Received: 28 September 2022 | Accepted: 14 January 2023

DOI: 10.1111/jfb.15326

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Are shark teeth proxies for functional traits? A framework to infer ecology from the fossil record

Jack A. Cooper[1] | John N. Griffin[1] | René Kindlimann[2] | Catalina Pimiento[1,3,4]

[1]Department of Biosciences, Swansea University, Swansea, UK

[2]Haimuseum und Sammlung R. Kindlimann, Aathal-Seegräben, Switzerland

[3]Paleontological Institute and Museum, University of Zurich, Zurich, Switzerland

[4]Smithsonian Tropical Research Institute, Balboa, Panama

Correspondence
Jack A. Cooper, Department of Biosciences, Swansea University, Swansea, UK.
Email: 2022207@swansea.ac.uk

Funding information
Fisheries Society of the British Isles, Grant/Award Number: PhD studentship; Swiss National Science Foundation, Grant/Award Number: PRIMA 185798; University of Florida, Grant/Award Number: International Travel Grant

Abstract

Modern sharks have an evolutionary history of at least 250 million years and are known to play key roles in marine systems, from controlling prey populations to connecting habitats across oceans. These ecological roles can be quantified based on their functional traits, which are typically morphological (*e.g.*, body size) or behavioural (*e.g.*, feeding and diet). Nonetheless, the understanding of such roles of extinct sharks is limited due to the inherent incompleteness of their fossil record, which consists mainly of isolated teeth. As such, establishing links between tooth morphology and ecological traits in living sharks could provide a useful framework to infer sharks' ecology from the fossil record. Here, based on extant sharks from which morphological and behavioural characteristics are known, the authors assess the extent to which isolated teeth can serve as proxies for functional traits. To do so, they first review the scientific literature on extant species to evaluate the use of shark dental characters as proxies for ecology to then perform validation analyses based on an independent data set collected from museum collections. Their results reveal that 12 dental characters have been used in shark literature as proxies for three functional traits: body size, prey preference and feeding mechanism. From all dental characters identified, tooth size and cutting edge are the most widely used. Validation analyses suggest that seven dental characters – crown height, crown width, cutting edge, lateral cusplets, curvature, longitudinal outline and cross-section outline – are the best proxies for the three functional traits. In particular, tooth size (crown height and width) was found to be a reliable proxy of all three traits; the presence of serrations on the cutting edge was one of the best proxies for prey preference; and tooth shape (longitudinal outline) and the presence of lateral cusplets were among the best indicators of feeding mechanism. Overall, the authors' results suggest that in the absence of directly measurable traits in the fossil record, these seven dental characters (and different combinations of them) can be used to quantify the ecological roles of extinct sharks. This information has the potential to provide key insights into how shark functional diversity has changed through time, including their ecological responses to extinction events.

KEYWORDS
body size, dental characters, ecological role, feeding mechanism, prey preference, tooth morphology

1 | INTRODUCTION

With over 500 extant species living in almost all marine habitats (Weigmann, 2016), sharks (Elasmobranchii, Selachii) play key ecological roles in today's oceans. Some well-studied roles include (a) apex predators (*e.g.*, the tiger shark, *Galeocerdo cuvier*), consuming large quantities of biomass and regulating the populations of their prey (Ferretti *et al*., 2010; Hammerschlag *et al*., 2019; Myers *et al*., 2007); (b) mesopredators (*e.g.*, the grey reef shark, *Carcharhinus amblyrhynchos*), a dual role as consumers of smaller organisms and as potential prey for larger carnivores (Barley *et al*., 2019; Frisch *et al*., 2016; Heupel *et al*., 2014; Roff *et al*., 2016); and (c) highly mobile animals (*e.g.*, the great white shark, *Carcharodon carcharias*), connecting habitats and populations and potentially transferring nutrients across sites (Bonfil *et al*., 2005; Weng *et al*., 2007; Williams *et al*., 2018). Several sharks are therefore considered keystone species given the large effects they can have on ecosystems (Heupel *et al*., 2014; Hammerschlag *et al*., 2019; but see Roff *et al*., 2016).

Species' ecologies can be quantified based on their functional traits – measurable intrinsic characteristics that broadly reflect how resources are obtained, used and transported, which ultimately impact biodiversity and how the ecosystem operates (Mouillot *et al*., 2013; Petchey & Gaston, 2006). A key functional trait in sharks is body size, which is fundamental to inform on the size of the prey they consume (Heupel *et al*., 2014; Lucifora *et al*., 2009) and the distance they can travel, and thus their ability to connect habitats and transport nutrients (Doughty *et al*., 2016; Estupiñán-Montaño *et al*., 2021). Another essential trait in shark ecology is diet (*i.e.*, the prey items they consume), which is inherently linked to trophic level, and therefore the ability of some sharks to alter ecosystem structure, resource distribution and partitioning *via* top-down control both directly through prey consumption and indirectly by altering prey behaviour and distribution (Burkholder *et al*., 2013; Cortés, 1999; Papastamatiou *et al*., 2006). Finally, feeding mechanism is an important functional trait in sharks, as it determines dietary specialisation (Ciampaglio *et al*., 2005), which can affect ecosystem structure by mitigating interspecific competition and influencing prey abundance and diversity (Munroe *et al*., 2013). Overall, these functional traits can provide fundamental information on ecological roles shark species play in marine systems.

The fossil record of modern sharks has evidenced their long evolutionary history, which dates back to at least 250 MYA (Cappetta, 2012). Sharks are represented in the fossil record primarily by their isolated teeth, which they shed constantly throughout their lives and, unlike their cartilaginous skeletons, have a hard composition, resulting in high preservation potential (Cappetta, 2012; Kent, 1994). Shark teeth are therefore abundant in the marine fossil record (Cappetta, 2012; Hubbell, 1996) and are often the only information available for understanding the ecological roles sharks played in the past. Importantly, many fossil sharks have living representatives (Paillard *et al*., 2020; Pimiento & Benton, 2020), allowing scientists to infer aspects of their natural history not preserved in the geological record.

