Received: 11 September 2019 | Accepted: 15 November 2019
DOI: 10.1111/2041-210X.13346

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Dermal denticle assemblages in coral reef sediments correlate with conventional shark surveys

Erin M. Dillon[1,2] | **Kevin D. Lafferty**[3] | **Douglas J. McCauley**[1,4] | **Darcy Bradley**[5] | **Richard D. Norris**[6] | **Jennifer E. Caselle**[4] | **Graziella V. DiRenzo**[1,7] | **Jonathan P. A. Gardner**[8] | **Aaron O'Dea**[2,9]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA, USA; [2]Smithsonian Tropical Research Institute, Balboa, Republic of Panama; [3]Western Ecological Research Center, U.S. Geological Survey, c/o Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, USA; [4]Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, USA; [5]Bren School of Environmental Science and Management, University of California, Santa Barbara, Santa Barbara, CA, USA; [6]Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA, USA; [7]Department of Ecosystem Sciences and Management, The Pennsylvania State University, University Park, PA, USA; [8]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand and [9]Department of Biological, Geological and Environmental Sciences, University of Bologna, Bologna, Italy

Correspondence
Erin M. Dillon
Email: erinmdillon@ucsb.edu

Funding information
Alfred P. Sloan Foundation; Marisla Foundation; U.S. Department of the Interior, Bureau of Ocean Energy Management, Environmental Studies Program; Sistema Nacional de Investigadores of SENACYT; Swerdlow Family; Worster Family; Victoria University of Wellington, New Zealand; UC Santa Barbara Chancellor's Fellowship

Handling Editor: Lee Hsiang Liow

Abstract

1. It is challenging to assess long-term trends in mobile, long-lived and relatively rare species such as sharks. Despite ongoing declines in many coastal shark populations, conventional surveys might be too fleeting and too recent to describe population trends over decades to millennia. Placing recent shark declines into historical context should improve management efforts as well as our understanding of past ecosystem dynamics.
2. A new palaeoecological approach for surveying shark abundance on coral reefs is to quantify dermal denticle assemblages preserved in sediments. This approach assumes that denticle accumulation rates correlate with shark abundances. Here, we test this assumption by comparing the denticle record in surface sediments to three conventional shark survey methods at Palmyra Atoll, Line Islands, central Pacific Ocean, where shark density is high and spatially heterogeneous.
3. We generally found a significant positive correlation between denticle accumulation rates and shark abundances derived from underwater visual census, baited remote underwater video and hook and line surveys.
4. Denticle accumulation rates reflected shark abundances, suggesting that denticle assemblages can preserve a signal of time-averaged shark abundance in low-energy coral reef environments. We offer suggestions for applying this tool to measure shark abundance over long time-scales in other contexts.

KEYWORDS
abundance estimation, dermal denticle assemblages, fossil record, *N*-mixture model, palaeoecology, Palmyra Atoll, shark, taphonomy

1 | INTRODUCTION

Long-term shark abundance data can help evaluate the extent of shark declines, set appropriate management targets and provide insight into how sharks influence food web ecology (Ferretti, Worm, Britten, Heithaus, & Lotze, 2010; Lotze & Worm, 2009; Myers & Worm, 2003; Roff et al., 2016). However, conventional surveys and fisheries catch data typically have short survey periods that only span the last few decades, cover small areas and can miss rare and mobile species like sharks (Burgess et al., 2005; Lotze & Worm, 2009; McClanahan et al., 2007). These limitations might explain, in part, why surveys conducted at the same sites can return shark abundance estimates that vary by orders of magnitude (Bradley, Conklin, et al., 2017; Ward-Paige, Flemming, & Lotze, 2010), confounding our understanding of shark community dynamics over time and space. This is a particularly pervasive issue in coral reef ecosystems, where sharks are important predators (Roff et al., 2016), cultural symbols (e.g. Riesenfeld, 1950) and ecotourism attractions (Cisneros-Montemayor, Barnes-Mauthe, Al-Abdulrazzak, Navarro-Holm, & Sumaila, 2013), yet are vulnerable to exploitation and have declined in many regions (Ferretti et al., 2010). Here, we examine the use of an alternate method for surveying sharks—dermal denticle counts—to improve contemporary and historical reference points of shark abundance on coral reefs.

Dermal denticles are small (<2 mm), tooth-like scales that cover the bodies of elasmobranchs (Figure 1). After being shed, denticles sink and become incorporated into marine sediments (Dillon, Norris, & O'Dea, 2017; Helms & Riedel, 1971; Sibert, Cramer, Hastings, & Norris, 2017). This accumulation of denticles in sediments is time-averaged, meaning that denticles shed by non-contemporaneous individuals appear together in a single temporally mixed assemblage. Denticle assemblages can preserve evidence of shark occurrences (Figure 2), even where sharks are rare or are not easily observed in conventional surveys (Dillon et al., 2017; Sibert et al., 2017). Denticles also preserve well in fossil sediments since they are composed of calcium phosphate (Helms & Riedel, 1971; Sibert & Norris, 2015), and they differ morphologically across taxa with different ecological life modes (Dillon et al., 2017; Ferrón & Botella 2017; Ferrón, Pla, Martínez-Pérez, Escudero-Mozo, & Botella, 2014; Reif, 1985), offering a window into shark community dynamics over deeper ecological and geological time. However, it is unclear if denticle accumulations reflect shark abundances or how taphonomic processes—which affect how organic remains and their ecological attributes become preserved in the fossil record (Behrensmeyer, Kidwell, & Gastaldo, 2000)—selectively alter the preservation, transport and temporal context of the denticle record (Kidwell, 2013; Kidwell & Flessa, 1995).

FIGURE 1 Light microscope image of a blacktip reef shark *Carcharhinus melanopterus* denticle. Scale bar = 200 μm. Image credit: V. Chan

We explored the relationship between denticles preserved in surface sediments and contemporary shark abundances measured by three conventional shark survey methods to test how well shark abundance can be estimated from the denticle record. Such live–dead comparisons are used to test the fidelity of death assemblages for other taxa (e.g. molluscs) in surface sediments (Kidwell, 2013), although they can also help indicate the reliability of buried historical layers, which are otherwise challenging to assess directly (Kidwell, 2009). In doing so, this approach assumes that denticle assemblages in surface sediments are reasonable analogues of the fully buried record (Kidwell, 2013). We conducted this study at Palmyra Atoll, a protected, remote island in the central Pacific Ocean where shark populations have been monitored for over a decade and are likely at or near their site-specific carrying capacity (Bradley, Conklin, et al., 2017). Consequently, mismatch between contemporary surveys and denticle assemblages is less likely to be caused by anthropogenic-driven shark declines than in fished regions and, instead, could indicate taphonomic biases, time-averaging or contemporary survey error. We found that denticle accumulation rates corresponded with shark abundances, supporting the denticle record's ability to record relative shark abundance in low-energy coral reef environments.

2 | MATERIALS AND METHODS

2.1 | Study area

Palmyra Atoll Fish and Wildlife Refuge, central Pacific Ocean (5°54′ N, 162°05′ W) is remote, unfished and uninhabited, apart from a limited research presence. Shark density at the atoll is high, spatially heterogeneous and has remained relatively stable over the past decade (Bradley, Conklin, et al., 2017). Blacktip reef sharks *Carcharhinus melanopterus* are the most common shark species in the lagoon and backreef habitats (Papastamatiou et al., 2017; Papastamatiou, Caselle, Friedlander, & Lowe, 2009), followed by grey reef sharks *Carcharhinus amblyrhynchos* and whitetip reef sharks *Triaenodon obesus*. However, at least 15 other shark species have been documented by deep reef

