Fossil dermal denticles reveal the preexploitation baseline of a Caribbean coral reef shark community

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Preexploitation shark baselines and the history of human impact on coral reef–associated shark communities in the Caribbean are poorly understood. We recovered shark dermal denticles from mid-Holocene (~7 ky ago) and modern reef sediments in Bocas del Toro, Caribbean Panama, to reconstruct an empirical shark baseline before major human impact and to quantify how much the modern shark community in the region had shifted from this historical reference point. We found that denticle accumulation rates, a proxy for shark abundance, declined by 71% since the mid-Holocene. All denticle morphotypes, which reflect shark community composition, experienced significant losses, but those morphotypes found on fast-swimming, pelagic sharks (e.g., families Carcharhinidae and Sphyrnidae) declined the most. An analysis of historical records suggested that the steepest decline in shark abundance occurred in the late 20th century, coinciding with the advent of a targeted shark fishery in Panama. Although the disproportionate loss of denticles characterizing pelagic sharks was consistent with overfishing, the large reduction in denticles characterizing demersal species with low commercial value (i.e., the nurse shark *Ginglymostoma cirratum*) indicated that other stressors could have exacerbated these declines. We demonstrate that the denticle record can reveal changes in shark communities over long ecological timescales, helping to contextualize contemporary abundances and inform shark management and ecology.

Bocas del Toro | conservation paleobiology | mid-Holocene | shark | subfossil

Historical accounts often depict remarkable numbers of sharks on Caribbean coral reefs (1–3), yet empirical evidence of past shark abundances is limited. Although declines in oceanic shark populations over the last century have been well documented (4–6), much less is known about how humans have shaped reef-associated, coastal shark communities, especially over long time periods. Sharks on many Caribbean coral reefs could have experienced earlier and more intense exposure to human stressors than their offshore counterparts, owing to their greater proximity to human populations (3, 7), the antiquity of fishing (8–10), and the widespread degradation of reef ecosystems, which preceded systematic monitoring (1, 11–13). Without baseline data to document what has been lost, it is challenging to implement effective management practices and to understand sharks' natural functions as mobile predators on reefs (14, 15).

To examine how shark abundances have changed over long ecological timescales, we used dermal denticles—the microscopic (<2 mm) tooth-like scales that cover elasmobranchs' bodies—to reconstruct shark communities on a Caribbean coral reef before major human impact. Denticles are shed naturally and accumulate in marine sediments, where they preserve as fossils (16). Denticle accumulations reflect shark abundances in low-energy reef habitats (17), and denticle morphology varies across sharks with different ecological modes, as it is coupled to denticle function (18–21) (Fig. 1). Because sharks have several orders of magnitude

more denticles than teeth, denticles are far more abundant in reef sediments, facilitating statistical analyses (17, 20, 21). As such, denticle assemblages can yield rigorous ecological information about past shark communities.

We extracted denticles from a mid-Holocene fringing reef in Bocas del Toro, Panama, that formed ~7 ka (22) (Fig. 2 and *SI Appendix*, Fig. S1), which predates the earliest evidence of human settlement in this region by several thousand years (23–26) yet represents a time when environmental conditions were similar to the modern day (27). We then compared this empirical baseline with denticle assemblages recovered from nearby modern reefs to quantify the magnitude of change between the mid-Holocene and modern time periods. To shed light on the timing and mechanisms driving shifts in shark abundance, we compiled and analyzed published archaeological, historical, ecological, and fisheries records, which offer insight into human interactions with sharks in the region during different cultural periods in Panama's history. Taken together, our findings revealed that shark communities on these reefs in western Caribbean Panama not only experienced severe declines but had been functionally restructured since the mid-Holocene.

Results

Denticle accumulation rates (denticles accumulating per kilogram sediment per year)—a proxy for shark abundance—were

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Significance

How abundant were sharks on Caribbean coral reefs before human impact? To explore this question, we recovered fossilized shark dermal denticles (scales) from a ~7,000-y-old reef in western Caribbean Panama and compared them with denticles found on modern reefs in the same area. Our data suggest that sharks were over three times more numerous before humans began using marine resources in the area and that shark communities were compositionally different in the past, containing a higher proportion of fast-swimming, pelagic sharks. This reconstruction of preexploitation shark communities using fossil denticle assemblages demonstrates their potential to help contextualize recent declines in shark abundance, examine the ecological consequences of those declines, and guide shark management.