Multiple studies have proposed that some shark functional traits are correlated to tooth morphology (*e.g.*, Ciampaglio *et al*., 2005; Frazzetta, 1988). As such, tooth measurements (here, dental characters) have been used to infer the ecology of fossil taxa. For instance, tooth height has been widely used as an indicator of body size (*e.g.*, Condamine *et al*., 2019; Shimada *et al*., 2020), whereas the presence of serrations on the cutting edge has been used to infer diet (*i.e.*, prey preference) and feeding mechanism (*e.g.*, Ciampaglio *et al*., 2005; Kent, 1994). Nonetheless, other studies have suggested that links between shark tooth morphology and ecology are cloudy at best. For example, biomechanical analyses indicate that different shark tooth morphologies lack functional differences, providing little support for their use as proxies for feeding mechanisms (Whitenack *et al*., 2011; Whitenack & Motta, 2010). Therefore, the extent to which measurable characteristics of shark dentition can be used to infer functional traits remains unclear. A deeper understanding of the relationships between dental characters and functional traits could allow a wider use of shark teeth as ecological proxies. This would be particularly useful in palaeontology, as the fossil record of sharks is mostly limited to isolated teeth. Connecting shark teeth with ecological traits can therefore provide insight into the roles that sharks played in ancient ecosystems and how they responded to past environmental changes.

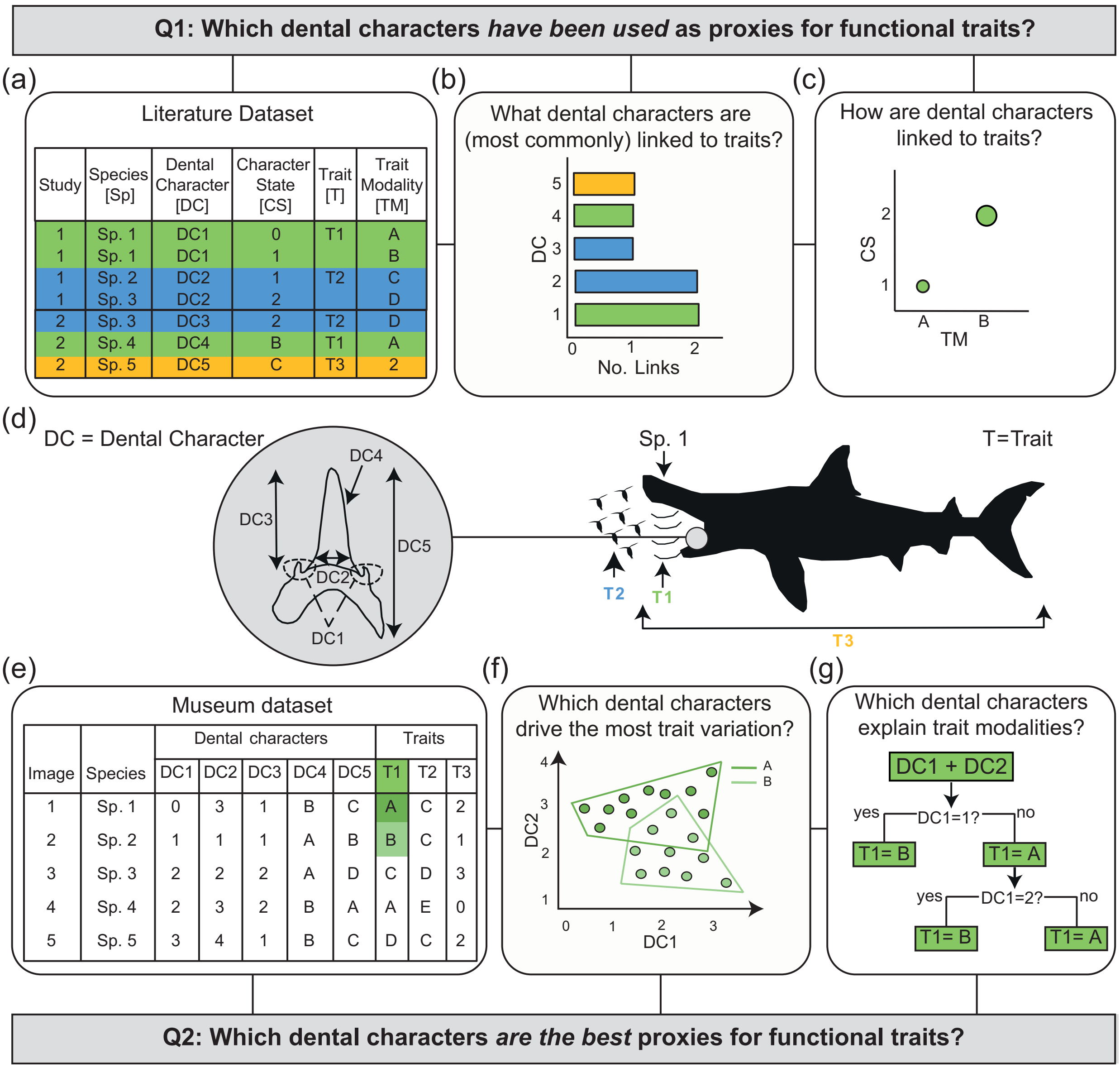
Here, the authors evaluate the use of shark dental characters as proxies for functional traits (Figure 1). They ask two questions: (Q1) which dental characters have been used as proxies for functional traits? and (Q2) which of these dental characters are the best proxies for functional traits? To answer these questions, they (a) review the literature (Figure 1a–c) focusing on extant sharks because their ecology is well documented (Ebert *et al*., 2021; Weigmann, 2016) and (b) use two validation analyses on an independent jaw data set of extant species (Figure 1e–g). Their results provide a framework to infer shark functional traits based on their teeth, which can potentially be applied to the fossil record.

2 | MATERIALS AND METHODS

2.1 | Q1 Which shark dental characters have been used as proxies for functional traits?

2.1.1 | Data

The authors conducted a survey of the literature to identify published studies that measure or record dental characters from extant shark teeth and link them to functional traits. The survey was performed in



Study	Species [Sp]	Dental Character [DC]	Character State [CS]	Trait [T]	Trait Modality [TM]
1	Sp. 1	DC1	0	T1	A
1	Sp. 1	DC1	1		B
1	Sp. 2	DC2	1	T2	C
1	Sp. 3	DC2	2		D
2	Sp. 3	DC3	2	T2	D
2	Sp. 4	DC4	B	T1	A
2	Sp. 5	DC5	C	T3	2

		Dental characters					Traits		
Image	Species	DC1	DC2	DC3	DC4	DC5	T1	T2	T3
1	Sp. 1	0	3	1	B	C	A	C	2
2	Sp. 2	1	1	1	A	B	B	C	1
3	Sp. 3	2	2	2	A	D	C	D	3
4	Sp. 4	2	3	2	B	A	A	E	0
5	Sp. 5	3	4	1	B	C	D	C	2

FIGURE 1 Conceptual approach. Q1 is answered using the following steps: (a) taxonomic, dental character (DC) and corresponding functional trait (T) data are extracted from the literature; (b) the dental characters most commonly and broadly used as proxies for individual traits are identified; and (c) individual links between dental character states (CS) and trait modalities (TM) are quantified. (d) A graphical example of dental characters and their use as proxies for functional traits. Q2 is answered using the following steps: (e) dental characters and trait values are recorded from jaw specimens from museum collections; and validation analyses performed on this data, specifically (f) PCA to identify which dental characters drive trait variation; and (g) classification tree analysis to find which dental characters best explain trait values.

the academic search engines Google Scholar, Scopus and Web of Science using the following terms: (a) Shark + tooth OR teeth + morphology, (b) Shark + tooth OR teeth + trait, (c) Shark + tooth OR teeth + ecology and (d) Shark + tooth OR teeth + morphology + function. Once traits studied in literature were identified, the authors repeated these searches using those traits as additional terms, for example, (e) Shark + tooth OR teeth + body size.

