male gonads, both of which demonstrate gametogenesis in *S. pugilis* [40]. We did not, however, conduct microscopic examination of gonad morphology. Nonetheless, given the observations of *S. pugilis* behaviour and macroscopic morphology, patterns of growth and demography, and the microscopic analysis of gonads in closely related species, we conclude that lip thickening precedes maturity in *S. pugilis*.

Shell middens demonstrate that conch harvesting has long been an important subsistence activity throughout the Caribbean [41], particularly of the queen conch (*L. gigas*). *S. pugilis* is smaller than *L. gigas* but has nonetheless contributed significantly to conch fisheries across the Caribbean for millennia. *S. pugilis* still forms an important component of the subsistence diet of coastal peoples in the Caribbean and Gulf of Mexico for its meat where it is generally boiled or roasted as a protein-rich food. *S. pugilis* is also used as an aphrodisiac in Brazil.

In Bocas del Toro, *S. pugilis* greatly outnumbers its larger cousin, *L. gigas*, in modern lagoons, archaeological middens [32] and mid-Holocene fossil assemblages [24], strongly suggesting that *L. gigas* is naturally rarer in Bocas than other Caribbean regions. Indeed, the massive accumulations of *L. gigas* shells from centuries of harvesting common in many parts of the Caribbean are notably absent. Contemporary harvesting of *S. pugilis* in Bocas del Toro is restricted to subsistence fishing, and there is no contemporary or historical evidence that the meat is or has been traded. The most frequent method of harvesting is to simply wade into shallow lagoons, collect the conch by hand without a mask and consume locally. It is fair to assume that prehistoric harvesting of *S. pugilis* was much the same.

In Bocas, *S. pugilis* is colloquially called *el raton del mar* (the mouse of the sea) reflecting its abundance and possibly alluding to the contemptuousness imparted on the (generally poor) people that consume it. For this reason, consumption of *S. pugilis* is not widely admitted in the region; during our surveys, people initially denied harvesting *S. pugilis* despite mounds of empty conch under their houses. Perhaps it is considered a low-grade food because it remains locally abundant in the region. Harvesters can year-round easily collect several conch for a family dinner within half an hour by wading across a silty lagoon. The attractive shells of *S. pugilis* are also sold as souvenirs to tourists in Bocas del Toro.

3. Methodology and approach

(a) Collections

Contemporary, prehistoric and pre-human material was collected from the Bocas del Toro archipelago (figure 1). Five contemporary sites were sampled using snorkel and bulk collection of modern refuse piles and souvenir shops. Prehistoric material was collected from two ceramic phases in two pits at the archaeological site 'Sitio Drago' [42]. The Bisquit Ware phase (0–40 cm) is dated to approximately AD 1200–AD 1410 and pre-Bisquit Ware phase (40–150+ cm) dates from
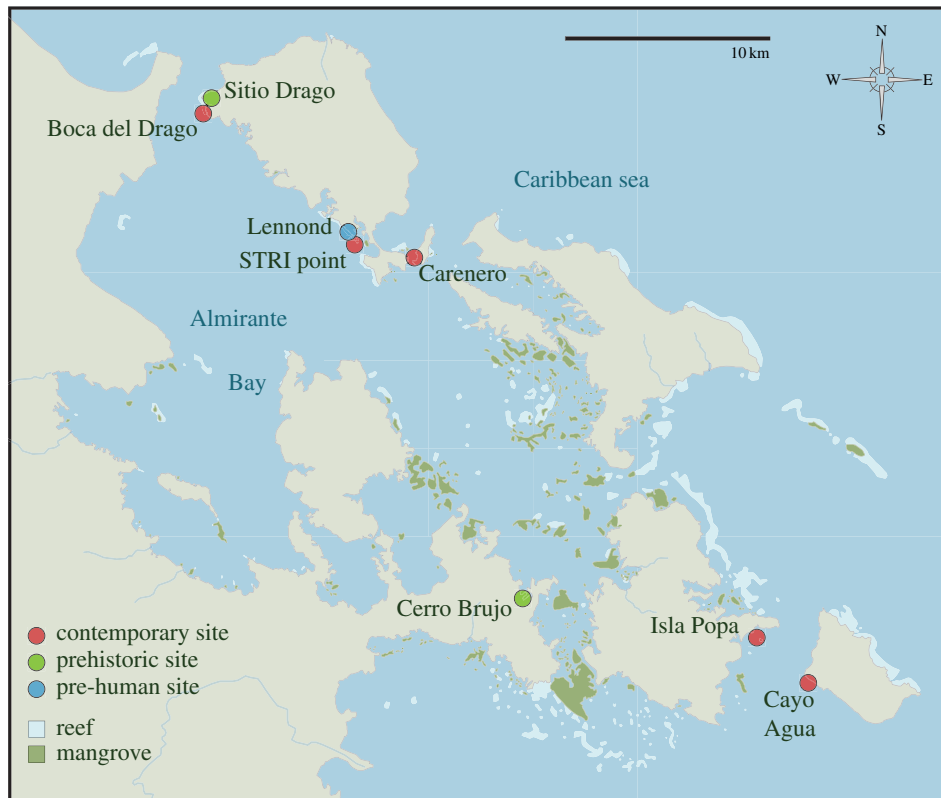
Figure 1. Bocas del Toro archipelago, Caribbean Panama, showing location of sites used or discussed in this study. (Online version in colour.)