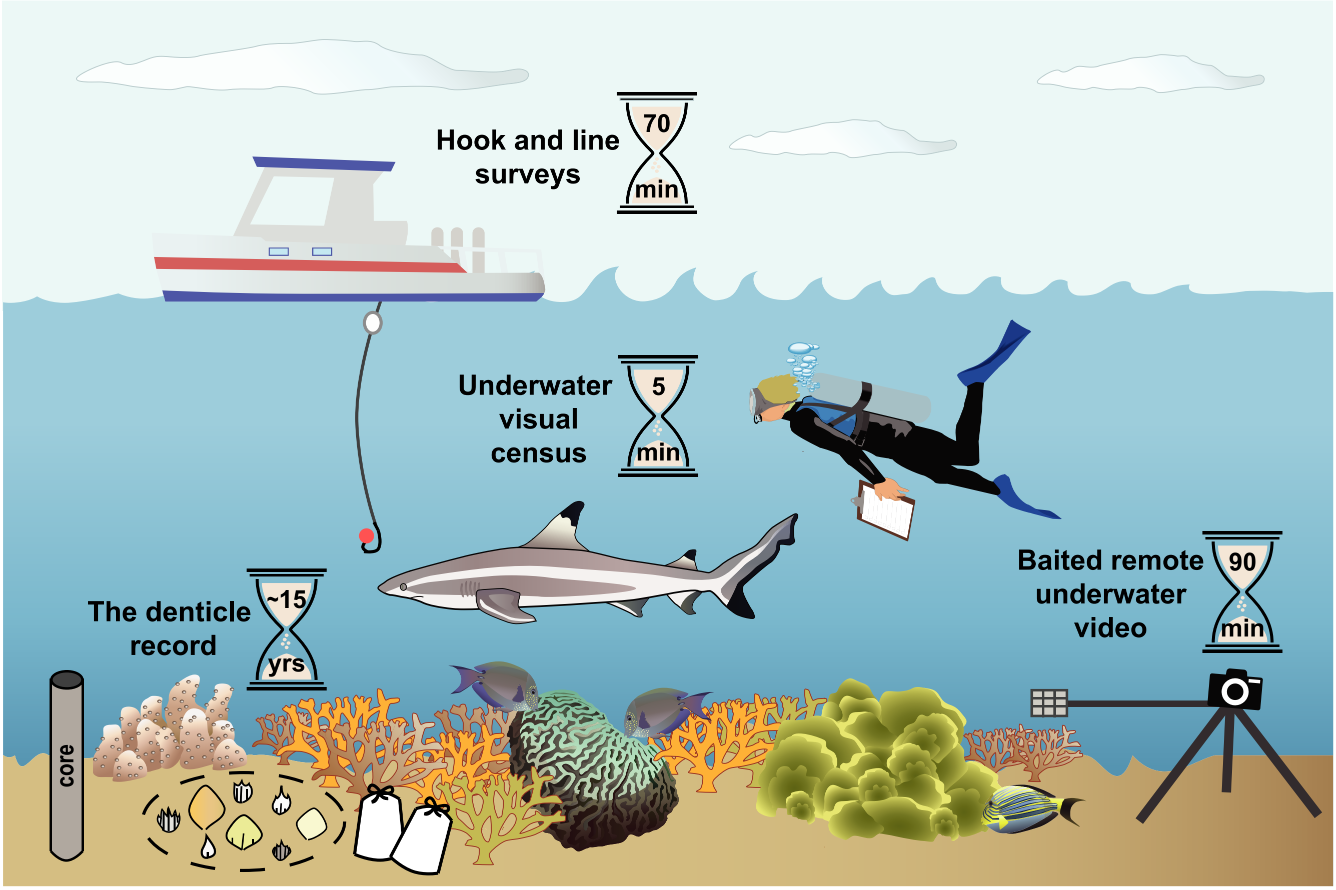

FIGURE 2 Sample durations for the denticle record and conventional survey methods used in this study. The hourglasses show the average duration of a single replicate. Underwater visual census and baited remote underwater video surveys had standardized durations, hook and line surveys varied from 7–274 min and the denticle record was averaged over years to decades. Several graphics were obtained from the Integration and Application Network image library: J. Hawkey, D. Kleine, T. Saxby, D. Tracey, and J. Woerner, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/)

cameras or shallow surveys (Mundy et al., 2010; Papastamatiou et al., 2014; Y. P. Papastamatiou & J. G. Eurich, pers. comm.).

2.2 | Collection and recovery of denticle assemblages

We collected surface sediments from 11 sites at Palmyra Atoll in the lagoon (*n* = 8) and backreef (*n* = 3) habitats (Figure 3). These sites were spread across five broadly defined areas: Western Terrace, West Lagoon, Center Lagoon, East Lagoon and Far East (following Gardner, Bartz, et al., 2014). Sampling was restricted to low-energy habitats to reduce the likelihood that the denticle assemblages had been transported, sorted, reworked or exposed to physical taphonomic biases (Kidwell, 2013; Kidwell & Flessa, 1995). We expect the sediment record to be relatively undisturbed by storms because Palmyra Atoll lies outside the path of nearly all tropical cyclones (Clark, 2008), although it does occasionally experience high wind and waves from distant storms (Gardner, Garton, Collen, & Zwartz, 2014). Sediment collection sites were selected to overlap with available shark abundance data from underwater visual census (UVC), baited remote underwater video (BRUV) and hook and line surveys, which varied by nearly an order of magnitude across sites (Figure S1; Table 1). In particular, sediment collection sites were matched with survey locations in the same habitat within a 0.5 km radius (*M* = 0.23 km) and were spaced 0.5–2.5 km apart.

At each site, we collected 10 replicate ~0.8 kg bulk samples of sediments from the top <10 cm via SCUBA in patches of mud, silt and sand in areas with scattered branching coral matrix or adjacent to coral heads. Water depths varied between 1.8 and 6.1 m. Replicate samples within a site were spaced 1–5 m apart. The substrate was moderately bioturbated by crustaceans, worms and holothurians, although the density of burrow holes and tracks was visibly similar across sites. Areas with high bioturbation by callianassid and alpheid shrimp were avoided. Sediment sampling was conducted in 2015 and 2016, with different sites sampled in each year.

Sediment samples were processed to extract denticles and describe sediment characteristics. First, we dried, weighed and sieved the sediments, from which grain size distributions, mean grain size and sorting were calculated (Folk & Ward, 1957). The 106–250 μm, 250–500 μm and 500 μm–2 mm size fractions were digested with 10% glacial acetic acid to eliminate the calcium carbonate components,

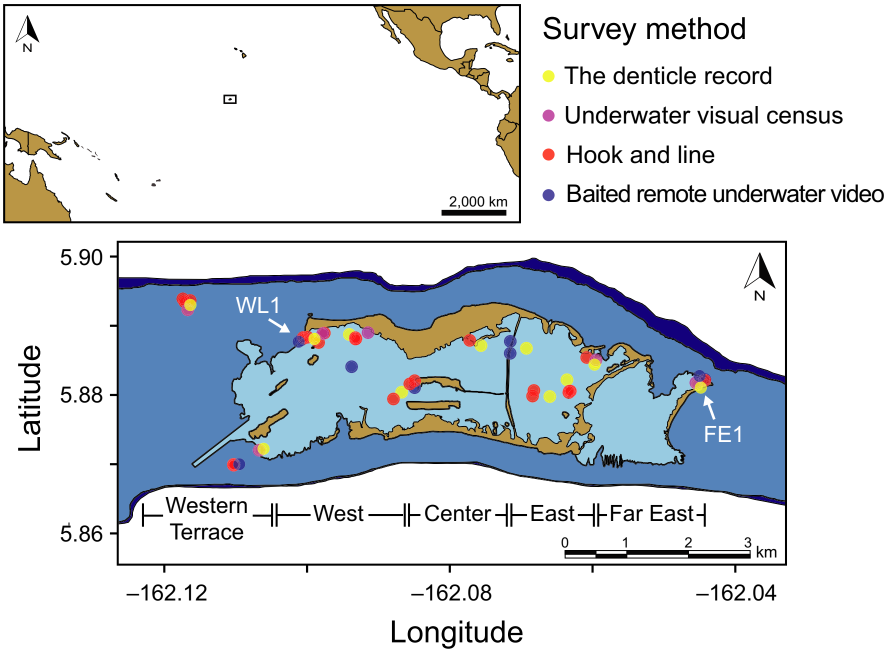

FIGURE 3 Survey locations at Palmyra Atoll, central Pacific Ocean. Conventional surveys were matched with the denticle record at 11 sites spread across five broadly defined areas of the atoll: Western Terrace, West Lagoon, Center Lagoon, East Lagoon and Far East. The arrows indicate the sites at Far East 1 (FE1) and West Lagoon 1 (WL1). The land is tan, the lagoon is light blue, the reef terrace and backreef are blue and the forereef is dark blue

and the remaining particles were treated with 100–200 ml of 5% hydrogen peroxide and heated for no more than 15 min to remove organic material (see Dillon et al., 2017; Sibert et al., 2017 for full protocol). Denticles were picked from the residue under a dissecting microscope and counted. Denticles missing more than half of their crown were excluded to avoid double counting; such fragments composed <7% of the total denticle assemblage. Denticle abundance was calculated as the total denticle count per sample divided by the dry weight of the sediment fractions, yielding denticles per kg sediment.

Denticle abundances were corrected by sedimentation rates at each site to produce denticle accumulation rates, measured as total denticle count per kg sediment per year (following Sibert et al., 2017). We used sedimentation data obtained from polyvinyl chloride (PVC) sediment traps over replicate 5–139 day periods between 2006 and 2009 from two sources, our own field collections and published data (Knapp et al., 2013; Williams, Knapp, Maragos, & Davy, 2011; see Supplementary Methods). Sedimentation rates were converted into vertical accumulation rates per year using mean sediment densities (Table 1).

Differences in denticle accumulation rates between sites (n = 11), areas of the atoll, (n = 5) and habitats (n = 2) were analysed using Welch's ANOVA (R Core Team, 2019). To assess the sampling effort needed to detect differences in denticle accumulation rates between sites, we performed a power analysis with a Type I error level of 0.05 for Welch's ANOVA (Levy, 1978; Shieh & Jan, 2013). To inform how best to invest field and laboratory sampling effort, the number of samples needed to capture the variation in denticle abundance between replicates at each site was explored via randomized resampling. Denticle abundances from the 10 replicate samples collected at each site were randomly resampled 10,000 times without replacement, and the cumulative mean denticle count per kg sediment was calculated. We then determined the difference between the cumulative mean as each replicate sample was added to the set and the final cumulative mean. The closer this difference was to zero, the more appropriate the number of replicates was for capturing within-site variation in denticle abundance, with the assumption that the 10 replicates did adequately capture this variation. This exercise was carried out for each sediment collection site, and the differences were plotted to visually examine the trade-offs between sampling effort and variance (Figure S2).

2.3 | Denticle classification

Denticle assemblage composition was determined by measuring and classifying the denticles from three randomly selected replicates per site (n = 574 denticles). We described the crown, peaks and ridges using a dissecting microscope (following Dillon et al., 2017; Table S1). We then visually categorized the denticles into previously recognized functional morphotypes: *drag reduction*, *ridged abrasion strength*, *abrasion strength*, *generalized functions* and *defense* (Dillon et al., 2017; Ferrón et al., 2014; Reif, 1985). To verify these classifications, a multinomial logistic regression was trained with our denticle reference collection (Dillon et al., 2017) and used to predict the functional morphotype of each denticle based on the measurements taken (see Supplementary Methods; Tables S1–S4).