From each study returned, the authors extracted the following information from the main text, tables, figures and supplementary material: taxonomy (*i.e.*, order, family, genus and species), tooth position if reported (*i.e.*, upper or lower), dental character recorded (*e.g.*, lateral cusplets; Figure 2) and its character state (*e.g.*, present or absent; Table 1), the functional trait linked to the dental character (*e.g.*, prey preference) and trait values (*e.g.*, plankton, invertebrates, fishes, high vertebrates; Figure 1a; Supporting Information Data S1). In addition, the authors recorded whether each taxon was represented in the fossil record by checking against Paillard *et al.* (2020) and the Paleobiology Database (http://paleobiodb.org/; last accessed August 2022).

The functional trait data were tabulated as follows. (a) Body size was recorded as total length (distance from the snout to the tip of the caudal fin) in centimetres. The authors further assigned these data to

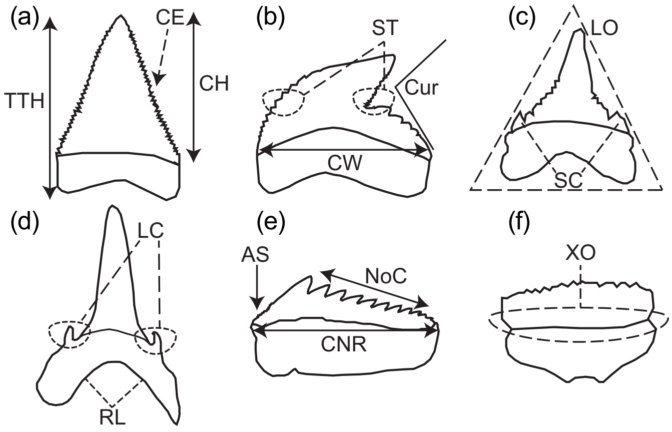


FIGURE 2 Schematic illustrations of all dental characters identified as proxies for functional trait in the literature review. Abbreviations are as follows: (a) CH, crown height; CE, cutting edge; TTH, total tooth height. (b) CW, crown width; Cur, curvature; ST, serration type. (c) LO, longitudinal outline; SC, serrational cusplets. (d) LC, lateral cusplets; RL, root lobes. (e) AS, acrocone serrations; NoC, number of cusps; CNR, cusp number ratio. (f) XO, cross-section outline. Descriptions for each dental character are presented in Table 1. Teeth used to illustrate these characters are from the following species: (a) *Carcharodon carcharias*, (b) *Galeocerdo cuvier*, (c) a juvenile *C. carcharias*, (d) *Carcharias taurus*, (e) *Hexanchus griseus* and (f) *Mustelus canis*

four size classes to facilitate analyses (Table 2). (b) Prey preference was defined as the most common prey item consumed as adults and was assigned using four broad categorisations (Table 2) following previous work (Pimiento *et al*., 2020). It should be noted that many shark species are opportunistic generalists feeding on a variety of food (Wetherbee & Cortés, 2004), with the prey preference of some species varying seasonally (Baremore *et al*., 2010; Dicken *et al*., 2017; MacNeil *et al*., 2005). Previous works attempting to standardise the diet composition of sharks have outlined up to 11 prey categories (Cortés, 1999). Nonetheless, even this fine categorisation scheme fails to fully capture the complex dietary spectrum of sharks. For example, the bonnethead shark (*Sphyrna tiburo*) primarily feeds on crustaceans (Mara *et al*., 2010) but also consumes seagrass (Leigh *et al*., 2018). Similarly, the whale shark (*Rhincodon typus*) mostly filter-feeds on plankton, but it has also been reported to feed on macroalgae (Meekan *et al*., 2022). Although the authors' broad prey preference categorisation scheme does not account for the full range of prey sharks can have during their lifetime, it allows to capture the most common diet of shark species, facilitating extrapolation to the fossil record. (c) Feeding mechanism was defined in terms of dentition types, which describe how sharks capture and process prey (Cappetta, 2012; Ciampaglio *et al*., 2005; Kent, 1994; Motta, 2004). The authors identified four different schemes defining such dentition types from the literature (Table S1) and selected Kent (1994) to record feeding mechanism hereafter as it was the only one that considered filter feeding as a separate mechanism ("vestigial"). Finally, although life stage is another trait associated with sharks' ecological roles (Tavares *et al*., 2019) and has been suggested to be linked to crown width changes in *C. carcharias*, particularly in males (French *et al*., 2017), the authors did not consider it here as its relations with tooth morphology have not been widely studied across shark species (Cappetta, 2012).

The authors defined *links* between dental characters and functional traits as any occurrence in literature in which a dental character is considered explanatory of a functional trait (Figure 1d). They assigned each link to two categories based on whether it was made quantitatively (*i.e*., established using an analytical approach such as a linear regression) or qualitatively (*i.e*., assigned based on observations or assumptions). Finally, they evaluated whether the collected data were independent (*i.e*., if the link was made using the study's own data and not based on previous studies; Supporting Information Data S2) to remove possible influence of prior assumptions.

2.1.2 | Analyses

All the authors' analyses were made using the data from the literature deemed to be independent. The authors first quantified the motivation for each study. Then, they assessed the number of extant orders, families, genera and species represented in the data following the nomenclature by Weigmann (2016). They additionally examined the distribution of crown heights and crown widths to assign size-based categorisations to these dental characters (Figure S1; Figure 2a,b; Table 1). Finally, they assessed the frequency in which dental characters are used as a proxy to each functional trait (Figure 1b), determined the dental characters most broadly used across the shark phylogeny and quantified the times each character state was linked to specific trait values (Figure 1c). Although all tooth positions were considered in the authors' analyses, for body size they ran an additional analysis using only anterior teeth as they have been proposed to be more directly associated to sharks' total length than other positions (Condamine *et al*., 2019; Shimada *et al*., 2020).