approximately 690 to AD 1200. Pre-human (fossil) shells were collected from the lagoonal sediments of a mid-Holocene fringing reef at the old town of Lennond (figure 1) which has been U–Th dated to 7187–5711 years before present [24]. We call this pre-human because, although humans had arrived to the isthmus long before this time, all evidence suggests they had little impact on Caribbean coastal ecosystems until approximately 6 ka [43]. See the electronic supplementary material for details on collection sites and methods.

(b) Morphometrics

Height, width and lip thickness of shells were measured using callipers. Shell height (SH) is the distance between the apex and the tip of the siphonal notch along the coiling axis (figure 2h). Shell width is the maximum distance perpendicular to height at the last body whorl where the lip is thickest and not including spines (figure 2g). Lip thickness is measured from the outer lip three quarters the way along from the siphonal canal (figure 2e,f).

The Ryan–Joiner test for normality (MINITAB v. 16) revealed non-normal distributions in SH and shell width data from some of the sites. All data were log-transformed, and the Ryan–Joiner test revealed all groups to be statistically normally distributed at $p = 0.05$. Levene's test for homogeneity of variances (MINITAB v. 16) revealed homoscedasticity in both heights and widths at $p > 0.05$. One-way ANOVA and Tukey's *post hoc* test (MINITAB v. 16) were therefore appropriate to analyse the differences in shell morphology through time and across sites.

(c) Estimating meat weight

There is no published relationship between edible meat weight (MW; dried tissue minus the visceral mass) and shell size for *S. pugilis*. There are, however, good data relating edible MW and shell size for *L. gigas*. We used the following equation established by CFMC/CFRAMP [44] that describes the relationship between MW (grams) and SH (centimetres) for juvenile *L. gigas* from La Parguera, Puerto Rico ($N = 94$, $r^2 = 0.926$).

$$\log_{10}(MW) = -2.535 + 3.486 \log_{10}(SH).$$

(d) Lip thickness at maturity

During juvenile growth, the outer lip of *S. pugilis* remains thin until whorl growth ceases, whereupon the outer lip flares and thickens considerably (figure 2). Plots of SH and width versus lip thickness compiled from all shells reveal two clusters that represent juveniles (thin-lipped) and mature (thick-lipped) individuals with the threshold between them occurring at a lip thickness of 1.8 mm (figure 3a). We conducted macroscopic observation of the gonads of 37 living *S. pugilis* from Bocas del Toro that revealed that the smallest individual expressing clear gametogenesis (see previously) had a lip thickness of 2.2 mm, corroborating the conclusion that lip thickening begins at or shortly before sexual maturity and our assumption for data analysis that shells with lips thinner than or equal to 1.8 mm are juveniles and those with a lip thickness greater than 1.8 mm are mature.