2.4 | Assessing denticle preservation

To assess preservation, the denticles in each randomly selected replicate were assigned a weathering score (n = 574). Weathering scores ranged from zero (pristine) to three (poor preservation) and were based on visual inspections of the crown, peaks and base (Figure S3; Table S5). Weathering scores were compared across functional morphotypes, denticle characters, habitats and areas of the atoll as well

TABLE 1 Sediment characteristics, denticle accumulation rates and abundances and shark abundances measured by underwater visual census (UVC), baited remote underwater video (BRUV) and hook and line surveys. Sites are ordered west to east across the atoll. Where applicable, the mean and standard deviation are reported (*M* ± *SD*)

Site name	Habitat	Area	Sorting	Mean grain size & sorting description	Days of sediment trap data	Sedimentation rate (g m^{-2} day^{-1}; *M* ± *SD*)	Vertical accumulation rate (cm/year; *M* ± *SD*)	Average estimated years per sample	Denticle accumulation rate (denticles kg^{-1} sediment $year^{-1}$; *M* ± *SD*)	Denticle abundance (denticles/kg sediment; *M* ± *SD*)	UVC surveys (sharks/m^2)	Hook and line surveys (shark catch/hr)	BRUV surveys (MaxN)
Western Terrace 1	Backreef	Western Terrace	1.61	Fine sand, poorly sorted	423	12.7 ± 6.6	0.46 ± 0.24	15	1.97 ± 1.4	29.7 ± 21.6	0.00053	0.84	–
Western Terrace 2	Backreef	Western Terrace	1.46	Fine sand, poorly sorted	377	41.8 ± 19.8	1.39 ± 0.66	5	1.98 ± 1.2	10 ± 5.9	0.00053	0.62	3
West Lagoon 1	Lagoon	West Lagoon	2.60	Medium sand, very poorly sorted	233	17.2 ± 7.0	0.57 ± 0.23	12	4.48 ± 1.7	54.8 ± 21.3	0.00159	0.90	1
West Lagoon 2	Lagoon	West Lagoon	2.32	Medium sand, very poorly sorted	118	13.7 ± 1.4	0.55 ± 0.06	13	2.71 ± 0.8	34.2 ± 10.4	0.00273	1.27	4
West Lagoon 3	Lagoon	West Lagoon	1.86	Coarse sand, poorly sorted	120	17.1 ± 7.2	0.52 ± 0.22	13	4.68 ± 1.9	62.9 ± 25.5	–	1.42	5
Central Lagoon 1	Lagoon	Central Lagoon	1.51	Fine sand, poorly sorted	209	25.3 ± 8.3	0.71 ± 0.23	10	0.85 ± 0.8	8.3 ± 7.7	–	0.00	2
East Lagoon 1	Lagoon	East Lagoon	1.74	Fine sand, poorly sorted	191	7.2 ± 2.0	0.20 ± 0.06	35	0.32 ± 0.3	10.9 ± 9.2	–	–	2
East Lagoon 2	Lagoon	East Lagoon	1.42	Medium sand, poorly sorted	191	7.2 ± 2.0	0.20 ± 0.06	35	1.19 ± 0.4	41.1 ± 13.7	–	0.00	–
East Lagoon 3	Lagoon	East Lagoon	1.23	Medium sand, poorly sorted	147	38.7 ± 24.9	1.09 ± 0.70	6	6.05 ± 1.9	39 ± 12.1	–	2.41	–
East Lagoon 4	Lagoon	East Lagoon	1.87	Fine sand, poorly sorted	115	26.2 ± 8.1	0.96 ± 0.30	7	8.85 ± 3.9	64.6 ± 28.7	0.00510	1.36	–
Far East 1	Backreef	Far East	2.10	Medium sand, poorly sorted	247	16.3 ± 9.7	0.66 ± 0.39	11	1.86 ± 1.3	19.7 ± 13.6	0.00053	4.57	3

as with sediment characteristics and denticle abundances to explore how preservation could affect our interpretation of the denticle record.

2.5 | Testing for concordance between the denticle record and conventional shark surveys

2.5.1 | Underwater visual census surveys

Stationary point counts were used to obtain diver-based visual measurements of relative shark abundance. During these surveys, a diver was positioned in the centre of a circle with a 10 m radius for 5 min (McCauley, McLean, Bauer, Young, & Micheli, 2012). Divers endeavoured to count individual sharks only once. Six sites corresponding to the sediment collection sites (Figure 3) were surveyed, with four to seven replicate surveys conducted at each site during daylight hours over a two-month period in 2006. Shark density was expressed as sharks/m^2.

2.5.2 | Baited remote underwater video surveys

Baited remote underwater video (BRUV) surveys were used to obtain video-based measurements of relative shark abundance. GoPro™ Hero4 cameras mounted on PVC or metal frames were deployed for 120 min at depths between 1 and 7 m at seven sites corresponding with the sediment collection sites (Figure 3), with one to three replicate surveys conducted at each site (Bradley, Papastamatiou, & Caselle, 2017). Each BRUV system was baited with 0.5 kg mackerel. All BRUVs were deployed during daylight hours between 2014 and 2016. We used the SeaGIS© software EventMeasure (version 4.4; Bacchus Marsh, Australia) to analyse the first 90 min of video footage. For each survey, we recorded the maximum number of individuals in a single video frame (MaxN)—a conservative metric of relative abundance in BRUV surveys—for each shark species.

2.5.3 | Hook and line fishing surveys

Hook and line surveys were conducted on six occasions between 2013 and 2014 during daylight hours (Bradley, Conklin, et al., 2017). Sampling trips lasted 7–10 days, and trips were spaced at least 58 days apart to decrease the likelihood of behavioural effects. Sampling was unstructured, and fishing locations were selected opportunistically to cover the lagoon and backreef habitats. Data were available for ten of the eleven sediment collection sites (Figure 3), with one to five replicate surveys conducted at each site. Chum was used to attract sharks to the boat, where they were caught using hand lines baited with a single barbless circle hook. Fishing effort (hours spent scientific fishing) varied across sampling trips and sites, and shark abundance was expressed as shark catch per hour. Recaptured individuals were not included in the abundance estimates.

2.5.4 | Between-methods comparisons

Data from the three conventional shark survey methods were not available at every sediment collection site, although there was overlap between at least two conventional methods and the denticle record at eight of the eleven sites (Table 1). Spatial autocorrelation between sediment collection sites was assessed using Moran's I but was non-significant. The three conventional survey methods primarily detected *C. melanopterus*, with *C. amblyrhynchos* rarely observed. The abundances of these two species were summed to yield total shark abundance with which the denticle record was compared. Pairwise comparisons between denticle accumulation rates and shark abundances, as detected by each of the conventional survey methods, were made using a series of one-sided Spearman's rank correlations with sequential Bonferroni corrections. This was done with denticle accumulation rates calculated using the mean (including $\pm 1\sigma$), minimum and maximum sedimentation rates at each site. Pairwise comparisons were also made between denticle abundances and shark abundances. Shark abundances from the conventional survey methods were compared using one-sided Spearman's rank correlations (R Core Team, 2019).

2.5.5 | *N*-mixture model

To better understand linkages between the denticle record and shark abundance given the challenges inherent in detecting rare, mobile taxa such as sharks, the temporally replicated data from the conventional survey methods were integrated using an *N*-mixture model to predict relative shark abundance at each site while accounting for differences in detection probability (Royle, 2004). We assumed a closed population with respect to mortality, recruitment and movement and that the counts were independent. Survey duration (effort) and method were included as covariates for detection, and habitat type (lagoon or backreef), substrate angle (along a sand-flat ledge or horizontal) and year were included as covariates for abundance. The data were fitted using a negative binomial mixing distribution with an upper index of integration (*K*) of 600 using the R package UNMARKED (Fiske & Chandler, 2011). Model support was assessed using a maximum likelihood-based approach (Table S6), and goodness-of-fit was examined using the R package NMIXGOF (Knape et al., 2018; see Supplementary Methods). No model received unequivocal support, so we model-averaged the predicted abundance values for each site across the top three models (Tables S7 and S8). Due to the potential limitations of this modelling approach given the use of unmarked animals and its sensitivity to statistical assumptions (Barker, Schofield, Link, & Sauer, 2018; Link, Schofield, Barker, & Sauer, 2018; but see Kéry, 2018), these predicted values were interpreted as relative abundances, rather than absolute abundances. Detection probabilities for each survey method were also estimated using model-averaging.

Multiple regression was used to determine the relationship between relative shark abundance (integrated across survey methods), environment and the denticle record. Shark abundance predicted from the *N*-mixture model (Table S8) and habitat type were included in the model as predictors, and the model was run twice—once with denticle accumulation rates and once with denticle abundances as the response variable (R Core Team, 2019).

2.5.6 | Denticle assemblage composition

To test how well the denticle record reflects shark diversity, we examined denticle assemblage composition in relation to the two species detected by the conventional survey methods. Using our reference collection, we determined the rank abundance of functional morphotypes that characterize *C. melanopterus* and *C. amblyrhynchos* (see Supplementary Methods) and compared this with the rank abundance of morphotypes found in the sediments. We also compared denticle assemblages between sites using Kruskal–Wallis tests (R Core Team, 2019).