2.2 | Q2 Which shark dental characters are the best proxies for functional traits?

2.2.1 | Data

The authors collected an independent tooth data set from all species identified in the literature review (Figure 1e) based on images of authentic jaw specimens (Supporting Information Data S3). Specimens were housed at the following museum collections: the British Natural History Museum (NHM); the Paleontological Institute and Museum, University of Zurich (PIMUZ); the collection of Haimuseum und Sammlung R. Kindlimann (RKC, a private collection with public access); the Royal Belgian Institute of Natural Sciences (RBINS); the Calvert Marine Museum (CMM); and the Gordon Hubbell Collection (GHC, Jaws International, Gainesville, FL), where each specimen was photographed (see Data Availability Statement).

TABLE 1 Summary of 14 dental characters identified by the literature review as proxies for each recorded functional trait, including two that were linked only to life stage

Character (abbreviation)	Description	States	Functional traits
Acrocone serrations (AS)	Serrations present on the main cusp of lower Hexanchiformes teeth (Adnet, 2006)	0 – absent 1 – present	Life stage
Cross-section outline (XO)	The shape profile of the tooth in a cross-section (Ciampaglio *et al*., 2005)	1 – round 2 – oval 3 – triangular 4 – lens 5 – rectangular 6 – polygonal 7 – multi-indented lens	Feeding mechanism
Crown height (CH)	Maximum vertical enamel height	1 – small (<5 mm) 2 – medium (5–20 mm) 3 – large (20–50 mm) 4 – huge (>50 mm)	Body size, prey preference, feeding mechanism
Crown width (CW)	Width of the tooth crown	1 – slender (<10 mm) 2 – wide (10–35 mm) 3 – vast (>35 mm)	Body size, prey preference, feeding mechanism
Curvature (Cur)	Angle of the main cusp	0 – none 1 – slight 2 – present	Prey preference, feeding mechanism
Cusp number ratio (CNR)	Number of cusps/crown width in Hexanchiformes (Adnet, 2006)	Number of cusps/crown width	Body size
Cutting edge (CE)	The mesial and distal edge of the main cusp, which can be smooth or serrated	0 – none 1 – smooth 2 – serrated	Prey preference, feeding mechanism
Lateral cusplets (LC)	Small secondary cusps found on either side of the tooth's main cusp	0 – absent 1 – present	Prey preference, feeding mechanism
Longitudinal outline (LO)	The shape profile of the whole tooth (Ciampaglio *et al*., 2005)	1 – triangular 2 – semi-circular 3 – piercing 4 – rectangular 5 – polygonal	Prey preference, feeding mechanism
Number of cusps (NoC)	The total number of cusps on a single tooth, including lateral cusplets	Count data	Body size, feeding mechanism
Root lobes (RL)	Edges of the root at the mesial or distal created by the nutrient groove	0 – none 1 – short 2 – moderate 3 – elongated	Feeding mechanism
Serrational cusplets (SC)	Cusplets developing as serrations on the main cusp (Bemis *et al*., 2015)	0 – absent 1 – present	Life stage
Serration type (ST)	Large primary serrations or small secondary "serrations within serrations" (Moyer & Bemis, 2017)	1 – primary 2 – secondary	Prey preference
Total tooth height (TTH)	Maximum height of the tooth from tip to root edge	1 – small (<5 mm) 2 – medium (5–20 mm) 3 – large (20–50 mm) 4 – huge (>50 mm)	Body size

Note: States for crown height, crown width and total tooth height states are based on tooth size distributions (see Figure S1). States for curvature, longitudinal outline and cross-section outline are based on Ciampaglio *et al*. (2005). Number of cusps is recorded as count data (*i.e.*, 1 = 1 cusp, 2 = 2 cusps, 3 = 3 cusps, etc.). Illustrations for each dental character are provided in Figure 2.

TABLE 2 Summary of the functional traits in sharks linked to dental character proxies in the literature review

Functional trait	Description	Functions	Services	Example study
Body size	Total length in centimetres and categorised in the following classes: 1 – small (1–200 cm) 2 – medium (201–400 cm) 3 – large (401–600 cm) 4 – giant (>600 cm)	Nutrient storage and transport	Nutrient cycling, food provision and promotion of biodiversity	Shimada (2003)
Prey preference	Categories 1 – plankton 2 – invertebrates 3 – fishes 4 – high vertebrates	Nutrient storage and trophic-dynamic regulations of populations	Nutrient cycling, biological control and maintenance of trophic interactions and ecosystem stability	Moyer and Bemis (2017)
Feeding mechanism	Categories 1 – crushing 2 – clutching 3 – grasping 4 – cutting 5 – vestigial	Nutrient storage and trophic-dynamic regulations of populations	Nutrient cycling, biological control and maintenance of trophic interactions and ecosystem stability	Frazzetta (1988)

Note: Categorisations of body size are based on classes from Shimada *et al*. (2020); broad categorisations of prey preference are based on Pimiento *et al*. (2020), and feeding mechanism categorisations are based on homodont dentition types from Kent (1994). Ecosystem functions and services are also recorded following Tavares *et al*. (2019). Example studies returned by the literature review that linked dental characters to each functional trait are included.

To take specimen images, jaws were positioned on a flat surface and photographed from above (*i.e*., at 90°) at the maximum open-gape angle to mitigate potential parallax error. Seven specimens were displayed on vertical walls, in which case they were photographed at 0°. One exception to this protocol was a *Megachasma pelagios* specimen (GHC-9; Supporting Information Data S3), where each jaw was photographed individually due to being separated during its curation. Whenever a taxon was identified to the genus level in the literature review, a jaw of a species of such a genus was selected in its place based on availability.

From each jaw, the authors selected the following upper and lower teeth to measure (a) first anterior, (b) third lateral and (c) final posterior tooth on the left side of the jaw, from the first functional row. The first anterior is the first tooth adjacent to the symphysis, and the final posterior is the last tooth along the mesio-distal axis of the jaw ramus. The third lateral is defined here as the sixth tooth adjacent to the symphysis, following an assumption of three anterior teeth in each jaw, a pattern typically seen in all macrophagous Lamniformes and some Carcharhiniformes (Cullen & Marshall, 2019; Shimada, 2002). These tooth positions were selected to account for monognathic (*i.e*., differences in tooth morphology across individual jaws, which is gradual in most species but particularly strong in Lamniformes and Heterodontiformes; Cappetta, 2012; Shimada, 2002) and dignathic heterodonty (*i.e*., differences between the upper and lower jaws, which is widespread in many species) as this can result in different relationships between dental characters and functional traits. Although the number of tooth files varies significantly between species, the authors' chosen positions account for morphological differences between anterior and posterior teeth (Cappetta, 2012) while also including more distinct lateral teeth of sharks like Lamniformes.