4. Results

(a) Size at maturity

Size at maturity of *S. pugilis* in Bocas del Toro decreases successively from pre-human to prehistoric to the contemporary period. This trend is observed in all metrics explored; the height and width of the largest juvenile (electronic supplementary material, table S1 and figure 3b,c), the height and width of

Figure 2. Growth of the West Indian fighting conch (*Strombus pugilis*) and morphometrics (height, width and lip thickness) taken in this study. (*a*–*d*) Juvenile shells with lips less than 1.8 mm. (*e*–*h*) Adult shells with lips thicker than 1.8 mm. (*e*) Dorsal view showing measurement of outer lip thickness. (*f*) A typically small mature contemporary shell from Isla Carenero with characteristic scorch markings from cooking. Arrow indicates location of outer lip thickness measurement. (*g*) One of the largest mature contemporary shells from Isla Popa. (*h*) A large pre-human mature shell. (*a*–*c,h*) are pre-human, whereas (*d*–*g*) are contemporary. Scale bar, 2 cm. (Online version in colour.)

the smallest mature shell (electronic supplementary material, table S1 and figure 3*b,c*), the height and width of the largest mature shell (electronic supplementary material, table S1 and figure 3*b,c*) and the distributions of heights and widths of only mature shells (figure 4). ANOVA reveals that both height and width of mature shells between pre-human, all prehistoric and all contemporary material is very highly significantly different (height, d.f. = 2, $F = 107.45$, $p < 0.0001$; width, d.f. = 2, $F = 77.94$, $p < 0.001$), and Tukey's post hoc test reveals the differences exist between all three comparisons (electronic supplementary material, table S2). Height and width of mature *S. pugilis* is likewise highly significantly different among individual sites and times (height, d.f. = 9, $F = 52.01$, $p < 0.001$; width, d.f. = 9, $F = 41.45$, $p < 0.001$). Tukey's post hoc test, summarized in electronic supplementary material, table S2, reveals where those significant differences exist. Pre-human mature *S. pugilis* is significantly higher and wider than any of the five contemporary populations, and all contemporary populations combined. The older, pre-Bisquit Ware prehistoric material is significantly higher and wider at maturity than any of the contemporary material. The younger Bisquit Ware material is significantly higher and wider at maturity than most contemporary populations, the only exception being material from Isla Popa from which it is higher and wider but not significantly so. Pre-human material is higher and wider at maturity than pre-Bisquit Ware prehistoric material but not significantly. However, pre-human material is significantly

higher at maturity than Bisquit Ware material and all of the combined archaeological material (pre-Bisquit Ware and Bisquit Ware). Pre-Bisquit Ware shells are both higher and wider at maturity than Bisquit Ware material, but the difference is not significant. Additionally, the size of *S. pugilis* is significantly different among several contemporary populations (electronic supplementary material, table S2); the Isla Popa material, for example, is significantly higher and wider at maturity than contemporary Cayo Agua material, despite their geographical proximity (figure 1).

(b) Estimated meat weight
Estimated mean edible dry MW of individual mature shells only is 2.93 g in pre-human, 2.42 g in prehistoric and 1.77 g in contemporary material. This represents, on average, 17% less meat in prehistoric compared with pre-human conch, 27% less meat in contemporary compared with prehistoric conch and 40% less meat in contemporary compared with pre-human conch.