3 | RESULTS

3.1 | Spatial variation in the denticle record

Denticle abundances ranged from 0 to 133 (*M* ± *SD*; 34 ± 26) denticles/kg sediment across sites (Figure 4; Figure S1). Sedimentation rates differed across sites and areas of the atoll ($F = 11.74$, $df_{\text{num}} = 9$, $df_{\text{denom}} = 20.9$, $p < .0001$ and $F = 3.67$, $df_{\text{num}} = 4$, $df_{\text{denom}} = 34.8$, $p = .013$ respectively; Figure S4) and, without accounting for mixing or reworking of older buried sediments, indicated that the samples spanned at least 15 years on average (Table 1). When denticle abundances were corrected by these sedimentation rates, denticle accumulation rates ranged from 0 to 18 (3.1 ± 3.0) denticles kg^{-1} sediment year^{-1}. Denticle accumulation rates were generally higher in the lagoon (3.6 ± 3.3) than on the backreef (1.9 ± 1.3), with the highest rates found in the East and West Lagoons ($F = 16.12$, $df_{\text{num}} = 4.0$, $df_{\text{denom}} = 38.9$, $p < .0001$; Figure 4). Denticle accumulation rates varied little across sites in the West Lagoon (4.0 ± 1.8) but were more variable across sites in the East Lagoon (4.0 ± 4.2). The Center Lagoon (0.8 ± 0.8) had the lowest denticle accumulation rates (Figure 4). Neither denticle abundances nor denticle accumulation rates were correlated with sorting ($S = 150$, $df = 9$, $r = .32$, $p = .3$ and $S = 168$, $df = 9$, $r = .24$, $p = .5$ respectively; Figure S5) or mean grain size (Kruskal–Wallis $H = 2.91$, $df = 2$, $p = .2$ and $H = 1.49$, $df = 2$, $p = .5$ respectively), which served as proxies for depositional environment.

In the randomized resampling exercise, the difference between the total cumulative site mean and the cumulative mean after adding each replicate in a randomized order levelled off at five to seven replicates, depending on the variance in denticle abundance (Figure S2). With five to seven replicates, there was a 5–9 denticles/kg sediment

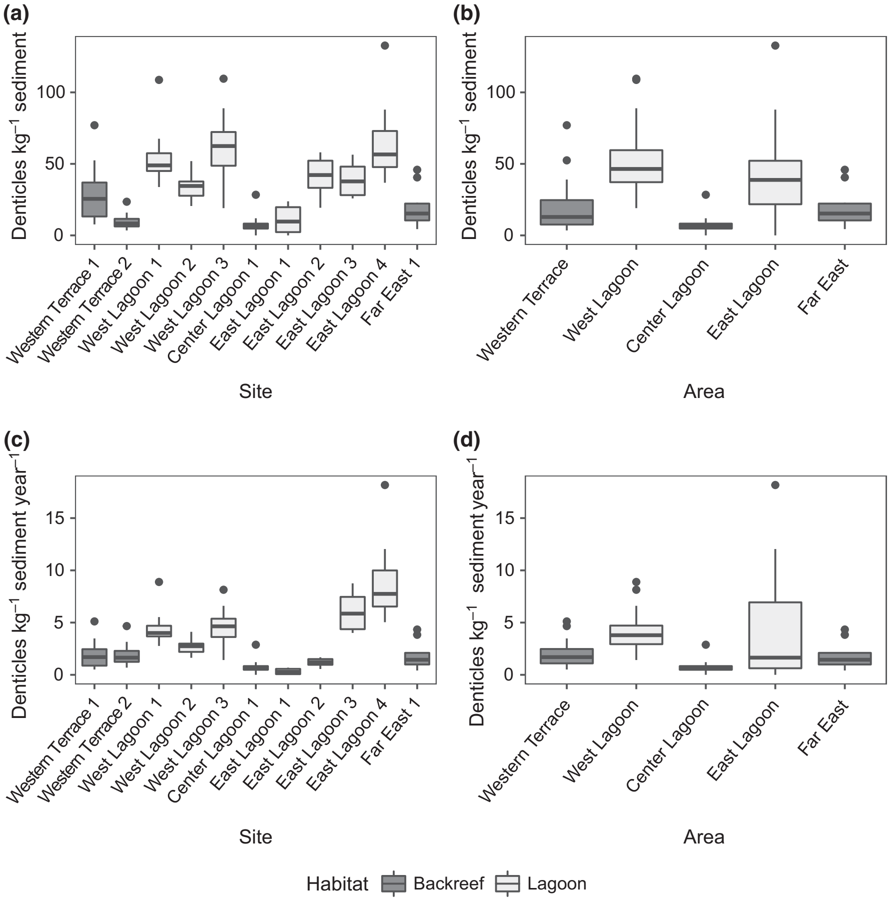

FIGURE 4 Boxplot of denticle abundances across (a) sites and (b) areas of the atoll and denticle accumulation rates across (c) sites and (d) areas of the atoll, coloured by habitat. Each boxplot shows the median (dark bar) and interquartile range (box), and outliers are displayed as points. In each plot, at least one group differed from the others ($p < .0001$)

maximum difference from the global cumulative mean at each site, which fell around each site's standard deviation (6–29 denticles/kg sediment). When comparing denticle accumulation rates across sites, analysing all 10 replicates per site yielded a power of 0.7, whereas analysing five to seven replicates per site yielded a power of 0.3–0.5. Thus, at least seven replicates should be collected per site to capture the spatial variability in the denticle record at Palmyra Atoll, and at least 10 replicates should be collected to detect differences across sites.

3.2 | Denticle preservation

Denticles were preserved at all sites and were only moderately weathered (median weathering score ± median absolute deviation: 2 ± 0.7). Although denticle bases were often missing, the crowns were usually intact, permitting measurement and classification. Weathering scores varied across functional morphotypes and denticle characters, although these differences were often inconsequential for classification. *Drag reduction* denticles (which characterize *C. melanopterus* and *C. amblyrhynchos*) were more weathered than the other functional morphotypes (Kruskal–Wallis $H = 41.835$, $df = 3$, $p < .0001$; Dunn's test $p < .01$; Figure 5a). Similarly, thin denticles (Mann–Whitney U = 21,574, $p < .0001$) and those with ridges (Mann–Whitney U = 8,882.5, $p < .0001$) were more weathered than thicker denticles without ridges. Weathering scores were not affected by other denticle characters, such as crown size (Kruskal–Wallis $H = 10.516$, $df = 8$, $p = .2$) or the number of peaks (Mann–Whitney U = 27,176, $p = .1$).

Denticles were better preserved in the lagoon than on the backreef (Mann–Whitney U = 22,881, $p = .008$; Figure 5b). Weathering scores were not correlated with sorting ($S = 230$, $df = 9$, $r = -.05$, $p = .9$), mean grain size (Kruskal–Wallis $H = 2.39$, $df = 2$, $p = .3$) or denticle abundance ($S = 190$, $df = 9$, $r = .1$, $p = .7$), suggesting that low denticle abundances were not purely due to poor preservation.

3.3 | Concordance between the denticle record and conventional shark surveys

The denticle record was well-aligned with the three conventional survey methods at all sites except two (Figure 6; Figure S6). There was a significant positive correlation between denticle accumulation rates and shark abundances measured by UVC surveys ($S = 4.19$, $df = 4$, $r = .88$, $p = .031$ adjusted; Figure 6a). Denticle accumulation rates and hook and line surveys were positively correlated at all sites except Far East 1 (Figure 3), which had a low denticle accumulation rate but high shark catch per hour ($S = 10.54$, $df = 7$, $r = .91$, $p = .0009$ adjusted; Figure 6b). Denticle accumulation rates and BRUV surveys were positively correlated at all sites except West Lagoon 1 (Figure 3), which had a high denticle accumulation rate but low MaxN value ($S = 1.01$, $df = 4$, $r = .97$, $p = .002$ adjusted; Figure 6c). These correlations were largely robust to variation in sedimentation rate, as over half the correlations remained statistically significant in the sensitivity analysis (Table S9). Furthermore, denticle abundances were positively correlated with UVC and BRUV surveys ($S = 4.19$, $df = 4$, $r = .88$, $p = .031$ adjusted and $S = 5.13$, $df = 4$, $r = .85$, $p = .046$ adjusted respectively; Figure S7a,c) but not with hook and line surveys ($S = 50.71$, $df = 7$, $r = .58$, $p = .16$ adjusted; Figure S7b). Finally, there were non-significant correlations between the three conventional survey methods ($p > .05$ for each pairwise comparison; Figure S6).