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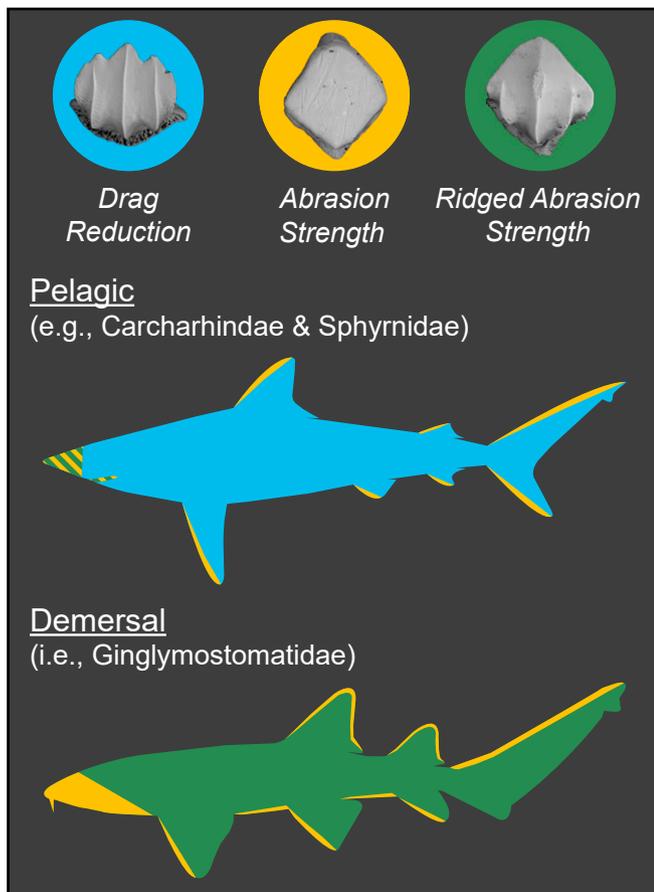
Fig. 1. Drag reduction, abrasion strength, and ridged abrasion strength denticles (*Inset*, scanning electron microscope images) are the three most common functional morphotypes found on reef-associa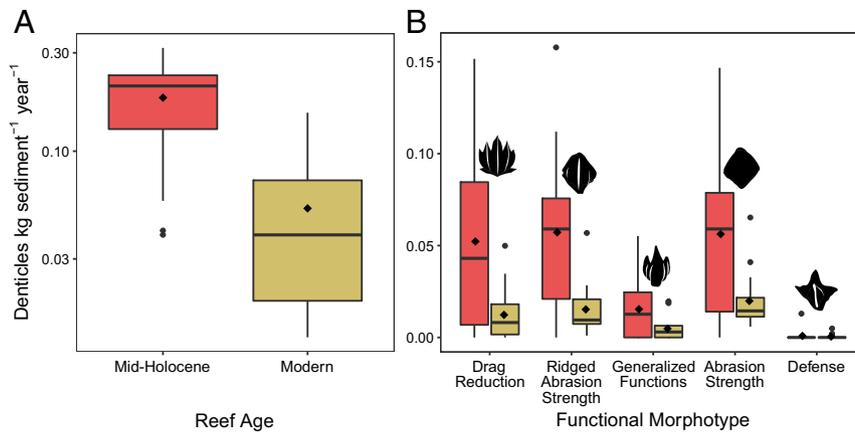ted sharks. Generalized functions and defense denticles (not shown) are less common. Fast-swimming, pelagic taxa, such as the families Carcharhinidae and Sphyrnidae (defined here as including both near-shore and oceanic species, following ref. 21), are characterized by hydrodynamic drag reduction denticles with riblets that improve swimming performance (often covering >80 to 90% of their bodies), although abrasion strength and ridged abrasion strength denticles are found along the leading edges of the fins and around the snout. The cross-hatching denotes a combination of morphotypes. Demersal taxa, such as the family Ginglymostomatidae, possess both ridged abrasion strength and abrasion strength denticles (often covering ~60 and 40% of their bodies, respectively), which provide protection during contact with sandy, hard, or coral-rich substrates. The dominance of different functional morphotypes on pelagic and demersal sharks enables changes in their relative abundances to be ascertained from the denticle record. Squamation patterns (lateral view) are portrayed from museum specimens (17, 20, 21), with a focus on species documented in Caribbean Panama.

To evaluate shifts in shark community composition over time, the denticles were classified into five previously recognized morphotypes (18–21), which have different functions and are associated with different ecological groups of sharks (Fig. 1). The accumulation rate of all five denticle functional morphotypes declined over time (Fig. 3B), mirroring the pattern in total denticle accumulation. Drag reduction denticles underwent the largest decline (76%; $\chi^2 = 7.83$, $P = 0.0051$), followed by ridged abrasion strength (73%; $\chi^2 = 6.60$, $P = 0.010$), generalized functions (69%; $\chi^2 = 7.23$, $P = 0.0072$), abrasion strength (65%; $\chi^2 = 7.36$, $P = 0.0067$), and defense denticles (42%; $\chi^2 = 4.15$, $P = 0.042$). Although the declines in drag reduction, abrasion strength, and ridged abrasion strength denticles differed by only 11%, together these shifts yielded a 45% decrease in the ratio of pelagic to demersal denticle accumulation rates between the mid-Holocene and modern time periods. Thus, despite these sweeping declines, the marginally greater decrease in the accumulation of drag reduction denticles relative to abrasion
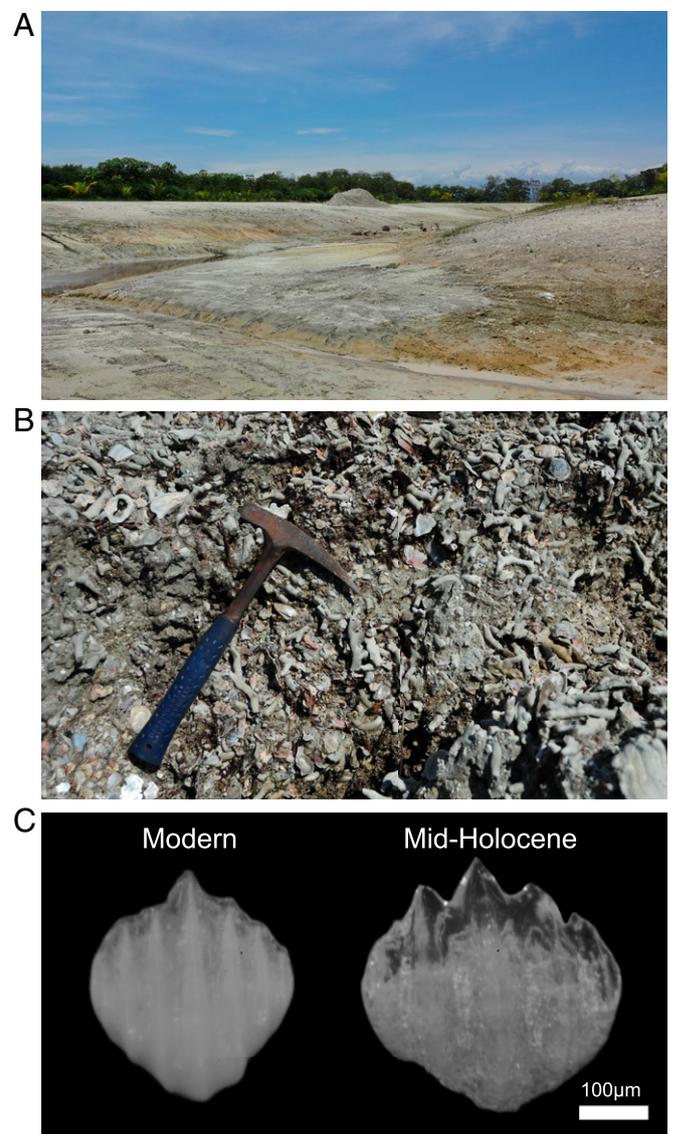
Fig. 2. Mid-Holocene coral reef in Almirante Bay, Bocas del Toro, Panama. (*A*) Samples were collected from a ~50 ha exposed area of this reef. (*B*) In situ and in life position branching coral framework and sediments were bulk sampled to access the denticle record. (*C*) Denticles recovered from the mid-Holocene and modern reefs were well preserved.