5. Discussion

(a) Long-term harvesting of *Strombus pugilis* and reduced size at maturity
Evolution of size at maturity driven by size-selective harvesting is commonly considered a blight of modern intensive
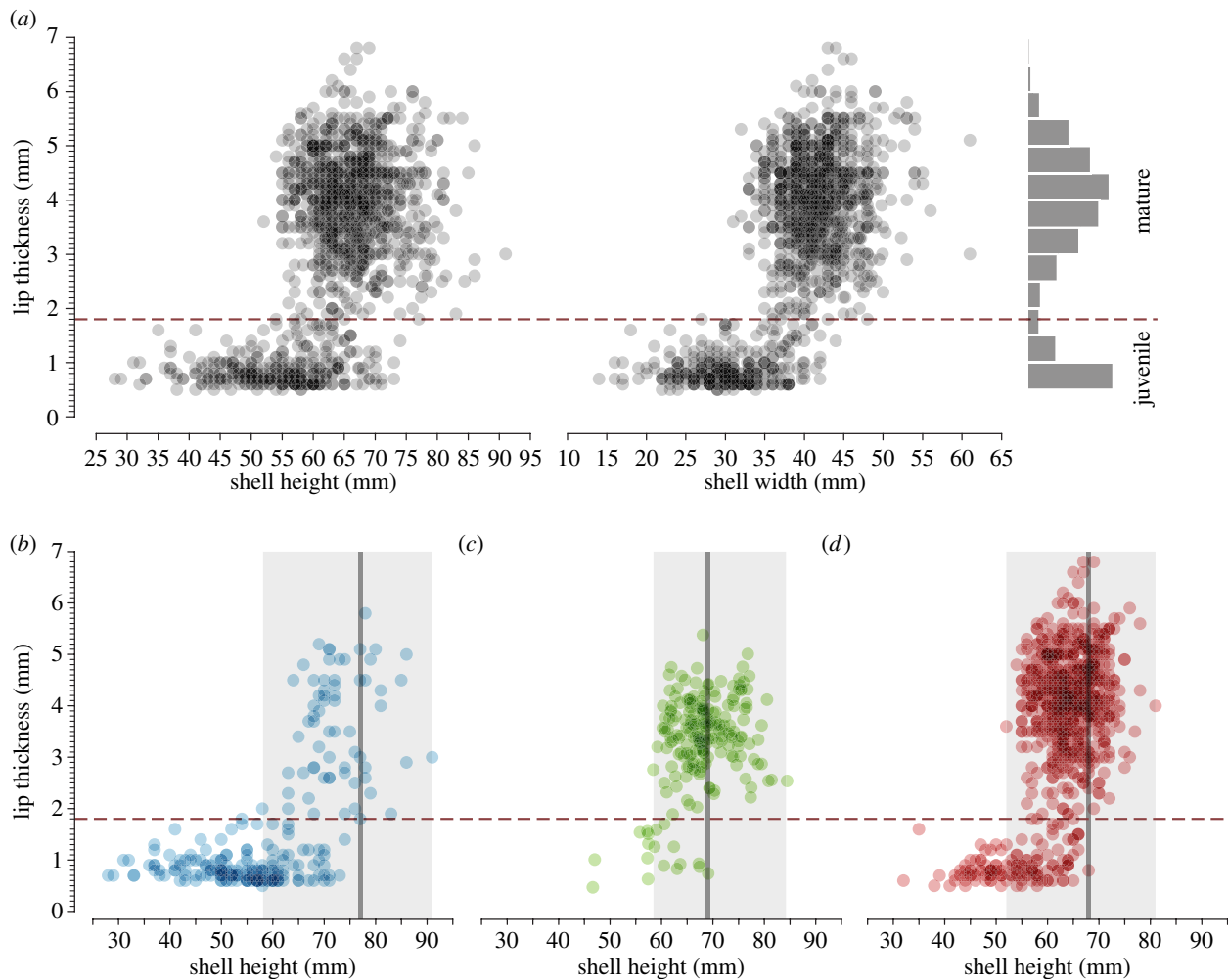
Figure 3. Shell size versus lip thickness in *Strombus pugilis* shells from Bocas del Toro. (*a*) All shells used in this study with frequency histogram of lip thickness. (*b*−*d*) Shell height versus lip thickness in (*b*) pre-human, (*c*) prehistoric and (*d*) all contemporary sites combined. Dashed lines indicates the cut-off from juvenile to sexually mature shells at a lip thickness of 1.8 mm. Light grey bars demarcate the smallest and largest sexually mature shells and dark lines the largest juvenile. (Online version in colour.)

methods of harvesting [45]. Our results contradict this widely held view demonstrating that millennia of low-intensity subsistence harvesting of the conch *S. pugilis* in Bocas del Toro caused evolution to reduced size at maturity. The data are particularly robust, because the declines in size occur in populations from the same island through time.