The *N*-mixture model demonstrated that the detection probability of each survey method increased with survey effort. When effort was held constant at one hour, detection probability was highest for UVC (0.56), followed by hook and line (0.42) and BRUV surveys (0.37). However, because survey effort varied across methods, hook and line and BRUV surveys had higher actual detection probabilities due to their longer durations. Survey year was associated with shark abundance in one of the top-ranked models, which likely indicated temporal variability, although a limited number of environmental parameters were included in the model due to data availability (Table S7). After accounting for these differences in detection, both relative shark abundance and habitat were decent predictors of denticle accumulation rate ($p = .037$ and $p = .041$ respectively;

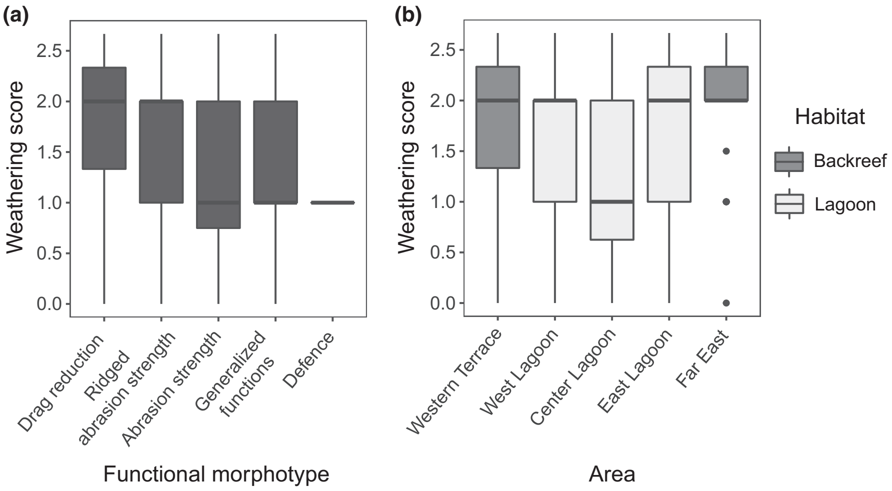

FIGURE 5 Denticle weathering scores by (a) functional morphotype and (b) area of the atoll, coloured by habitat. Weathering scores ranged from zero (pristine) to three (poorly preserved). Each boxplot shows the median (dark bar) and interquartile range (box), and outliers are displayed as points. Preservation was lowest in *drag reduction* denticles and denticles recovered from the backreef

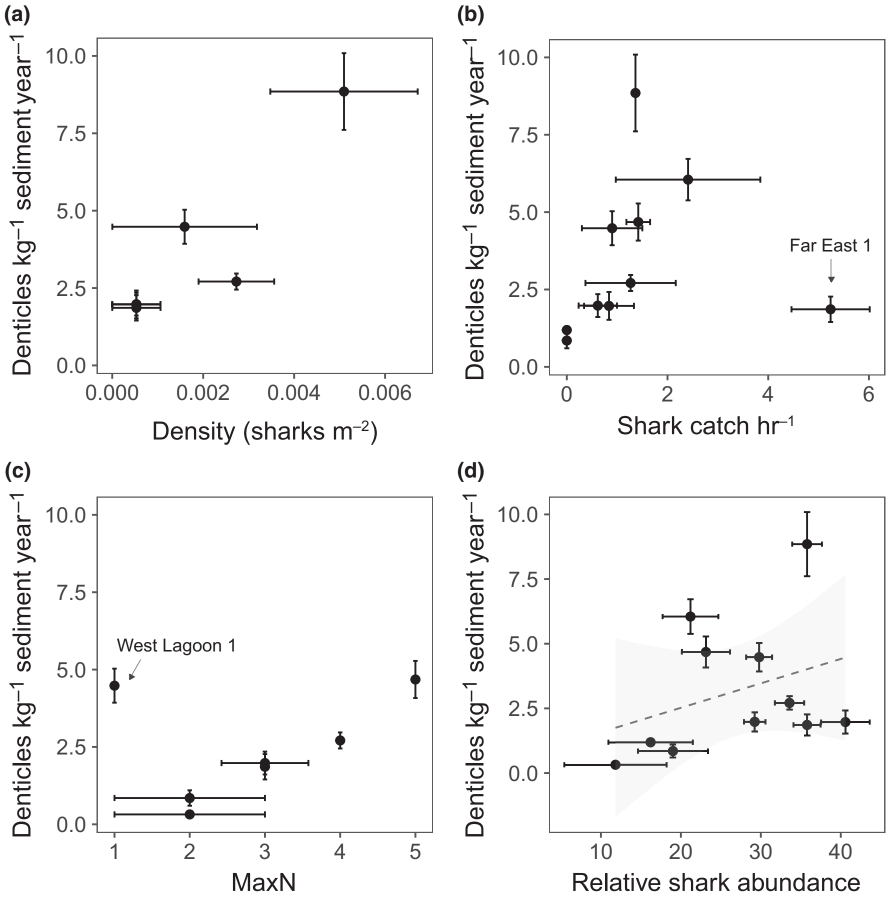

FIGURE 6 Correlation between denticle accumulation rates (denticles kg^{-1} sediment year^{-1}) and (a) shark density derived from UVC surveys, (b) shark catch per hour derived from hook and line surveys, (c) MaxN derived from BRUV surveys, and (d) relative shark abundance integrated across methods (dashed regression line with 95% confidence intervals). Points represent *M* ± *SE* at each site with corresponding data

$R^2 = .36$; Figure 6d) and denticle abundance ($p = .04$ and $p = .019$ respectively; $R^2 = .43$) in the multiple regression models (Table S10).

3.4 | Denticle assemblage composition

The subset of denticles that was identified to functional morphotype was comprised primarily of *drag reduction* denticles (69.0%), followed by *ridged abrasion strength* (12.8%), *abrasion strength* (8.1%), *generalized functions* (7.8%) and *defense* denticles (0.2%). Around 2% remained unclassified. One *defense* denticle closely resembled a diagnostic tiger shark *Galeocerdo cuvier* denticle (Dillon et al., 2017; Muñoz-Chápuli, 1985) from our reference collection (Figure S8). The relative abundance of each functional morphotype did not differ across sites ($p > .05$ for all morphotypes). Notably, denticle assemblage composition overlapped with the functional morphotypes possessed by the two species detected by the conventional surveys. Most of the body and fins of *C. melanopterus* and *C. amblyrhynchos* in our reference collection were characterized by *drag reduction* denticles (75.0% of denticles examined; Figure 1), although *ridged abrasion strength* (14.3%), *abrasion strength* (9.7%) and *generalized functions* (1.0%) denticles were also present. Overall, the rank abundance of functional morphotypes recovered from the sediments resembled that of the commonly observed species at the atoll.

4 | DISCUSSION

4.1 | Denticle accumulation rates reflect relative shark abundances at Palmyra Atoll

Denticle accumulation rates were, in almost all instances, highly correlated with shark abundances detected by UVC, BRUV and hook and line surveys at Palmyra Atoll. This is likely because sites with more sharks accumulated more denticles. Moreover, patterns of residency and movement shape the distribution of shark abundance and could influence denticle accumulation. For example, denticle accumulation rates were highest in the East and West Lagoons, where *C. melanopterus* shows strong site fidelity and small home ranges (Papastamatiou, Friedlander, Caselle, & Lowe, 2010; Papastamatiou, Lowe, Caselle, & Friedlander, 2009). In contrast, *C. melanopterus* occasionally transits through the backreef and Center Lagoon (Papastamatiou et al., 2017, 2010; Papastamatiou, Caselle, et al., 2009), where shark abundances and denticle accumulation rates were lower. The denticle record therefore could be recording long-term spatial variation in the abundance and habitat use of this species.

The denticle record did not align with all the individual surveys—namely the hook and line survey at Far East 1 and the BRUV survey at West Lagoon 1. Far East 1 is a shallow backreef site that can become isolated from the adjacent forereef at low tide

(Rogers, Monismith, Fringer, Koweek, & Dunbar, 2017), so shark catch per hour could have been abnormally high due to the presence of sharks from the neighbouring forereef that were attracted by the bait plume at high tide or, alternatively, sharks that were trapped at low tide. In the lagoon, *C. melanopterus* uses the sand-flats in a tidally dependent manner, and larger individuals patrol the sand-flat ledges (Papastamatiou, Lowe, et al., 2009). The BRUV deployment at West Lagoon 1 faced the sand-flat rather than the ledge, so it might not have been well-positioned to detect sharks in the vicinity. Although bait was used, the small quantity of bait and relatively low water movement in the lagoon (Rogers et al., 2017) could have limited the area of attraction. Therefore, whereas these short surveys might have captured ephemeral, behaviourally driven fluctuations in shark abundance, the denticle record likely recorded longer-term averages.

There was no significant correlation between the three conventional survey methods, matching previous observations of imperfect correspondence (Bradley, Conklin, et al., 2017; McCauley et al., 2012; Ward-Paige et al., 2010). They took different approaches to measuring shark abundance, had varying detection probabilities and sampling effort, and were conducted in different years, all of which likely contributed to their lack of agreement (Figure 2). Regardless, relative shark abundance was positively correlated with denticle accumulation rate, even when we accounted for imperfect shark detection probability and estimated population size using an *N*-mixture model. This suggests that the shark abundance gradient across sites, which was reflected in the denticle record, did not purely stem from each method's observational biases.

4.2 | Denticle assemblage composition captures a signal of shark functional diversity

Most isolated denticles cannot be identified to species, in contrast to the high taxonomic resolution of conventional shark surveys. Regardless, we found that the relative proportions of functional morphotypes recovered from sediments were similar to those characterizing the two species detected by the conventional surveys. In contrast, the tiger shark denticle was an unexpected find, considering that this species has only been anecdotally reported at Palmyra Atoll (J. D. Collen, pers. comm.). The denticle record might therefore be capturing a larger proportion of shark functional diversity than the conventional surveys used in this study, perhaps due to the longer time-scales over which denticles accumulate (Figure 2).

4.3 | Applying the denticle record to survey sharks

In low-energy coral reef environments, the denticle record can preserve a time-averaged signal of relative shark abundance. Here, we provide several suggestions for using the denticle record to explore shark communities in other regions.

4.3.1 | Site selection

To improve the fidelity of denticle assemblages, sampling should be constrained to low-energy habitats such as lagoons, bays or backreefs. Under these conditions, denticles are likely to sink quickly after being shed, given that their primary constituent (hydroxyapatite) is ~3.1 times denser than seawater (Helms & Riedel, 1971), and are less likely to be size-sorted. Under high-energy conditions, denticles are more likely to be sorted, selectively lost or damaged, resulting in mismatch between denticle accumulation and shark abundance or skewing denticle assemblage composition toward thicker, more durable morphotypes. In Palmyra Atoll's lagoon, denticles were well-preserved, consistent with results from mid-Holocene lagoonal reefs (Dillon et al., 2017) and deep-sea cores (Sibert & Norris, 2015). Denticles found in the backreef tended to be more weathered and might have experienced selective loss or sorting. Two samples from the forereef not used in this study contained few denticles despite sharks being abundant in this habitat, and those denticles were in poor condition, strongly suggesting the avoidance of such high-energy sites.