3.4 times higher on the mid-Holocene reef ($n = 15$ sediment samples, $n = 183$ denticles, and 0.18 ± 0.090 [mean $\pm$ SD]) than on the modern reefs ($n = 16$ sediment samples, $n = 389$ denticles, and 0.053 ± 0.042), representing a 71% decline (59 to 79% decline with jackknife sampling) in mean denticle accumulation between the two time periods ($\chi^2 = 4.68$, $P = 0.030$; Fig. 3A). This significant difference largely persisted when we accounted for uncertainty in the Uranium–Thorium dates used to establish the sample ages and calculate denticle accumulation rates (*SI Appendix*, Tables S1 and S2). Denticle accumulation also varied between sites within each time period, with a 5.4-fold difference observed across the modern reef means and a 5.6-fold difference observed across the mid-Holocene reef means ($\chi^2 = 33.88$, $P < 0.001$; *SI Appendix*, Figs. S2–S4).

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Fig. 3. Change in denticle accumulation rates between the mid-Holocene (red) and modern (gold) time periods. (*A*) The mean denticle accumulation rate declined by 71% between the two time periods (*P* = 0.030). (*B*) The mean accumulation rate of each morphotype also declined over time, ranging from a 76% decline in drag reduction denticles to a 42% decline in defense denticles (*P* < 0.05). Morphotypes are ordered from left to right by the amount of decline. Mid-Holocene and modern accumulation rates were calculated from 15 sediment samples (*n* = 183 denticles) and 16 sediment samples (*n* = 389 denticles), respectively. Each boxplot shows the median (dark bar), mean (diamond), and interquartile range (box), and outliers are displayed as points. The vertical axis is $\log_{10}$ transformed in *A* but not in *B* because of the presence of zeros. Denticle illustrations credit: Ashley Diedenhofen (artist).

strength and ridged abrasion strength denticles suggested a proportionally larger reduction in denticles characteristic of fast-swimming, pelagic sharks (75% decline)—defined here as including both near-shore and oceanic species—as compared to denticles characteristic of demersal sharks (69% decline).

Differences in the absolute magnitude of decline across each denticle morphotype, although ostensibly subtle, were enough to alter the functional composition of denticle assemblages over time. Drag reduction, abrasion strength, and ridged abrasion strength morphotypes dominated both the mid-Holocene and modern denticle assemblages (>90%), yet the assemblage composition shifted significantly between the two time periods (permutational multivariate analysis of variance [PERMANOVA] *F* = 3.24, *P* = 0.024; Fig. 4*A*), even after accounting for differences across sites (PERMANOVA *F* = 2.34, *P* = 0.006; *SI Appendix,* Fig. S5). Abrasion strength denticles were proportionally more abundant and drag reduction denticles were proportionally less abundant in the modern samples relative to the mid-Holocene samples (Fig. 4*B*). In contrast, the proportion of ridged abrasion strength

denticles remained similar over time (Fig. 4*B*). Furthermore, the relative abundances of abrasion strength and ridged abrasion strength denticles shed from pelagic sharks, which cover only a small proportion of their bodies (Fig. 1), were consistently low in both time periods (*SI Appendix,* Fig. S6). Consequently, although there was overlap in the functional morphospace that encompassed the modern and historical ranges of variability (Fig. 4*A*), the modern denticle assemblage reflected the persistence of demersal sharks.

Because denticle accumulation is driven by shark abundance (17), the higher denticle abundances discovered on the mid-Holocene reef indicated that sharks might have been over three times more numerous in the region historically. Alternatively, this pattern could have resulted from the presence of larger sharks, which possess more denticles and, accordingly, might contribute more to the denticle record. To investigate this counter hypothesis, we compared patterns of denticle size over time, as denticle crowns scale allometrically with shark length within species (28). The size–frequency distribution of all denticles combined was not
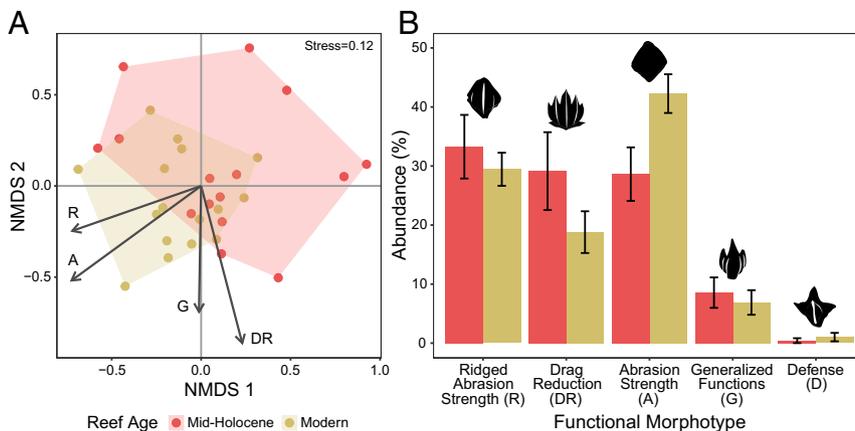

Fig. 4. The mid-Holocene (red) denticle assemblage (*n* = 183) was compositionally different from the modern (gold) assemblage (*n* = 389). (*A*) Nonmetric multidimensional scaling ordination depicts the assemblages in functional morphospace, with each point representing a sediment sample within the shaded convex hull. Although there was overlap between the mid-Holocene and modern assemblages, the centroid of the modern assemblage shifted (*P* = 0.024), corresponding with a higher proportion of denticles characteristic of demersal sharks. (*B*) The relative abundances of ridged abrasion strength, drag reduction, and abrasion strength denticles were similar in the mid-Holocene assemblage. In contrast, drag reduction denticles were proportionally less common, and abrasion strength denticles were proportionally more common in the modern assemblage. Error bars indicate the SE around each mean.