The directional selection pressure to evolve reproduction at a smaller size could have been applied by persistent, low-intensity harvesting or it may have involved ephemeral bursts of more intensive harvesting. Size at sexual maturity declined from pre-Bisquit Ware to Bisquit Ware periods when harvesting pressure upon *S. pugilis* increased substantially as populations of the apparently more desirable *Lobatus raninus* became depleted [32]. The two periods are separated by around 100 years suggesting rapid evolution [6]. Variation in size at maturity among contemporary populations also correlates with observed harvesting intensities. Mature shells at Cayo Agua are the smallest, whereas those from Isla Popa, which is less than 4 km from Cayo Agua (figure 1), were the largest of all contemporary populations. Cayo Agua has tens of habitations that overlook the reef, many of which have large accumulations of consumed and discarded *S. pugilis* shells, and people can often be observed harvesting *S. pugilis* in the lagoon. The Isla Popa site has a single family dwelling close to the lagoon, and people have never been observed collecting *S. pugilis*. Additionally,

contemporary mature *S. pugilis* shells from Boca del Drago were particularly small. Shells here are frequently harvested for sale as souvenirs to tourists, which may impart a strong selection pressure for the largest most valuable conch. Mature *S. pugilis* at Carenero and STRI Point were larger than the contemporary average. Although Carenero is surrounded by relatively dense human habitation, people there tend to prefer to source their protein from farmed meats rather than shellfish. The largest contemporary shells were found at STRI Point, which has been somewhat protected from harvesting for several years owing to the frequency of scientific work carried out there and the distance from subsistence harvesters. Thus, areas that experience less harvesting pressure today have shells that reach sexual maturity at larger size implying rapid evolution.

Despite this, none of the contemporary populations reached a size at maturity similar to pre-human baseline sizes. However, this may be because relaxation of selection by humans may not be sufficient to reverse the evolutionary effects of long-term harvesting because of the relatively weaker agents of selection towards larger size [46].

(b) Alternative explanations

These results are, to the best of our knowledge, the first to provide evidence that prehistoric subsistence harvesting
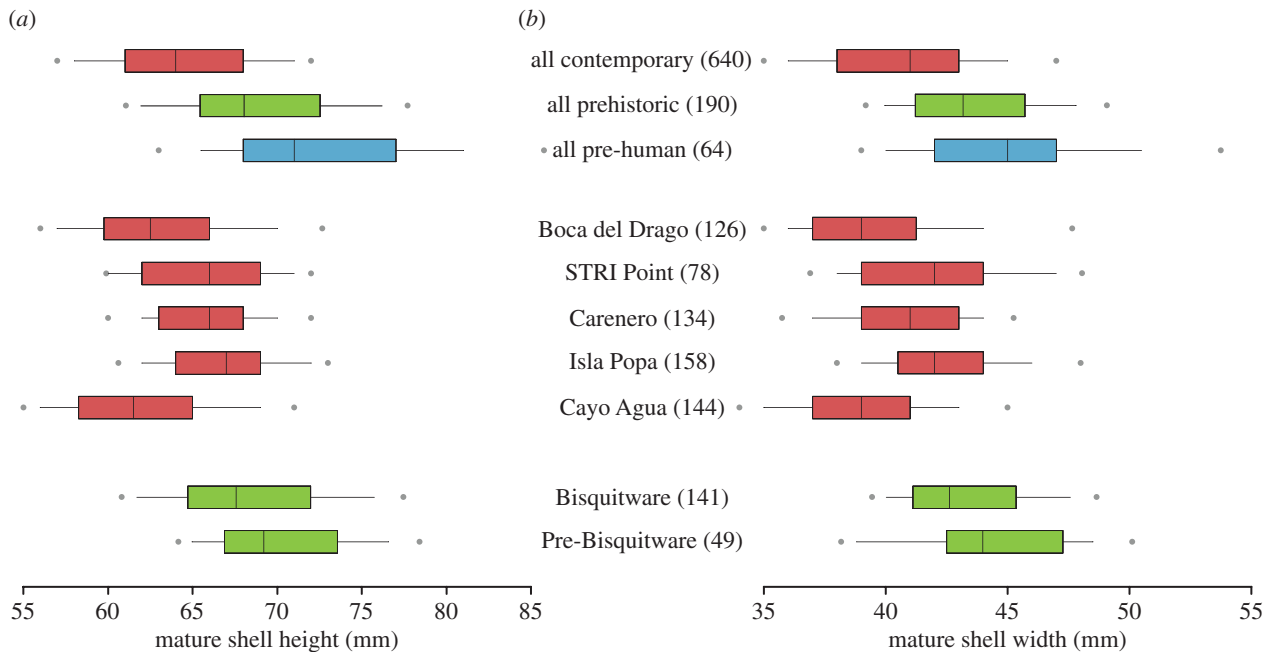
Figure 4. Box plots of (a) shell height and (b) shell width of sexually mature *Strombus pugilis* from pre-human, prehistoric and contemporary sites in Bocas del Toro. Mid bar line represents the median. Box width represents the 25% quartiles either side of the median. Bars represent the 95% quartiles. Dots indicate outliers. *N* in parentheses. (Online version in colour.)