For each tooth selected, the authors measured crown height and crown width in millimetres using ImageJ (Abràmoff *et al*., 2004) and a scale bar present in all photographs. Furthermore, they recorded the states of all other dental characters identified as a trait proxy in literature (Table 1), including tooth size categories as described earlier (Figure S1; Table 1). Total tooth height was not measured from the jaws due to its categorisation being identical to crown height (Table 1). Finally, to each species, they assigned functional trait values (Table 2; Figure 1e) based on Weigmann (2016) and Ebert *et al*. (2021).

Some limitations to authors' data set should be acknowledged. First, given the reduced availability of jaw specimens, the authors were able to photograph only a single specimen per taxon. Second, only 12 specimens (20.7%) had sex data, and 21 (36.2%) had body size or life-stage data available. As such, neither gynandric nor ontogenetic heterodonty (*i.e*., differences in tooth morphology between sexes and life stages, respectively) could be accounted for in these analyses. Nonetheless, whereas monognathic and dignathic heterodonty are known in many shark species, gynandric and ontogenetic heterodonty are more poorly studied in sharks and better studied in rays (Cappetta, 2012). Of the studies that have been conducted, gynandric and ontogenetic heterodonty have been described in only a few species (*e.g*., *C. carcharias*, *Carcharhinus leucas*, *Scyliorhinus stellaris*, *Etmopterus spinax* and *G. cuvier*; Berio *et al*., 2020; Cullen & Marshall, 2019; French *et al*., 2017; Straube & Pollerspöck, 2020; Turtscher *et al*., 2022). Nonetheless, because the aim of this research was to apply resulting dental character–functional trait relationships to isolated fossil teeth (from which life stage and sex are often unknown), the authors contend that the absence of gynandric and ontogenetic heterodonty from their analyses should not distort the interpretation and application of the resulting framework to fossils.

2.2.2 | Analyses

With the museum data set, the authors performed two separate sets of analyses in the R environment (R Core Team, 2017). First, they used PCA to illustrate variation in tooth morphology (*i.e*., morphospace) and associated trait values. Recorded dental characters were used as the variables for these analyses. They used crown height and crown width as both numerical (*i.e*., measured in millimetres) and categorical (*i.e*., size classes) variables to assess the different contributions to morphological variation. Functional trait values (Table 2) were used to define convex hulls along the morphospace, allowing the authors to identify morphological clusters. Overall, their analyses allowed them to identify which dental characters were the most important drivers of variation along the tooth morphospace (Figure 1f). Although exploratory, PCA has been previously used to link shark ecology to both tooth (Ciampaglio *et al*., 2005) and dermal denticle morphology (Dillon *et al*., 2017).

Second, a classification and regression tree analysis was used to assess which dental characters best explain functional trait values (Figure 1g). This approach uses decision tree modelling to explain each response variable by splitting the explanatory data into mostly homogenous groups using the rpart R package (De'ath & Fabricius, 2000; Therneau *et al*., 2015). The authors used classification rather than regression trees to perform the analyses whereby functional traits were the response variables and dental characters the explanatory variables, because most of the data collected were categorical. As such, crown height and crown width categorisations were considered in these analyses (Table 1; Figure S1). Tooth position was also included as an explanatory variable to account for monognathic and dignathic heterodonty, which can, for example, lead to different feeding mechanisms across or between jaws (Cappetta, 2012; Cullen & Marshall, 2019; Kent, 1994). Including tooth position further allowed the authors to determine if it was a more important predictor of functional trait values than the dental characters. To assess reliability of the trees, the authors used cross-validation in which they partitioned the data into two sets: (a) the train set, comprising two-thirds of the data, used to fit the tree; and (b) the test set, comprising the last one-third of the data and run against the tree to evaluate its accuracy (De'ath & Fabricius, 2000). Their two sets of analyses were performed considering all tooth positions and then repeated considering only anterior teeth given their supposed more direct correlation with traits such as body size (Condamine *et al*., 2019; Shimada *et al*., 2020).

3 | RESULTS AND DISCUSSION

3.1 | Q1 Which dental characters have been used as proxies for functional traits in sharks?

The authors' review returned 56 studies published between 1959 and 2020. They obtained data from 5056 teeth (Supporting Information Data S1) across 63 extant shark species belonging to 39 genera, 25 families and 7 orders (Table S2). Five taxa were identified only to genus level, resulting in 68 taxa in the whole data set. From teeth data collected, 68% belonged to modern taxa and the remaining to fossil specimens of extant taxa, with the majority (90%) of modern taxa having a fossil record (Paillard *et al*., 2020). All extant orders except Echinorhiniformes and Pristiophoriformes were represented in the authors' data set (Figure S2a). This was unsurprising as both orders are relatively poorly studied (Ebert *et al*., 2021). Data were notably skewed towards two orders: Lamniformes (64.5%) and Carcharhiniformes (32.1%; Supporting Information Data S1; Figure S2a), suggesting that these are the most well-studied shark orders in literature on tooth morphology. Carcharhiniformes is by far the most species-rich order today (*c*. 290 species; Ebert *et al*., 2021), whereas Lamniformes, with just 15 living species, displays high ecological and dental disparity (Ebert *et al*., 2021). Moreover, several species in these orders have relatively large tooth sizes (Cappetta, 2012), likely explaining this bias.