significantly different between the mid-Holocene and modern time periods (Kolmogorov–Smirnov $D = 0.11$, $P = 0.13$), although the median denticle crown size was marginally larger in the modern samples (Wilcoxon $W = 29500$, $P = 0.021$). This was likely due to the higher representation of abrasion strength and ridged abrasion strength denticles, which are typically larger than the other morphotypes. When disaggregated by ecological mode, median denticle crown size and size–frequency distributions were not significantly different over time for both demersal (Wilcoxon $W = 11889$, $P = 0.44$; Kolmogorov–Smirnov $D = 0.12$, $P = 0.25$) and pelagic (Wilcoxon $W = 2481$, $P = 0.17$; Kolmogorov–Smirnov $D = 0.15$, $P = 0.41$) sharks (*SI Appendix*, Fig. S7 and Table S3), suggesting that, in aggregate, shark sizes remained similar between the two time periods. However, because the allometric relationship between denticle size and shark length varies among species (28), changes in individual species' size structures could have been obscured by the functional-level resolution of the denticle classifications used here.

To determine whether taphonomic processes might have affected our interpretation of the denticle record, we examined patterns of denticle weathering and relationships between denticle abundance and sediment characteristics. The denticles recovered were, on the whole, well preserved (Fig. 2*C*), and the assemblages reinforced previous findings that macro- and microskeletal remains

on these reefs represent time-averaged, autochthonous accumulations of foraminifera (29), fish (30), mollusks (22, 31), and corals (27) in three notable ways. First, denticle abundances were not correlated with reef accretion rates (Spearman $r = 0.52$, $P = 0.19$), the weight of coral in each sample (Spearman $r = -0.27$, $P = 0.14$), or sorting estimates (Spearman $r = -0.05$, $P = 0.79$), suggesting that denticle deposition was independent from reef growth and sediment production and that denticles had not been preferentially swept away by water movement. Second, the denticle assemblages were dominated by functional morphotypes characteristic of species in the families Ginglymostomatidae, Carcharhinidae, and Sphyrnidae (20), consistent with the shark communities typically observed on Caribbean reefs (32). Third, median denticle weathering scores were similar across time periods (Wilcoxon $W = 38391$, $P = 0.59$; *SI Appendix*, Fig. S8*A*) and sites (Kruskal–Wallis $H = 3.88$, $df = 7$, $P = 0.79$; *SI Appendix*, Figs. S8*B* and S9), suggesting that the mid-Holocene assemblage had not undergone greater taphonomic alteration than its modern counterpart. There was also no correlation between weathering scores and denticle abundances (Spearman $r = 0.08$, $P = 0.65$; *SI Appendix*, Fig. S10), implying no selective dissolution or winnowing. Drag reduction denticles were more weathered than the other morphotypes (Kruskal–Wallis $H = 95.28$, $df = 5$, $P < 0.001$, Dunn's test $P < 0.05$;
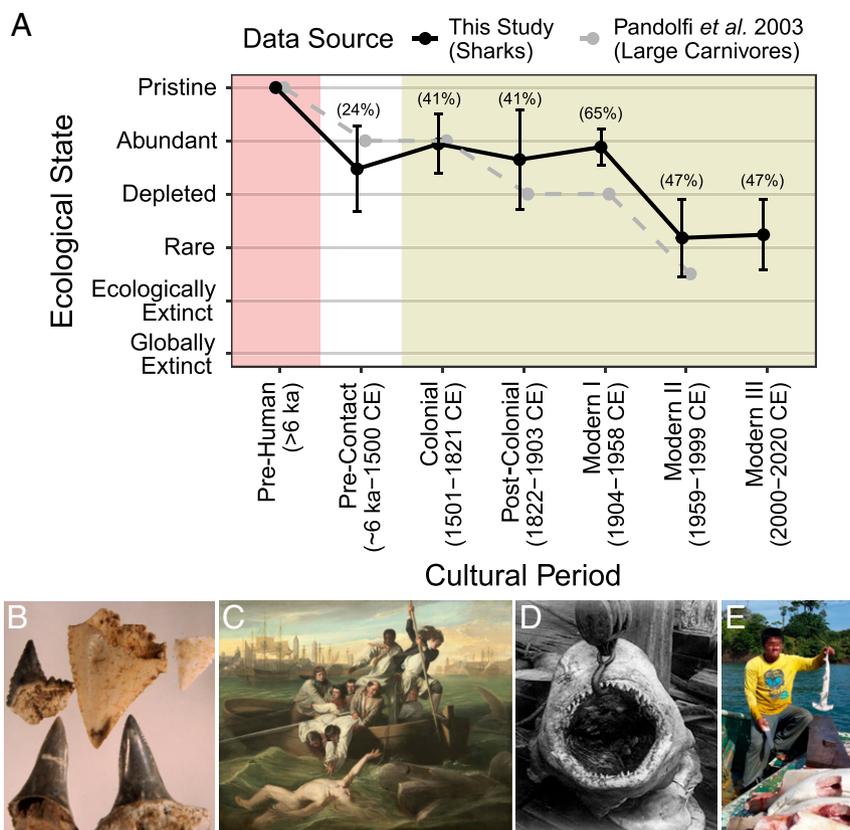
Fig. 5. Historical ecology of sharks in Caribbean Panama. (*A*) The ecological state of sharks was inferred from 91 published records and revealed an apparent decline in shark abundance since humans arrived in the region. The steepest decline occurred after the mid-20th century when sharks became described as rare. This pattern closely tracks an assessment of all large marine carnivores in the region using the same evaluation criteria (gray dotted line) (12). The points and error bars show the mean and SD of ecological state scores across respondents ($n = 17$), and the percentages indicate the prevalence of self-reported "high confidence" responses (44% across all cultural periods). The shading indicates the maximum time span of the modern (gold) and mid-Holocene (red) denticle record (the mid-Holocene record extends beyond the lower limit of the horizontal axis). Cultural periods are defined in *SI Appendix*, Table S6, and the ecological state of sharks in the prehuman cultural period was assigned to be pristine (following ref. 12). Human interactions with sharks are also depicted in imagery from across the Caribbean: shark teeth recovered from a midden in the settlement at Black Creek, Costa Rica (4000 to 2500 B.P.) (*B*); shark attack rescue in Havana, Cuba (1778 CE) (*C*); shark caught in the Panama Canal Zone (1910 CE) (*D*); and shark fishing in Bocas del Toro, Panama (2015 CE) (*E*). Images credits: Norberto Francisco Baldi Salas (photographer)/National Gallery of Art, Washington/John Singleton Copley/Library of Congress, Prints & Photographs Division, LC-USZ62-98280.