caused size-selective evolution of a marine resource. Here, we explore alternative explanations (cf. [10]).

(i) Natural environmental change

Coastal configuration and bottom topography around the Bocas del Toro archipelago have evolved over the past 8000 years through de-glaciation and associated sea-level rise. It is unlikely that these changes drove the successive decreases in size at maturity in *S. pugilis* observed here because (i) the modern day configuration of mangrove, seagrass and fringing reef were established at some time before 7.2 ka when the archipelago flooded as observed in the establishment of coral reefs at this time [24]. (ii) Sea-level rise had slowed substantially by the Mid-Holocene and sea level was less than 3 m lower than today [47] or possibly much less [48]. As such, differences in topography and thus habitat availability for *S. pugilis* would have been essentially the same as today, especially given that (iii) topography in the archipelago is widely variable (figure 1) so flooding would have both increased and decreased the availability of habitat for *S. pugilis* depending on location. And finally (iv) all contemporary populations are smaller at reproduction than prehistoric and fossil material, which would not be expected if habitat differences were driving size given the variability among our contemporary sites.

(ii) Human-induced environmental changes

Human-induced changes include increased water temperatures which may have reduced body size of invertebrates via the temperature–size rule [49,50], and anecdotal evidence suggesting increased hypoxia which could impart limits to growth of *S. pugilis*. Neither of these, however, can adequately account for the patterns observed here because they began only in the last few decades, whereas the amount of decrease in size at maturity in *S. pugilis* between the pre-human and prehistoric material is approximately as great as that observed between prehistoric and contemporary material.

(iii) Demographic changes driven by harvesting

Because we were able to discriminate sexually mature from juvenile shells we can be sure that declines in mean size over time were not caused by a simple increase in the relative proportion of juveniles. However, within those sexually mature shells the removal of the largest shells, as predicted by optimal foraging theory, may have caused a decline in mean size at sexual maturity rather than evolution *per se*. However, this is unlikely because (i) the size of smallest mature and the largest juvenile also declined through time. (ii) The distribution of size of mature individuals did not become more positively skewed over time (figure 4). (iii) All contemporary populations, even those with low or no harvesting pressure, were smaller than prehistoric and pre-human material. (iv) Lip thickness did not decline over time (figure 3b,c). It is therefore unlikely that demographic shifts driven by harvesting caused declining size at sexual maturity.

(iv) Selection bias

Prehistoric and contemporary shells were selected by humans and therefore biased towards larger size as predicted by optimal foraging theory and the increased calorific value of larger shells [51]. Indeed, discussion with contemporary harvesters revealed *S. pugilis* is sufficiently abundant and that the largest individuals are preferentially selected for consumption. Pre-human shells, on the other hand, derive from natural death assemblages that were sampled non-randomly and thus include a much greater proportion of juveniles (electronic supplementary material, table S1). They too may have incurred selection bias towards larger individuals, but we consider this minimal given the very high proportion of very small and fragile shells collected, and certainly not as strongly biased as the archaeological and contemporary

material. Thus, selection of shells used in this study should have led to a bias towards *larger* prehistoric and contemporary material only making our results *more* robust. We assume that the strength of selection biases between prehistoric and contemporary material were similar given that the same artisanal methods are used today in their collection.