4.3.2 | Establishing temporal context

Temporal context is needed to infer shark abundance from denticle abundance. While sedimentation and reef accretion rates determine the minimum amount of time encompassed by a sample, biological (e.g. bioturbation, deposit feeding) and physical (e.g. wave energy) processes can mix sediments (Flessa, Cutler, & Meldahl, 1993; Kosnik, Hua, Kaufman, & Zawadzki, 2015; Olszewski, 2004). This mixing is a key process affecting death assemblage composition, as it blends new inputs from the living community with older buried cohorts (Kidwell, 2013; Tomašových, Gallmetzer, et al., 2019; Tomašových & Kidwell, 2011). For this reason, the amount of time-averaging should be resolved and, depending on the study aims, constrained.

Examining changes in the denticle record over human time-scales requires high-resolution samples (e.g. sediment cores). One way to constrain time-averaging is to collect samples from branching coral framework, which forms an interlocking matrix that restricts the vertical movement of sediment particles trapped within. Reef accretion rates can be measured by dating pieces of coral (Cramer, O'Dea, Clark, Zhao, & Norris, 2017) or smaller particles like otoliths (Lin et al., 2019) and used to calculate denticle accumulation rates and estimate sample age.

Although denticles accumulating in moderately bioturbated sediments cannot reveal fine-scale historical trends, they can help describe spatial patterns of abundance and indicate recent change. The bulk samples used in this study were collected from well-oxygenated sediments with little to no branching coral framework, which can increase time-averaging (Kosnik et al., 2015; Kowalewski, 1996), leaving us unable to interpret changes in shark abundance over time. However, shark populations at

Palmyra Atoll have remained relatively stable over at least the last decade (Bradley, Conklin, et al., 2017), and, with the exception of a brief period of human occupation during World War II, there has not been a strong human presence at the atoll (Collen, Garton, & Gardner, 2009). Given this low anthropogenic pressure, Palmyra Atoll is an ideal location to reveal taphonomic patterns in the denticle record. In contrast, areas that have experienced rapid and recent shark declines are likely to show mismatch between time-averaged denticle assemblages and contemporary surveys (c.f. Albano et al., 2016; Roff et al., 2013; Tomašových & Kidwell, 2017).

Quantifying the amount of time encompassed by bioturbated sediments can be challenging and time-intensive. Here, we used sedimentation rates to calculate denticle accumulation rates, as methods to date denticles and build denticle-specific time-averaging models have not yet been developed. However, using sedimentation rates has several drawbacks. First, we expect the samples to be more time-averaged than indicated by sedimentation rates alone due to the presence of bioturbating fauna (Kosnik et al., 2015; Olszewski, 2004; Tomašových, Kidwell, Alexander, & Kaufman, 2019). Moreover, bioturbation depths were not known, so time-averaging could have differed across sites. Second, sedimentation was measured over three years, which might not scale linearly over decades (Sadler, 1981). However, sedimentation rates measured from a gravity core collected in the West Lagoon, spanning a period from 1840 to 2003 (Collen et al., 2011), corresponded with the rates used in this study. Third, resuspension could have artificially inflated sedimentation rates. To reduce resuspension, we used sediment traps with a diameter-to-length ratio of 10, well in excess of the recommended ratio of three to five for low-energy habitats (Bloesch & Burns, 1980). Finally, given that denticle accumulation rates can be sensitive to the accuracy of the time-scale used to calculate them (Sibert et al., 2017), we ran sensitivity analyses to ensure that correlations between denticle accumulation rates and shark abundances were robust to variation in sedimentation.

4.3.3 | Sample volume and replication

Denticles comprise a small fraction of coral reef sediments, so large volumes are needed to obtain enough denticles for robust statistical analyses. The minimum per-sample volume should aim to recover at least ~30 denticles when estimating total abundance (Sibert et al., 2017) and likely more when examining community composition (Heck, van Belle, & Simberloff, 1975), depending on the standing diversity and taxonomic identification attainable. Sample volumes can be determined with preliminary sampling or estimated using information about reef accretion rates and contemporary shark abundance. For example, if shark abundance is high and/or reef accretion is low, <1–3 kg replicates should be sufficient, whereas if shark abundance is low and/or reef accretion is high, 10 kg replicates might be needed.

4.3.4 | Implications for fully buried denticle assemblages

Reconstructing shark abundances over millennia requires sampling the fossil record using sediment cores or fossil reefs. Although the differential loss of taxa or diagnostic characters during burial can hinder interpretations of the fossil record (Kidwell, 2013), ichthyoliths have relatively little preservation bias (Helms & Riedel, 1971; Doyle & Riedel, 1979; see *Site selection*), supporting the ability of denticle assemblages in surface sediments to be reasonable proxies for permanently buried assemblages. Nonetheless, quantifying down-core trends in denticle weathering and radiometrically dating denticles might help verify whether the preservation and age-frequency distribution (temporal resolution) of denticle assemblages changes during burial.

4.3.5 | Future work and limitations

Several uncertainties remain about the relationship between denticle assemblages and shark communities. First, little is known about denticle shedding rates and whether they differ between demersal and pelagic species or as a function of shark age, body size, behaviour or denticle morphology, which could cause some species to be over- or under-represented in the denticle record. Second, models should be built to test how water velocity and denticle morphology affect denticle sinking rates and horizontal transport. Third, variability in denticle morphology across sharks' bodies and between taxa currently limits identification to functional group and shark family (Dillon et al., 2017; Reif, 1985). Machine learning techniques could help identify denticles to genus or species, improving comparisons between denticle assemblage composition and diversity metrics derived from conventional shark surveys. Finally, although we found correlations between denticle accumulation rates and shark abundances at the scale of several kilometres at Palmyra Atoll, additional work is needed to resolve whether this association holds across islands with different shark densities and community compositions.

5 | CONCLUSIONS

As coral reefs accrete, they preserve a record of the abundances and composition of a variety of taxa, including corals, urchins and fish (Cramer et al., 2017; Lin et al., 2019; Pandolfi & Jackson, 2006). Our results add sharks to this list. The correspondence between denticle accumulation rates and shark abundances supports the use of the denticle record as a proxy for estimating relative shark abundance in low-energy coral reef environments. For example, mismatch between denticle assemblages in surface sediments and contemporary surveys can be used to demonstrate recent change. Furthermore, although these surface assemblages receive input from the contemporary shark community and might undergo additional taphonomic processes during burial (Behrensmeyer et al., 2000), testing their fidelity can aid the interpretation of deeper palaeoecological records (Kidwell, 2009). Denticles recovered from fossil reefs present a valuable opportunity to define historical ranges of variation (O'Dea, Dillon, Altieri, & Lepore, 2017) and reconstruct patterns of change over millennia. Such long-term data can help determine baseline shark abundance, understand natural variation, interpret sharks' roles in natural and human-impacted systems and set management targets informed by local historical conditions.

ACKNOWLEDGEMENTS

We thank the Palmyra Atoll National Wildlife Refuge, U.S. Fish and Wildlife Service, U.S. Department of the Interior, The Nature Conservancy staff, the Palmyra Atoll Research Consortium, D. Schroeder and D. Morton for their assistance in the field, A. Bagla, V. Chan, P. Borgogno, N. Minouei, M. Schofield, T. Correll, J. Faessel, C. McQueen, M. Rivera, G. Bergman, K. Plioplys, K. Remige, L. Ruff, I. Hauser, K. Thornton and A. Nguyen for their help in processing samples, and E. Sibert for her thoughtful review. We thank G. Williams and I. Knapp for their help in compiling and interpreting the sedimentation data, and Y. Papastamatiou and J. Eurich for discussions about shark diversity. We also thank the Smithsonian National Museum of Natural History Museum Support Center Division of Fishes staff, especially D. Pitassy, K. Murphy, L. Parenti, S. Raredon and collection manager J. Williams, for facilitating access to their ichthyology collections. Finally, we thank Lee Hsiang Liow and four anonymous reviewers for their insightful comments. This research was conducted under U.S. Fish and Wildlife special use permits (#12533-14011, #12533-13011, #12533-12011, #12533-11007, #12533-10011, #12533-09010, #12533-08011 and #12533-07006), and the methods were carried out in accordance with relevant guidelines and regulations stated in our Institutional Animal Care and Use Committee, University of California, Santa Barbara, Protocol no. 856. Study collaboration and funding were provided by the U.S. Department of the Interior, Bureau of Ocean Energy Management, Environmental Studies Program, Washington, DC under Agreement Number MP1400039 (K.D.L.). Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government. Additional funding was obtained from the Alfred P. Sloan Foundation (D.J.M.), the Swerdlow Family (D.J.M.), the Worster Family (E.M.D.), the Sistema Nacional de Investigadores of SENACYT (A.O.), the Marisla Foundation (J.E.C.) and the Victoria University of Wellington, New Zealand (J.P.A.G.). E.M.D. is supported by a UC Santa Barbara Chancellor's Fellowship. This is contribution PARC-155 of the Palmyra Atoll Research Consortium. The authors declare no competing financial interests.