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SI Appendix, Fig. S8C), although this difference was consistent between time periods (*SI Appendix*, Fig. S8D). Therefore, selective preservation or sorting likely did not affect the observed patterns of denticle abundance or assemblage composition.

To independently reconstruct the ecological history of sharks in the region and constrain when shark abundance declined between the mid-Holocene and modern time periods represented by the time-averaged denticle assemblages, we analyzed published archaeological, historical, ecological, and fisheries data (*SI Appendix*, Tables S4 and S5). These records (*n* = 91) were divided into seven cultural periods in Caribbean Panama's history (*SI Appendix*, Table S6) and were blindly reviewed (*n* = 17 reviewers) to assign a semiquantitative ecological state to each cultural period based on perceived shark abundance (*SI Appendix*, Table S7). Shifts in the ecological state of sharks in Caribbean Panama over the last several millennia corroborated the declines in denticle accumulation rates that we report here. Furthermore, these records suggested that the most precipitous decline occurred in the late 20th century, when perceived shark abundance dropped from abundant to rare (Fig. 5 and *SI Appendix*, Fig. S11). The ecological state of sharks subsequently remained rare throughout the most recent cultural period.

Discussion

Caribbean coral reefs and their associated shark communities suffer from the shifting baseline syndrome, as substantial human impacts were manifest long before monitoring began (1, 8, 13, 22, 31, 33–38). Reef sharks have been depleted in many regions (6, 39) including the Caribbean (3), yet we do not know what shark carrying capacities were on Caribbean reefs before people began fishing and altering the landscape, thus hindering efforts to set management targets informed by local expected conditions. It is also unclear whether shark communities were compositionally different in the past and how any structural changes might have affected their ecological functions on reefs (15). Our approach, which leverages shark dermal denticles preserved in mid-Holocene and modern reef sediments, helps resolve this issue. As a first application, we used the denticle record here to gain insight into the state of shark communities before harvesting in one area of western Caribbean Panama.

We found that the overall denticle accumulation rate decreased by 71% since the mid-Holocene on reefs in Bocas del Toro, suggesting that sharks were over three times more abundant before humans began using marine resources in the region. All denticle functional morphotypes declined over time, indicating a loss of sharks with different ecological modes. However, the accumulation rate of denticles found on fast-swimming, pelagic taxa, such as near-shore and oceanic species in the families Carcharhinidae and Sphyrnidae (i.e., drag reduction denticles; Fig. 1), declined more than those characterizing demersal taxa, such as the nurse shark *Ginglymostoma cirratum* (i.e., ridged abrasion strength and abrasion strength denticles). The high representation of demersal sharks in the modern denticle assemblage mirrors survey data, which show that the shark community today in Bocas del Toro is dominated by nurse sharks (40)—a finding which extends to many Caribbean reefs (3). Yet, by revealing that nurse sharks were relatively less common in the past, the denticle record suggests that their current dominance likely does not reflect the historical state of shark communities in the area.

The 71% decline in denticle accumulation rates between the mid-Holocene and modern time periods echoes postindustrial shark declines estimated using fishery-dependent and -independent data (e.g., refs. 4–6 and 41–43) and space-for-time substitutions, which rely on surveys in protected areas to infer unfished shark biomass (e.g., refs. 44–47). For example, longline data from the Gulf of Mexico showed declines of 45 to 99% in oceanic sharks between the 1950s and 1990s (5) (although see ref. 48 for criticism), and reef shark densities across the central-western

Pacific Ocean have declined by more than 90% from simulated baselines (46). Likewise, a 71% decline in abundance since 1970 was reported across 18 oceanic shark and ray species globally using the Living Planet Index, including a 46% decline in the Atlantic Ocean (43).

Although this congruence between methods builds confidence in the denticle record, time series data for sharks—particularly those inhabiting coastal habitats such as coral reefs—are temporally and geographically limited, and prehuman baselines are largely unknown (6, 7). In some instances, recent estimates of decline could easily underestimate the full magnitude of change from preexploitation baselines because significant losses could have occurred prior to the reference points used (e.g., ref. 49), given some species' vulnerability to even mild artisanal fishing pressure (3, 50, 51). In other instances, such as in Bocas del Toro where this study was conducted, no long-term data exist as shark surveys have only recently been implemented (40). Denticle-based reconstructions of reef shark communities can complement these ecological and fishery-based approaches by 1) documenting historical changes in shark abundance where data are sparse and 2) producing empirical baselines that can predate human impact and characterize natural variability. Our study illustrates this method's potential to access millennial-scale records of shark communities in other regions with different human histories, contemporary human impact, and oceanographic settings by sampling exposed fossil reefs and reef cores.

Our analysis of the perceived ecological state of sharks in Caribbean Panama based on historical records mirrored the decline in denticle accumulation and indicated that it might have occurred relatively recently. Archaeological evidence shows that shark harvesting began as early as 4000 to 2500 B.P. (25). Despite this prehistorical fishing, European explorers described sharks as numerous, and anecdotes of seas teeming with sharks continued into the early 20th century, contradicting their rarity in the region today (*SI Appendix*, Table S4). The absence of sharks was most apparent in these historical sources after the mid-20th century, corroborating trajectories of change reconstructed for all large marine carnivores in the region, including sharks, using a similar approach (12) (Fig. 5). Marine carnivores in aggregate, however, experienced earlier and larger declines, which was anticipated given that this group included the heavily harvested loggerhead and hawksbill sea turtles (38) and the now extinct Caribbean monk seal (33). If taken at face value, these findings suggest that although sharks have been harvested in the region for millennia, intensive harvesting did not occur or did not have a significant impact on sharks until after more valuable resources had been depleted.