The sub-set of data deemed to be independent included 40 studies (71% of the full data set). These studies investigated the relationship between tooth morphology and functional traits to (a) apply it to specimens (both fossil and extant) with unknown trait data (*e.g*., unknown body size, 19 studies, 47.5%); (b) assess it through tooth replacement and/or ontogeny (6 studies, 15%); (c) verify trait values (7 studies, 17.5%); (d) study tooth performance in cutting prey (7 studies, 17.5%); and (e) perform evolutionary analyses (1 study, 2.5%). From these studies, the authors extracted 4605 teeth data (91% of the total data collected; Table S2) comprising all 68 taxa. Of these data, 72% belong to modern specimens and the remaining to fossil specimens of extant taxa. They initially identified 14 dental characters (Figure 2) used as proxies for their three functional traits in sharks (body size, prey preference and feeding mechanism; see "Materials and Methods" section and Table 1). Two of these dental characters (*i.e*., acrocone serrations and serrational cusplets) were linked to life stage (Table 1). Nonetheless, life stage and associated dental characters were discarded from the analyses because they were not found broadly across shark phylogeny. In particular, acrocone serrations were unique to Hexanchiformes (Adnet, 2006), and serrational cusplets were described only in juvenile *C. carcharias* teeth (Bemis *et al*., 2015). As such, the authors' analyses considered the remaining 12 dental characters. A total of 400 links (*i.e*., where a dental character was considered explanatory of trait values) were identified from the literature (Supporting Information Data S2) – 150 (37.5%) attributed to body size, 71 (17.8%) to prey preference and 173 (43.3%) to feeding mechanism. All three identified traits are

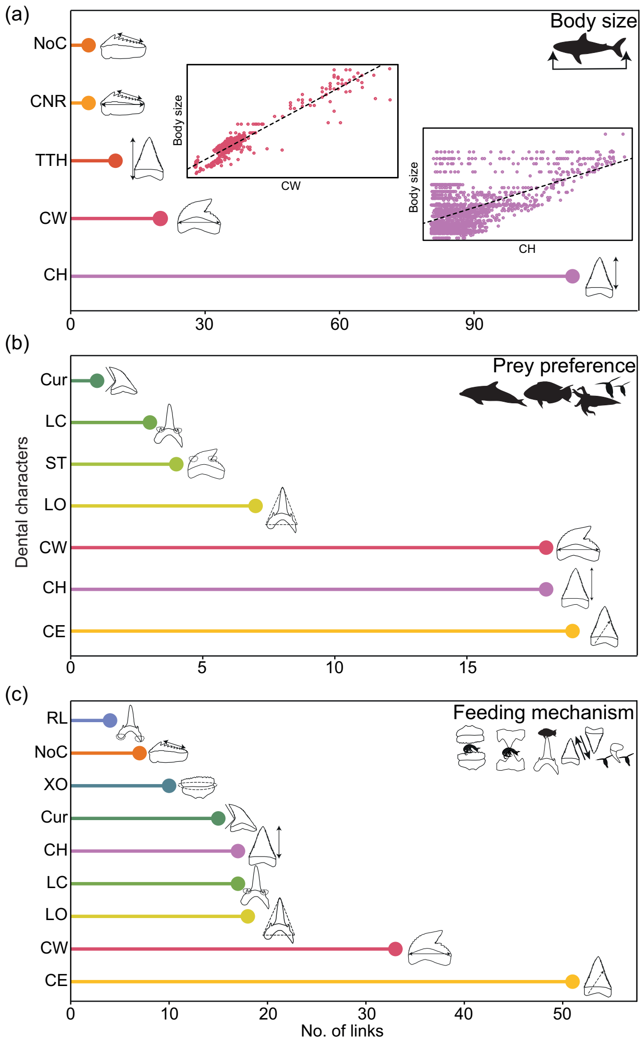


FIGURE 3 Dental characters used in literature as proxies for (a) body size, (b) prey preference and (c) feeding mechanism. Dental character abbreviations are as follows: NoC, number of cusps; CNR, cusp number ratio; TTH, total tooth height; CW, crown width; CH, crown height; Cur, curvature; LC, lateral cusplets; ST, serration type; LO, longitudinal outline; CE, cutting edge; RL, root lobes; and XO, cross-section outline. Scatter plots in (a) show linear regressions between crown height (purple plot) and crown width (pink plot) versus body size considering all tooth positions (see text and Figure S5 for details)

among the most relevant for studying ecological function in marine megafauna (Tavares *et al*., 2019).

3.1.1 | Body size

The literature review found five dental characters used as proxies for body size: crown height, crown width, total tooth height, cusp number ratio and number of cusps (Table 1; Figure 3a). These characters were identified from 24 studies, recorded numerically (*i.e*., measured in millimetres) and used across 52 shark taxa belonging to four orders: Hexanchiformes, Squaliformes, Lamniformes and Carcharhiniformes (Table S2; Figure S2b). Crown height was by far the most common proxy for body size (112 links, 74.7%), followed by crown width (20 links, 13.3%; Figure 3a). Despite its commonness, crown height was linked to body size in just two orders, Carcharhiniformes and Lamniformes, whereas crown width was the only proxy used across all four orders (Table S2; Figure S3a). Cusp number ratio and number of cusps were proxies limited only to Hexanchiformes (Adnet, 2006; Adnet & Martin, 2007), whereas total tooth height was a proxy used in Squaliformes, Lamniformes and Carcharhiniformes (Table S2; Figure S3a). Total tooth height had only four recorded links to body size, whereas cusp number ratio and number of cusps each had two (Figure 3a). Consistent results were found when only anterior teeth were considered, where crown height and crown width were the most commonly used dental characters (Figure S4a). Overall, authors' literature review reveals that the most common and most broadly used proxies for body size are crown height and crown width, respectively.

With regard to this finding, the authors performed linear regressions considering body size *vs*. crown height and crown width from the literature. They found that both dental characters were positively correlated with body size even when examining all taxonomic orders together (Figure 3a; Figure S5). The correlation between crown height and body size was weaker when all tooth positions were considered ($R^2 = 0.32$, $P < 0.001$; Figure 3a; Figure S5a) and stronger when only anterior teeth were used ($R^2 = 0.71$, $P < 0.001$; Figure S5c). This is most likely due to shark teeth progressively decreasing in crown height antero-posteriorly along the jaw (*e.g*., Pimiento *et al*., 2010). As such, large sharks can have tall anterior teeth, as well as short lateral and posterior teeth. Conversely, crown width was found to be highly correlated with body size when considering both all tooth positions ($R^2 = 0.90$, $P < 0.001$; Figure 3a; Figure S5b) and only anterior teeth ($R^2 = 0.89$, $P < 0.001$; Figure S5d). A positive linear relationship between tooth size and body size was also observed when using categorised size classes where larger body size classes are linked with larger tooth sizes (Figure 4a,b; crown height Kruskal–Wallis test: $X^2 = 431.08$, $df = 3$, $P < 0.001$; crown width Kruskal–Wallis test: $X^2 = 250.24$, $df = 2$, $P < 0.001$). This was also found when using only anterior teeth (Figure S4b,c; crown height Kruskal–Wallis: $X^2 = 206.5$, $df = 3$, $P < 0.001$; crown width Kruskal–Wallis: $X^2 = 202.5$, $df = 2$, $P < 0.001$). The authors' results are in line with current knowledge of the relationship between shark tooth size and total length (*e.g*., Chavez *et al*., 2012; Litvinov *et al*., 1983; Shimada, 2003; Strasburg, 1963). In fact, these relationships in individual species are often extrapolated to extinct sharks to predict body size. For example, the relationship between tooth size and total length in *C. carcharias* is commonly used to predict the size of the extinct *Otodus megalodon* (Pimiento *et al*., 2010; Pimiento & Balk, 2015; Shimada, 2019). In this species, crown width has recently been shown to be a more robust proxy than crown height across different tooth positions (Perez *et al*., 2021), mirroring the authors' regression results (Figure 3a; Figure S5). It should be noted, however, that non-macrophagous sharks (*M. pelagios*; *Cetorhinus maximus* and *R. typus*) represent exceptions to these findings given their small teeth (*i.e*., <5 mm in crown height; Table 1) relative to their large body sizes (5–18 m; Table 2;