AUTHORS' CONTRIBUTIONS

E.M.D., A.O., K.D.L., D.J.M. and R.D.N. designed the study and methodology; E.M.D. and K.D.L. collected the sediment samples; J.E.C., D.J.M., D.B. and J.P.A.G. contributed data; E.M.D. processed the samples and analysed the data; G.V.D. assisted with the analysis; E.M.D. and A.O. wrote the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available at the Dryad Data Repository https://doi.org/10.25349/D9CP4C (Dillon et al., 2020)

ORCID

Erin M. Dillon https://orcid.org/0000-0003-0249-027X
Kevin D. Lafferty https://orcid.org/0000-0001-7583-4593
Douglas J. McCauley https://orcid.org/0000-0002-8100-653X
Darcy Bradley https://orcid.org/0000-0003-2581-8768
Richard D. Norris https://orcid.org/0000-0001-5288-1733
Graziella V. DiRenzo https://orcid.org/0000-0001-5264-4762
Jonathan P. A. Gardner https://orcid.org/0000-0002-6943-2413
Aaron O'Dea https://orcid.org/0000-0001-5495-4764

REFERENCES

Albano, P. G., Filippova, N., Steger, J., Kaufman, D. S., Tomašových, A., Stachowitsch, M., & Zuschin, M. (2016). Oil platforms in the Persian (Arabian) Gulf: Living and death assemblages reveal no effects. *Continental Shelf Research*, *121*, 21–34. https://doi.org/10.1016/j.csr.2015.12.007

Barker, R. J., Schofield, M. R., Link, W. A., & Sauer, J. R. (2018). On the reliability of *N*-mixture models for count data. *Biometrics*, *74*(1), 369–377. https://doi.org/10.1111/biom.12734

Behrensmeyer, A. K., Kidwell, S. M., & Gastaldo, R. A., (2000). Taphonomy and paleobiology. *Paleobiology*, *26*, 103–147. https://doi.org/10.1017/S0094837300026907

Bloesch, J., & Burns, N. M. (1980). A critical review of sediment trap technique. *Aquatic Sciences*, *42*(1), 15–55.

Bradley, D., Conklin, E., Papastamatiou, Y. P., McCauley, D. J., Pollock, K., Pollock, A., … Caselle, J. E. (2017). Resetting predator baselines in coral reef ecosystems. *Scientific Reports*, *7*, 43131. https://doi.org/10.1038/srep43131

Bradley, D., Papastamatiou, Y., & Caselle, J. (2017). No persistent behavioural effects of SCUBA diving on reef sharks. *Marine Ecology Progress Series*, *567*, 173–184. https://doi.org/10.3354/meps12053

Burgess, G. H., Beerkircher, L. R., Cailliet, G. M., Carlson, J. K., Cortés, E., Goldman, K. J., … Simpfendorfer, C. A. (2005). Is the collapse of shark populations in the Northwest Atlantic Ocean and Gulf of Mexico real? *Fisheries*, *30*(10), 19–26. https://doi.org/10.1577/1548-8446(2005)30[19:ITCOSP]2.0.CO;2

Cisneros-Montemayor, A. M., Barnes-Mauthe, M., Al-Abdulrazzak, D., Navarro-Holm, E., & Sumaila, U. R. (2013). Global economic value of shark ecotourism: Implications for conservation. *Oryx*, *47*(3), 381–388. https://doi.org/10.1017/S0030605312001718

Clark, O. (2008). *The recent carbonate sediments of Palmyra Atoll, Northern Line Islands, Central Pacific Ocean*. MSc thesis, Victoria University of Wellington, New Zealand.

Collen, J. D., Baker, J. A., Dunbar, R. B., Rieser, U., Gardner, J. P. A., Garton, D. W., & Christiansen, K. J. (2011). The atmospheric lead record preserved in lagoon sediments at a remote equatorial Pacific location: Palmyra Atoll, northern Line Islands. *Marine Pollution Bulletin*, *62*, 251–257. https://doi.org/10.1016/j.marpolbul.2010.11.004

Collen, J. D., Garton, D. W., & Gardner, J. P. A. (2009). Shoreline changes and sediment redistribution at Palmyra Atoll (Equatorial Pacific

Ocean): 1874-Present. *Journal of Coastal Research*, *25*(3), 711–722. https://doi.org/10.2112/08-1007.1

Cramer, K. L., O'Dea, A., Clark, T. R., Zhao, J., & Norris, R. D. (2017). Prehistorical and historical declines in Caribbean coral reef accretion rates driven by loss of parrotfish. *Nature Communications*, *8*, 14160. https://doi.org/10.1038/ncomms14160

Dillon, E. M., Lafferty, K. D., McCauley, D. J., Bradley, D., Norris, R. D., Caselle, J. E., … O'Dea, A., (2020), *Data from: Dermal denticle assemblages in coral reef sediments correlate with conventional shark surveys*. v2, Dataset, Santa Barbara, CA: UC Santa Barbara. https://doi.org/10.25349/D9CP4C

Dillon, E. M., Norris, R. D., & O'Dea, A. (2017). Dermal denticles as a tool to reconstruct shark communities. *Marine Ecology Progress Series*, *566*, 117–134. https://doi.org/10.3354/meps12018

Doyle, P. S., & Riedel, W. R. (1979).Ichthyoliths: Present status of taxonomy and stratigraphy of microscopic fish skeletal debris. Scripps Institution of Oceanography Reference Series, 79-16. Scripps Institution of Oceanography, University of California, San Diego.

Ferretti, F., Worm, B., Britten, G. L., Heithaus, M. R., & Lotze, H. K. (2010). Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters*, *13*, 1055–1071. https://doi.org/10.1111/j.1461-0248.2010.01489.x

Ferrón, H. G., & Botella, H. (2017). Squamation and ecology of thelodonts. *PLoS ONE*, *12*(2), e0172781. https://doi.org/10.1371/journal.pone.0172781

Ferrón, H., Pla, C., Martínez-Pérez, C., Escudero-Mozo, M. J., & Botella, H. (2014). Morphometric discriminant analysis of isolated chondrichthyan scales for palaeoecological inferences: The Middle Triassic of the Iberian Chain (Spain) as a case of study. *Journal of Iberian Geology*, *40*(1), 87–97. https://doi.org/10.5209/rev_JIGE.2014.v40.n1.44089

Fiske, I., & Chandler, R. (2011). Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, *43*(10), 1–23.

Flessa, K. W., Cutler, A. H., & Meldahl, K. H. (1993). Time and taphonomy: Quantitative estimates of time-averaging and stratigraphic disorder in a shallow marine habitat. *Paleobiology*, *19*(2), 266–286. https://doi.org/10.1017/S0094837300015918

Folk, R. L., & Ward, W. C. (1957). Brazos River Bar: A study in the significance of grain size parameters. *Journal of Sedimentary Petrology*, *27*(1), 3–26.

Gardner, J. P. A., Bartz, R. J., Brainard, R. E., Collen, J. D., Dunbar, R. B., Garton, D. W., & Powell, S. (2014). Conservation management options and actions: Putative decline of coral cover at Palmyra Atoll, Northern Line Islands, as a case study. *Marine Pollution Bulletin*, *84*, 182–190. https://doi.org/10.1016/j.marpolbul.2014.05.013

Gardner, J. P. A., Garton, D. W., Collen, J. D., & Zwartz, D. (2014). Distant storms as drivers of environmental change at Pacific Atolls. *PLoS ONE*, *9*(1), e87971. https://doi.org/10.1371/journal.pone.0087971

Heck, K. L. Jr, van Belle, G., & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, *56*(6), 1459–1461. https://doi.org/10.2307/1934716

Helms, P. B., & Riedel, W. R. (1971). Skeletal debris of fishes. In E. L. Winterer & W. R. Riedel (Eds.), *Initial reports of the deep sea drilling project* (Vol. 7 (Part 2), pp. 1709–1720). Washington, DC: U.S. Government Printing Office.

Kéry, M. (2018). Identifiability in *N*-mixture models: A large-scale screening test with bird data. *Ecology*, *99*(2), 281–288. https://doi.org/10.1002/ecy.2093

Kidwell, S. M. (2009). Evaluating human modification of shallow marine ecosystems: Mismatch in composition of molluscan living and time-averaged death assemblages. In G. P. Dietl & K. W. Flessa (Eds.), *Conservation paleobiology: Using the past to manage the future*. The Paleontological Society Papers (Vol. *15*, pp. 113–139). Chicago, IL: University of Chicago Press, The Paleontological Society.