The pattern, timing, and rate of these declines implicate human activities. Overfishing, which is recognized as the primary threat to shark populations globally (6, 8, 52), appears to be the most parsimonious explanation for the pronounced loss of pelagic sharks observed in this study. In Caribbean Panama, sharks first became described as rare in the cultural period spanning 1959 to 1999, coinciding with, although potentially preceding, the advent of a targeted shark fishery in the 1980s (53). Today, sharks continue to be caught and sold along Panama's Caribbean coast (54). Over a 13-mo-long fisheries survey in the city of Colón, all but one shark landed were species with drag reduction denticles (*SI Appendix*, Fig. S12), indicating that modern day Panamanian fisheries selectively catch pelagic sharks. Similar selectivity is apparent in historical accounts (55) and prehistorical records from Caribbean Panama, with teeth and vertebrae belonging to sharks in the families Carcharhinidae and Sphyrnidae, but not Ginglymostomatidae, found in middens (25, 26). Fishing mortality can therefore help explain the large selective loss of sharks with drag reduction denticles since the mid-Holocene in Bocas del Toro. However, we also observed a substantial reduction in the accumulation of abrasion strength and ridged abrasion strength

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denticles, which are primarily found on the nurse shark *G. cirratum* in our study region. Nurse sharks are rarely landed (25, 26, 53) (*SI Appendix*, Fig. S12), exhibit low at-vessel mortality (56), and have little commercial value (57, 58), suggesting that fishing alone cannot explain their decline over time.

The large reduction in denticles belonging to shark taxa that are infrequently harvested highlights the additional contribution of indirect human pressures to shark declines in Caribbean Panama. The Bocas del Toro region has experienced major environmental and ecological changes since the beginning of the 20th century, stemming from agriculture, land clearing, and coastal development (59). Benthic habitats across the archipelago have undergone dramatic transformations, including shifts in the dominant reef builders as well as decreased coral cover, due to deteriorating water quality, disease, bleaching, deep water hypoxia, and hydrological change (22, 27, 35, 37, 60)—a pattern of degradation documented across the greater Caribbean (13, 61). These anthropogenic disturbances, in turn, could have degraded habitat for both sharks and their prey, in addition to lowering prey nutritional quality (62). This habitat loss was compounded by the intensification of fish and invertebrate harvesting in the 1970s (53), which likely reduced available prey for all sharks. In addition to human impacts, oceanographic variability (46) or natural population fluctuations (63) could have contributed to the changes observed in the denticle record. Continuous time series of denticle accumulation rates could refine the timing and pattern of shark decline between the two end members presented in this study and, when combined with coeval abiotic and biotic proxies, could help further disentangle the relative importance of these human and nonhuman drivers.

The size–frequency distribution of denticle crowns, which scale allometrically with shark length within species, was similar between the mid-Holocene and modern assemblages, suggesting that the observed decline in denticle accumulation did not result purely from changes in shark body size. This lack of change in denticle size structure deviates from well-substantiated declines in the mean length of exploited shark populations in the Caribbean and other regions (5, 42, 49, 50) but should not be construed here as evidence that size shifts did not occur in Bocas del Toro. There are at least two reasons why changes in shark population size structure might not have been detected in the denticle assemblages sampled in this study. First, lagoonal areas within Bocas del Toro provide habitat for multiple species of juvenile sharks, as documented by the denticle record (*SI Appendix*, Fig. S7A) and modern observations (64). As such, this record might provide a truncated view of the shark community size structure. Such a view is sufficient to measure shifts in relative abundance over time, but it would not provide adequate insight into shifts in the size structure of the whole shark community (e.g., if larger pelagic sharks that spent more time offshore than in these shallow reef habitats were preferentially culled, their loss would not be recorded at these sites). Second, at present, we were unable to resolve these patterns at the species level, which would be needed to measure shifts in population size structure. Although we cannot conclusively reject the possibility that some species became smaller over time, a strong and systematic shift in shark length would likely be reflected in denticle size at the functional level due to the low species selectivity of fishing in the region. The absence of such a pattern within denticle morphotypes suggests that demographic changes were not a dominant mechanism driving their decline over time. Further work to increase the taxonomic resolution of denticle classifications and establish the allometric scaling relationship for each shark species in the region, in addition to conducting work in locations with only adult shark habitat, could help unlock the potential to use denticle assemblages to study the size structure of shark populations.

The decline in reef shark abundance, reflected by denticle assemblages in Bocas del Toro, parallels global losses across marine megafauna (65) and apex consumers (66), yet the ecological consequences are still being unraveled. The denticle record can contribute historical perspective to how shark declines might have affected ecosystem processes and can help test predictions rooted in ecological theory. Theory predicts that the threefold loss of meso and apex predators likely altered food web structure and stability through a decrease in predation and scavenging and a possible loss of functional redundancy (15, 67–69). The removal of predators might have also diminished nonconsumptive effects on prey behavior and foraging (70), nutrient cycling (15, 66), and cross-ecosystem linkages (71). However, it is less clear if these declines drove cascading effects or if such effects were dampened by harvest pressure exerted on both shark and teleost predators. Likewise, if we assume consistency in sharks' ecological functions through time, theory predicts that the shifts we documented in shark community composition likely altered predation pressure, given the trophic differences between pelagic and demersal sharks. Nurse sharks are sedentary, have one of the slowest reported metabolisms of any shark species, and primarily consume benthic invertebrates and small teleost fish (58, 72). They, therefore, occupy a lower trophic position than many adults in the families Carcharhinidae and Sphyrnidae (15, 69) and likely would have a smaller impact on reef food webs because of their reduced energy requirements (72). Nonetheless, additional evidence would be needed to demonstrate how lower trophic guilds responded to the heightened dominance of this demersal mesopredator over time. These predictions could be tested by analyzing the skeletal remains of shark prey items. Fish teeth, otoliths, and mollusk shells are preserved alongside denticles in the fossil record (22, 27, 30, 34) and could reconstruct components of sharks' trophic interactions through time. If paired with contemporaneous oceanographic (e.g., $\delta^{18}O$) and habitat (e.g., coral abundance) proxies, these data could help reveal whether historical shark declines precipitated a trophic cascade or, alternatively, whether lower trophic guilds were shaped by bottom-up forces (see refs. 8, 15, and 73). Additionally, nitrogen isotopes (74) could document temporal changes in predator and prey trophic levels and quantify trophic overlap between mesopredatory sharks and teleost predators, which is known to buffer against trophic cascades (15). The historical context derived from these analyses could augment the contemporary evidence used to assess sharks' trophic roles on reefs.