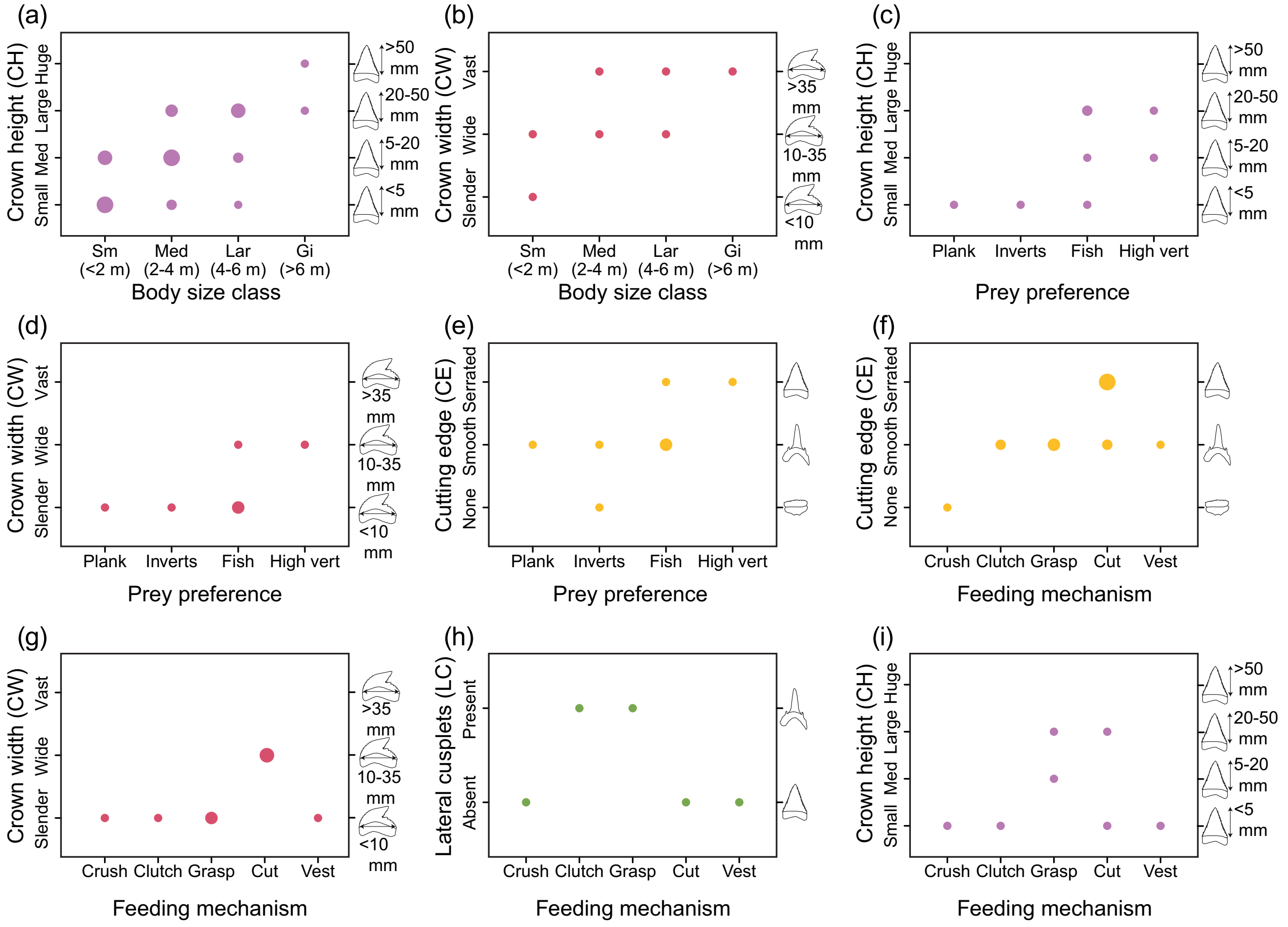


FIGURE 4 Links between dental character states and functional trait values recorded from literature. Links to body size classes from (a) crown height and (b) crown width. Links to prey preference from (c) crown height, (d) crown width and (e) cutting edge. Links to feeding mechanism from (f) cutting edge, (g) crown width, (h) lateral cusplets and (i) crown height. Note that crown height and crown width and body size were recorded numerically *via* measurement data but here are converted to categorical values (Tables 1 and 2). Abbreviations are as follows: Sm, small; Med, medium; Lar, large; Gi, giant; Plank, plankton; Inverts, invertebrates; Fish, fishes; High vert, high vertebrates; Crush, crushing; Clutch, clutching; Grasp, grasping; Cut, cutting; Vest, vestigial. • 1–5, • 6–10, ● 11–15, ● 16–20, ● >20

Ebert *et al*., 2021). As such, there were no studies in the literature linking body size and tooth size in these species. Overall, the authors' linear regression analyses indicate that from the two most common proxies for body size, crown width displays a stronger linear correlation across tooth positions than crown height (crown width *vs*. body size $R^2 > 0.85$; crown height *vs*. body size $R^2 > 0.32 < 0.71$; Figure 3a; Figure S5).