Kidwell, S. M. (2013). Time-averaging and fidelity of modern death assemblages: Building a taphonomic foundation for conservation palaeobiology. *Palaeontology*, *56*(3), 487–522. https://doi.org/10.1111/pala.12042

Kidwell, S. M., & Flessa, K. W. (1995). The quality of the fossil record: Populations, species, and communities. *Annual Review of Ecology and Systematics*, *26*(1), 269–299. https://doi.org/10.1146/annurev.es.26.110195.001413

Knape, J., Arlt, D., Barraquand, F., Berg, Å., Chevalier, M., Pärt, T., … Żmihorski, M. (2018). Sensitivity of binomial *N*-mixture models to overdispersion: The importance of assessing model fit. *Methods in Ecology and Evolution*, *9*(10), 2102–2114. https://doi.org/10.1111/2041-210X.13062

Knapp, I. S. S., Williams, G. J., Carballo, J. L., Cruz-Barraza, J. A., Gardner, J. P. A., & Bell, J. J. (2013). Restriction of sponges to an atoll lagoon as a result of reduced environmental quality. *Marine Pollution Bulletin*, *66*(1–2), 209–220. https://doi.org/10.1016/j.marpolbul.2012.08.017

Kosnik, M. A., Hua, Q., Kaufman, D. S., & Zawadzki, A. (2015). Sediment accumulation, stratigraphic order, and the extent of time-averaging in lagoonal sediments: A comparison of 210Pb and 14C/amino acid racemization chronologies. *Coral Reefs*, *34*(1), 215–229. https://doi.org/10.1007/s00338-014-1234-2

Kowalewski, M. (1996). Time-averaging, overcompleteness, and the geological record. *Journal of Geology*, *104*, 317–326. https://doi.org/10.1086/629827

Levy, K. J. (1978). Some empirical power results associated with Welch's robust analysis of variance technique. *Journal of Statistical Computation and Simulation*, *8*(1), 43–48. https://doi.org/10.1080/00949657808810246

Lin, C. H., De Gracia, B., Pierotti, M. E. R., Andrews, A. H., Griswold, K., & O'Dea, A. (2019). Reconstructing reef fish communities using fish otoliths in coral reef sediments. *PLoS ONE*, *14*(6), e0218413. https://doi.org/10.1371/journal.pone.0218413

Link, W. A., Schofield, M. R., Barker, R. J., & Sauer, J. R. (2018). On the robustness of *N*-mixture models. *Ecology*, *99*(7), 1547–1551. https://doi.org/10.1002/ecy.2362

Lotze, H. K., & Worm, B. (2009). Historical baselines for large marine animals. *Trends in Ecology & Evolution*, *24*(5), 254–262. https://doi.org/10.1016/j.tree.2008.12.004

McCauley, D. J., McLean, K. A., Bauer, J., Young, H. S., & Micheli, F. (2012). Evaluating the performance of methods for estimating the abundance of rapidly declining coastal shark populations. *Ecological Applications*, *22*(2), 385–392. https://doi.org/10.1890/11-1059.1

McClanahan, T. R., Graham, N. A. J., Maina, J., Chabanet, P., Bruggemann, J. H., & Polunin, N. V. C. (2007). Influence of instantaneous variation on estimates of coral reef fish populations and communities. *Marine Ecology Progress Series*, *340*, 221–234. https://doi.org/10.3354/meps340221

Mundy, B. C., Wass, R., DeMartini, E., Greene, B., Zgliczynski, B., Schroeder, R. E., & Musberger, C. (2010). Inshore fishes of Howland Island, Baker Island, Jarvis Island, Palmyra Atoll, and Kingman Reef. *Atoll Research Bulletin*, *585*, 1–131. https://doi.org/10.5479/si.00775630.585

Muñoz-Chápuli, R. (1985). Sobre la clasificacion tipologica del esqueleto dermico de escualos (Chondrichthyes). *Miscellania Zoológica*, *9*, 396–400.

Myers, R. A., & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, *423*, 280–283. https://doi.org/10.1038/nature01610

O'Dea, A., Dillon, E. M., Altieri, A. H., & Lepore, M. L. (2017). Look to the past for an optimistic future. *Conservation Biology*, *31*(6), 1221–1222. https://doi.org/10.1111/cobi.12997

Olszewski, T. D. (2004). Modeling the influence of taphonomic destruction, reworking, and burial on time-averaging in fossil accumulations. *Palaios*, *19*(1), 39–50. https://doi.org/10.1669/0883-1351(2004)019<0039:MTIOTD>2.0.CO;2

Pandolfi, J. M., & Jackson, J. B. C. (2006). Ecological persistence interrupted in Caribbean coral reefs. *Ecology Letters*, *9*(7), 818–826. https://doi.org/10.1111/j.1461-0248.2006.00933.x

Papastamatiou, Y. P., Bodey, T. W., Friendlander, A. M., Lowe, C. G., Bradley, D., Weng, K., … Caselle, J. E. (2017). Spatial separation without territoriality in shark communities. *Oikos*, *127*(6), 767–779. https://doi.org/10.1111/oik.04289

Papastamatiou, Y. P., Caselle, J. E., Friedlander, A. M., & Lowe, C. G. (2009). Distribution, size frequency, and sex ratios of blacktip reef sharks *Carcharhinus melanopterus* at Palmyra Atoll: A predator-dominated ecosystem. *Journal of Fish Biology*, *75*(3), 647–654. https://doi.org/10.1111/j.1095-8649.2009.02329.x

Papastamatiou, Y. P., Friedlander, A. M., Caselle, J. E., & Lowe, C. G. (2010). Long-term movement patterns and trophic ecology of blacktip reef sharks (*Carcharhinus melanopterus*) at Palmyra Atoll. *Journal of Experimental Marine Biology and Ecology*, *386*, 94–102. https://doi.org/10.1016/j.jembe.2010.02.009

Papastamatiou, Y. P., Lowe, C. G., Caselle, J. E., & Friedlander, A. M. (2009). Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. *Ecology*, *90*(4), 996–1008. https://doi.org/10.1890/08-0491.1

Papastamatiou, Y., Wood, C., Bradley, D., McCauley, D., Pollock, A., & Caselle, J. (2014). First records of the sicklefin lemon shark, *Negaprion acutidens*, at Palmyra Atoll, central Pacific: A recent colonization event? *Marine Biodiversity Records*, *7*, 1–3. https://doi.org/10.1017/S175526721400116X

R Core Team. (2019). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Reif, W. E. (1985). Squamation and ecology of sharks. *Courier Forschungsinstitut Senckenberg*, *78*, 1–255.

Riesenfeld, A. (1950). *The megalithic culture of Melanesia*. Leiden: E. J. Brill.

Roff, G., Clark, T. R., Reymond, C. E., Zhao, J.-X., Feng, Y., McCook, L. J., … Pandolfi, J. M. (2013). Palaeoecological evidence of a historical collapse of corals at Pelorus Island, inshore Great Barrier Reef, following European settlement. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122100. https://doi.org/10.1098/rspb.2012.2100

Roff, G., Doropoulos, C., Rogers, A., Bozec, Y.-M., Krueck, N. C., Aurellado, E., … Mumby, P. J. (2016). The ecological role of sharks on coral reefs. *Trends in Ecology and Evolution*, *31*(5), 395–407. https://doi.org/10.1016/j.tree.2016.02.014

Rogers, J. S., Monismith, S. G., Fringer, O. B., Koweek, D. A., & Dunbar, R. B. (2017). A coupled wave-hydrodynamic model of an atoll with high friction: Mechanisms for flow, connectivity, and ecological implications. *Ocean Modelling*, *110*, 66–82. https://doi.org/10.1016/j.ocemod.2016.12.012

Royle, J. A. (2004). *N*-mixture models for estimating population size from spatially replicated counts. *Biometrics*, *60*(1), 108–115. https://doi.org/10.1111/j.0006-341X.2004.00142.x

Sadler, P. M. (1981). Sediment accumulation rates and the completeness of stratigraphic sections. *The Journal of Geology*, *89*(5), 569–584. https://doi.org/10.1086/628623

Shieh, G., & Jan, S. L. (2013). Determining sample size with a given range of mean effects in one-way heteroscedastic analysis of variance. *Journal of Experimental Education*, *81*(3), 281–294. https://doi.org/10.1080/00220973.2012.731020

Sibert, E. C., Cramer, K. L., Hastings, P. A., & Norris, R. D. (2017). Methods for isolation and quantification of microfossil fish teeth and shark dermal scales (ichthyoliths) from marine sediments. *Palaeontol Electron*, *20*, 1–14. https://doi.org/10.26879/677

Sibert, E. C., & Norris, R. D. (2015). New age of fishes initiated by the Cretaceous-Paleogene mass extinction. *Proceedings of the National Academy of Sciences USA*, *112*(28), 8537–8542. https://doi.org/10.1073/pnas.1504985112

Tomašových, A., Gallmetzer, I., Haselmair, A., Kaufman, D. S., Mavrič, B., & Zuschin, M. (2019). A decline in molluscan carbonate production driven by the loss of vegetated habitats encoded in the Holocene sedimentary record of the Gulf of Trieste. *Sedimentology*, *66*(3), 781–807. https://doi.org/10.1111/sed.12516

Tomašových, A., & Kidwell, S. M. (2011). Accounting for the effects of biological variability and temporal autocorrelation in assessing the preservation of species abundance. *Paleobiology*, *37*(2), 332–354. https://doi.org/10.1666/09506.1

Tomašových, A., & Kidwell, S. M. (2017). Nineteen-century collapse of a benthic marine ecosystem on the open continental shelf. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170328. https://doi.org/10.1098/rspb.2017.0328

Tomašových, A., Kidwell, S. M., Alexander, C. R., & Kaufman, D. S. (2019). Millennial-scale age offsets within fossil assemblages: Result of bioturbation below the taphonomic active zone and out-of-phase production. *Paleoceanography and Paleoclimatology*, *34*(6), 954–977. https://doi.org/10.1029/2018PA003553

Ward-Paige, C., Flemming, J. M., & Lotze, H. K. (2010). Overestimating fish counts by non-instantaneous visual censuses: Consequences for population and community descriptions. *PLoS ONE*, *5*(7), 1–9. https://doi.org/10.1371/journal.pone.0011722

Williams, G. J., Knapp, I. S., Maragos, J. E., & Davy, S. K. (2011). Proximate environmental drivers of coral communities at Palmyra Atoll: Establishing baselines prior to removing a WWII military causeway. *Marine Pollution Bulletin*, *62*(8), 1842–1851. https://doi.org/10.1016/j.marpolbul.2011.05.002

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dillon EM, Lafferty KD, McCauley DJ, et al. Dermal denticle assemblages in coral reef sediments correlate with conventional shark surveys. *Methods Ecol Evol*. 2020;00:1–14. https://doi.org/10.1111/2041-210X.13346