Denticle-informed shark baselines can help guide ecosystem management by reshaping perceptions of what a natural shark community in Caribbean Panama, or elsewhere, looked like before human disturbance. Shark abundances on remote, protected islands have often been used to estimate preexploitation baselines, although these spatial reference points are only available in a limited number of regions and arguably not in the Caribbean (2, 8). The denticle accumulation rates on the mid-Holocene reef in Panama were around an order of magnitude lower than modern accumulation rates found on a remote, unfished Pacific atoll (17). This disparity suggests that preexploitation shark abundance on this inshore Caribbean reef was much lower than the high abundances observed on many uninhabited, oceanic islands today and supports the prediction that there could be important bottom-up forcing that regulates shark populations and contributes to natural geographic heterogeneity in shark carrying capacities (46, 47). Therefore, making generalizations using baselines derived from regions or time periods with dissimilar environments or ecological histories could yield impractical restoration targets for sites that historically supported different shark densities. Rather, comparing prehuman and modern shark communities can be insightful for evaluating site-specific management strategies and goals, even if these historical abundances cannot be restored.

The denticle record has several limitations that must be considered when using it to reconstruct shark communities. First, variation in denticle morphology across a shark's body currently precludes the identification of isolated denticles beyond the family level (18, 20, 21). Nonetheless, interpreting the denticle record at the level of functional morphotype and broadly relating those morphotypes to shark taxa, as we have done here, can provide an ecologically meaningful assessment of higher-level taxonomic and functional shifts in shark communities. Second, because the bulk samples in this study represent time-averaged accumulations, the modern denticle assemblages were estimated to encompass the last ~50 to 360 y, which could dampen the extent of decline observed in denticle accumulation over time. One advantage of this time averaging, however, is that the denticle assemblages capture some of the natural fine-scale temporal variability across the modern and mid-Holocene sites, representing an average shark community by integrating over many points in time. These samples also incorporate natural spatial variability in shark abundance, as habitats interdigitate over decades to centuries. Third, we sampled five localities across a single mid-Holocene reef tract as it is, at present, the only known exposed reef of this age in Caribbean Panama. This fossil reef offers unique insight into preexploitation shark baselines in the local region, although the rarity of such sites hinders large-scale spatial replication. Nonetheless, variation in denticle accumulation across the sites we sampled was similar between time periods and comparable to contemporary shark surveys in Bocas del Toro (40). As additional Holocene sites are detected, our study provides a framework for comparing denticle assemblages over time and across locations to describe geographic patterns of shark decline. Lastly, variation in denticle densities (19), shedding rates, and taphonomic biases could confound estimates of absolute shark abundance derived from denticle accumulation rates (*SI Appendix, SI Materials and Methods*). In this study, we found no evidence to suggest that the trends in denticle accumulation were caused by taphonomic processes, such as size sorting, selective dissolution, or preservation, or by reef accretion rates. However, denticle shedding rates likely vary across sharks with different ecological modes and denticle quantities, decoupling true abundances from denticle accumulation. Instead, reconstructing relative shark abundances, as we have done here, provides a conservative metric of shark community shifts.

Conclusions

Our evidence adds to the growing body of paleoecological research investigating the effects of overharvesting (31, 34, 36) and habitat change (22, 27, 35, 37) on reef-associated coral, mollusk, sponge, and teleost fish communities in Bocas del Toro, Panama. In this study, we quantify shark abundance before major human impact using the fossil record. Our data show that reef-associated sharks in this area of the Caribbean have been severely depleted by both long-term harvesting, which accelerated in the second half of the 20th century, as well as by habitat degradation, which began even earlier. We also demonstrate that denticles are abundant and well preserved in reef sediments, providing a record of reef shark abundance and functional diversity over millennia. This first application establishes denticle assemblages as a promising approach for answering long-standing questions about the baseline conditions of shark communities, the drivers of shark declines over long ecological timescales, and their ultimate ecological and conservation implications.

Materials and Methods

General Setting. Sampling was conducted in Almirante Bay, Bocas del Toro, Caribbean Panama (centered at 9.2993° N and 82.2312° W), a sheltered, semienclosed lagoonal system that sits outside the hurricane belt. Over 30 shark species have been observed in, or their ranges cover, the Bocas del Toro archipelago (32), and Almirante Bay could provide a nursery habitat for small coastal shark species (64). Surveys conducted in the bay since 2016 have reported just seven shark species, with the nurse shark *G. cirratum* accounting for most of the sightings (40). Although contemporary shark abundance varies spatially across the archipelago, reported abundances were similarly low near all reefs sampled in this study, including those adjacent to the fossil site (40).

Mid-Holocene Reef. The mid-Holocene reef tract (Fig. 2) occupies a ~50-ha area on the leeward side of Isla Colón, buffered from waves and currents by the Plio-Pleistocene sediments that comprise the island (75). The reef is located alongside the modern coastline and accreted ~7 ka under similar oceanographic and climatic conditions to the reefs in Almirante Bay today (22, 27, 29, 76). Foraminiferal assemblages characterize this mid-Holocene site as a patch reef with seagrass facies and molluscan muds, similar to modern habitats within the bay (29). This congruence suggests that the mid-Holocene reef should be reasonably representative of shark communities found in similar habitats today. The reef matrix was found to be well preserved, consisting of corals in life position without indication of physical disturbance and unsorted carbonate muds and silts containing autochthonous biogenic material accumulating within this branching coral framework (22, 27, 30). Human settlements are not recorded on Panama's Caribbean coast until after ~6 ka (23, 24), and the earliest evidence in the Bocas del Toro region dates to ~4 ka (25, 26). Being the only known exposed mid-Holocene reef in this region, this site provides a unique, albeit rare, window into the shark community inhabiting a Caribbean reef before major human impact at a time when the environment was similar to the modern day.