(c) Consequences and future considerations

Size-selection-driven evolutionary change can lead to reduced fitness through what has been termed 'unnatural selection' [46]. Fecundity, the quality of offspring, survival rates and other life-history attributes can be damaged, whereas competitive interactions, parasite loading and other interactions among community members may increase [3,52]. In the case of *S. pugilis*, the consequences of over 1500 years of size-selective harvesting are not easily determined and require further study. Nonetheless, we estimate that effects on yield are of considerable consequence for subsistence harvesters. People inhabiting Bocas del Toro approximately 1500–500 years ago would have obtained 37% more meat per conch than contemporary harvesters, and the earliest humans collecting *S. pugilis* from 'pristine' habitats would have received a remarkable 66% more meat per conch than contemporary harvesters.

All contemporary populations are smaller at maturity than prehistoric and pre-human populations, even where harvesting pressure is very low or non-existent. Declining size at maturity therefore likely represents a genetically based rather than phenotypic change. Models suggest that reversal of genetic evolution caused by size-selection when selective harvesting is relaxed will be more protracted and stubborn than their initial accumulation because selection driven by harvesting is stronger than the various natural agents of selection towards larger size [46]. Given this, it may be impossible to reverse the effects of over 1500 years of size-selective harvesting in *S. pugilis*. The slightly larger body sizes of *S. pugilis* in areas that experience lower intensity harvesting do, however, hint that release from harvesting pressure could reverse the evolutionary trend. The establishment of marine protected areas (MPAs), where harvesting *Strombus* is not permitted, may assist in halting or reversing size-selective evolution [46], and if there is sufficient migration or gene flow between populations inside and outside of the MPAs, *Strombus* yields may stop declining or even increase [45,53].

(d) The role of prehistoric harvesting

Despite a growing body of evidence that humans have long affected marine ecosystems, Baisre [10] argued that the role of prehistoric harvesting has been overplayed and that the majority of human-induced change in the seas occurred within the twentieth century. Baisre justifiably raised a number of important challenges that archaeological studies must overcome to effectively demonstrate the role of prehistoric harvesting on ecosystems, communities and populations. These included the often relatively poor sampling that is available to zoo archaeologists compared with ecologists, preservation biases and challenging taxonomy [54]. Baisre also highlighted the need to thoroughly test possible alternative explanations for patterns observed through time in archaeological and historical records. In our study, we reveal that significant changes in size at maturity of a staple marine resource had occurred by at least 1500 years ago. Preservation biases, cultural changes, taxonomic issues and

poor sampling can be discounted and, as we have shown, there is no evidence that environmental change, anthropogenic or not, could explain the patterns observed.

One important element generally missing from the debate provoked by Baisre [10] is that all archaeological material must originate from a time *after* humans had interacted with coastal ecosystems. Although they can give strong indications of trajectories, archaeological and historical data, by their very nature, can never reveal true baseline conditions. Terminal Pleistocene or Holocene palaeontological studies can reveal conditions before the arrival of humans and should be considered a valuable resource for historical ecologists [55–58]. As an example, if we had conducted this study without pre-human palaeontological material, then we would only be able to conclude that sometime *after* prehistoric time did significant declines in size at maturity in *S. pugilis* take place. As it turns out, the decline in size at maturity from pre-human 'pristine' baseline to prehistoric material is almost as great as the decline from prehistoric to contemporary times, greatly suggestive of persistent and pervasive evolution driven by long-term subsistence selection by humans.

6. Conclusion

(1) The fighting conch, *S. pugilis*, is naturally abundant in the Bocas del Toro region of Caribbean Panama, and the largest individuals have been preferentially selected by humans through non-intensive subsistence harvesting for at least 1500 years.

(2) Size at maturity in *S. pugilis* declined progressively and significantly over the last 7000 years in concert with this prolonged subsistence harvesting.

(3) Long-term size-selective subsistence harvesting of *S. pugilis* in Bocas del Toro has resulted in evolution to reach sexual maturity at smaller sizes, one unassailable consequence of which is that the yield of meat per conch has declined by over a third since harvesting began.

(4) Prehistoric and subsistence harvesting can be an effective agent of size-selective evolution with persistent detrimental consequences, but it can only be fully revealed with baseline data from pre-human palaeontological material.

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