Sample Collection. To compare the denticle-defined shark baseline with the modern assemblage, we collected replicate ~9-kg bulk samples of fine surface sediments and reef framework from five localities on the mid-Holocene reef (n = 15 samples; n = 3 replicates per locality) and three modern reefs in Almirante Bay (n = 16 samples; n = 4 to 6 replicates per site) (*SI Appendix*, Fig. S1) in 2014. At the mid-Holocene reef site, samples were collected from the uppermost section of the reef facies, covering a stratigraphic depth of ~10 cm. On the modern reefs, samples were excavated from the uppermost <10 cm at water depths of 2 to 4 m, which overlap with the estimated paleodepths at the mid-Holocene site (27) and constitute a similar environmental setting (22, 29). Sampling was constrained to low-energy habitats with branching coral framework, which restricts vertical mixing and reworking (27, 30, 34), to reduce the influence of taphonomic processes and facilitate comparisons over time.

Quantifying the Denticle Assemblages. Sediment samples were sieved and processed to isolate the denticles. The 106 to 250 μm, 250 to 500 μm, and 500 μm to 2 mm size fractions were treated with 10% acetic acid to eliminate the calcium carbonate components and then with 5% hydrogen peroxide to remove excess organic material (20, 77). Denticles were picked from the residue and counted, and denticles missing more than half of their crown were excluded to avoid double counting. The total denticle count per sample was divided by the dry weight of the sediment fractions to calculate denticle abundance.

To determine assemblage composition, denticles were measured and visually classified using a reference collection into five recognized functional morphotypes: drag reduction, ridged abrasion strength, abrasion strength, generalized functions, and defense (18–21). These classifications were verified with a multinomial logistic regression model trained on the reference collection (20), which was used to predict the morphotype of each denticle (*SI Appendix*, Tables S8–S10 and *SI Appendix, SI Materials and Methods*).

Temporal Context and Accumulation Rates. Uranium–Thorium and calibrated radiocarbon dating of coral pieces were used to estimate the age and amount of time encompassed by the sediment samples and to calculate reef accretion rates (*SI Appendix*, Table S1 and *SI Appendix, SI Materials and Methods*). Dates from the mid-Holocene site corroborated previous work, demonstrating that this reef accreted over a period of at least 1,500 y from 7.2 to 5.7 ka (22, 27), whereas the modern samples spanned the last ~50 to 360 y (mean = 159 y; expressed relative to the collection year). Reef accretion rates were estimated using linear interpolation between dates after removing age reversals (*SI Appendix*, Fig. S13). Denticle abundances were corrected by reef accretion rates at each site to calculate absolute denticle accumulation rates. The 2σ errors on each date were incorporated into a sensitivity analysis to determine how much this analytical uncertainty affected our interpretation of change in denticle accumulation rates (*SI Appendix*, Table S2).

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Analyzing Change over Time in Denticle Assemblages. Generalized linear mixed models using a Gamma error distribution and site as a random effect were used to test for differences in denticle accumulation rates over time, while accounting for variation across sites. A negative binomial error distribution was used to test for differences in the counts of each functional morphotype, offset by kilograms sediment per year, over time. Models were compared using small-sample corrected Akaike information criterion, and nested likelihood ratio tests were used to obtain *P* values. Models were implemented using the R package *glmmTMB*, and the assumptions were checked using the package *DHARMa*. Jackknife sampling was used to estimate bias, given natural spatial variation. Spearman rank correlations were used to explore relationships between denticle abundance, weathering, and sediment characteristics (sorting was calculated using the Folk and Ward method in the package *G2Sd*). Differences in the shapes and medians of the denticle size–frequency distributions were evaluated with Kolmogorov–Smirnov and Wilcoxon tests.

To assess changes in denticle assemblage composition, denticle counts were square root transformed, and Bray–Curtis dissimilarities were ordinated using nonmetric multidimensional scaling. The function *envfit* was applied to overlay biplot vectors and identify the morphotypes that contributed to the ordination patterns. We used PERMANOVA to test for differences in dissimilarities over time, while controlling for site differences using the function *adonis2* in the package *vegan*. Unidentified denticles were removed from the analyses. Changes were reported in terms of the relative abundance of each morphotype, which was positively correlated with the absolute count (*SI Appendix*, Fig. S14). All analyses were performed in R (78).

Weathering Analysis. Each denticle was assigned a weathering score, which ranged from zero (pristine) to three (poor preservation) and was based on visual inspection of the crown, peaks, and base (criteria are described in ref. 17). Scores were compared across time periods, sites, and functional morphotypes to assess denticle preservation.

Exploring Changes in the Perceived Ecological State of Sharks. Published archaeological studies (*n* = 15), anecdotes and ethnographic accounts (*n* = 47), ecological surveys (*n* = 12), and fisheries reports (*n* = 17) from Caribbean Panama were compiled to evaluate human perceptions and harvesting of sharks over the last ∼4 ka (*SI Appendix*, Table S5). These records were separated into seven cultural periods in Caribbean Panama's history, which

were described in terms of human resource use (*SI Appendix*, Table S6). To evaluate these disparate data types, the records (e.g., *SI Appendix*, Table S4) were interpreted using established criteria (12, 79) to assign a semiquantitative ecological state to each cultural period based on perceived shark abundance (*SI Appendix*, Table S7). Ecological states were determined using the data in aggregate for each cultural period, and they were based on the most frequent state given the potential for variation in perceptions of shark abundance. To constrain personal biases, the accounts were reviewed by 17 individuals. The study protocol was approved and designated as exempt by the Human Subjects Committee, which serves as the Institutional Review Board of the University of California, Santa Barbara (IRB Protocol #3–20-0211). Written consent was obtained through completion of the questionnaire. Identifying information was removed from the metadata before evaluation, and the cultural periods were blinded (following ref. 80). Respondents were also asked to report how confident they were in each of their responses (high, neutral, or low) and to provide a short justification for each response in the questionnaire (*SI Appendix, SI Materials and Methods*).

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