3.1.2 | Prey preference

The authors identified seven dental characters used as proxies for prey preference in the literature review: cutting edge, crown height, crown width, longitudinal outline, serration type, lateral cusplets and curvature (Table 1; Figure 3b). These were recorded categorically (*e.g*., cutting edge: smooth, serrated or absent; Table 1) in 9 studies across 5 orders (Squantiniformes, Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes) and 25 taxa (Table S2; Figure S2c). A robust correlation between tooth morphology and prey preference is expected given that the primary function of teeth is to capture and process prey (Cappetta, 2012). Of the seven identified dental characters, all except curvature were used as proxies across multiple orders (Table S2; Figure S3b), with crown height being studied in all five aforementioned orders, cutting edge being studied in all except Heterodontiformes and crown width and lateral cusplets being studied in three orders (Orectolobiformes, Lamniformes and Carcharhiniformes; Table S2; Figure S3b). Cutting edge, crown height and crown width were by far the most common proxies for prey preference (20, 18 and 18 links, respectively; Figure 3b), making up 78.9% of all documented links. As such, they were selected for further analysis.

Quantifying links between dental character states and functional trait values revealed that small and slender crowns and smooth cutting edges were associated with smaller prey (*i.e.*, plankton and invertebrates), whereas large and wide crowns and serrated cutting edges were associated with larger prey items (*i.e.*, fishes and high vertebrates; Figure 4c–e). Prey preferences of plankton and invertebrates were exclusively linked to small crown heights (<5 mm) and widths (<10 mm) and smooth cutting edges. Moreover, the absence of cutting edges was linked only to invertebrate preferences, representing plate-like teeth used in the consumption of typically armoured prey (Cappetta, 2012; Cullen & Marshall, 2019; Kent, 1994). A dietary preference for fishes occurred across multiple states for the most common dental characters (*i.e.*, cutting edge, crown height and crown width), likely reflecting the fact that fishes are widely consumed across shark species (Ebert *et al*., 2021; Wetherbee & Cortés, 2004). Moreover, fishes display a wide diversity of body forms, with shark tooth morphologies varying accordingly. Prey preferences for high vertebrates, on the contrary, were associated only with larger tooth sizes (*i.e*., medium-large crown heights, wide crown widths) and serrated cutting edges, likely reflecting the need of slicing chunks of flesh to consume large prey with thick skin such as marine mammals (Ciampaglio *et al*., 2005; Cortés, 1999; Frazzetta, 1988; Lucifora *et al*., 2009). The authors' results therefore suggest that the combination of crown size and cutting edge is the most common proxy for prey preference in sharks.

3.1.3 | Feeding mechanism

The authors found nine dental characters used as proxies for shark feeding mechanism in literature: cutting edge, crown width, longitudinal outline, lateral cusplets, crown height, curvature, cross-section outline, number of cusps and root lobes (Table 1; Figure 3c). All were measured categorically (*e.g*., lateral cusplets: absent or present; Table 1) in relation to this functional trait, with the exception of number of cusps which was recorded based on countable elements (*i.e*., discrete numerical data; Supporting Information Data S1). Both qualitative (without analysis) and quantitative links (with analysis) – 86 (49.7%) and 87 (50.3%), respectively – were returned within the literature review across 11 studies and 37 taxa from 6 orders: Hexanchiformes, Squaliformes, Heterodontiformes, Orectolobiformes, Lamniformes and Carcharhiniformes (Table S2; Figure S2d). Of the nine identified dental characters, cutting edge, cross-section outline and longitudinal outline were proxies used in all six orders mentioned earlier. The presence of lateral cusplets was used as a proxy for feeding mechanism within five orders, whereas crown height, crown width and number of cusps were used in four orders. Finally, curvature and root lobes were proxies used in three and two orders, respectively (Table S2; Figure S3c). Root lobes were the least common (five links) and least broadly used proxy, so they were discarded from subsequent analyses. Number of cusps was also not investigated further due to redundancy as this character includes all lateral cusplets (Ciampaglio *et al*., 2005). As such, the seven most commonly used dental characters (Figure 3c) were selected for further analyses.

Of the seven dental characters investigated further, three – curvature, longitudinal outline and cross-section outline – did not have clear relationships with feeding mechanism that could be detected from literature (Figure S6). For instance, although curvature was found to be present in teeth with grasping and vestigial feeding mechanisms and absent in cutting feeding, no data were found for clutching or crushing feeding (Figure S6a). Not all character states of longitudinal outline and cross-section outline were accounted for in the authors' data either. Notably, some states of both characters were linked to multiple feeding mechanisms and *vice versa* (Figure S6b,c). For example, a "lens" cross-section outline was found in clutching, grasping and cutting feeding (Figure S6c). As both longitudinal outline and cross-section outline are shape-based metrics (Ciampaglio *et al*., 2005), the lack of a clear relationship between these dental characters and feeding mechanism in the literature may support suggestions that although overall tooth morphology appears to correspond to dietary preference (Bazzi *et al*., 2021; Cappetta, 2012; Frazzetta, 1988), its relationship with feeding function may be more cloudy (Whitenack *et al*., 2011; Whitenack & Motta, 2010).

The remaining four dental characters (*i.e*., cutting edge, crown width, lateral cusplets and crown height) had clearer associations with feeding mechanisms (Figure 4f–i). For instance, serrated cutting edges and wide crowns were exclusively linked to cutting feeding (Figure 4f,g); the absence of a cutting edge was linked only to crushing feeding (Figure 4f); and the presence of lateral cusplets was linked only to clutching and grasping feeding (Figure 4h). The links between other dental character states and feeding mechanisms were less clear, with single character states being linked to multiple feeding mechanisms (Figure 4f–i). Notably, whereas large crown heights were linked only to both grasping and cutting feeding mechanisms, small crowns were also linked to cutting and medium crowns also to grasping (Figure 4i). The literature review therefore indicates that cutting edge, crown width and lateral cusplets are the most widely used proxies for feeding mechanisms, with crown height also being largely used, but showing less-clear associations.

3.2 | Q2 Which dental characters are the best proxies for functional traits in sharks?

The authors' museum data set included 63 of the 68 taxa initially collated in the literature review – 58 identified to species level and 5 to genus level – for which proxy species were used based on collection availability (Supporting Information Data S3). Missing species included *Carcharhinus sealei*, *C. maximus*, *Rhizoprionodon longurio*, *Scoliodon laticaudus* and *Scyliorhinus retifer*. From the 12 dental characters identified in the literature review as proxies for functional traits (Table 1), cusp number ratio and serration type (Figure 2) were excluded due to limited representation across shark phylogeny. In particular, cusp number ratio occurs only in Hexanchiformes (Adnet, 2006; Adnet & Martin, 2007), whereas serration type occurs only in serrated teeth. Indeed, secondary serrations (Table 1) have been reported only in *G. cuvier* teeth (Moyer & Bemis, 2017). The authors also excluded total tooth height because crown height was found to be much more widely used in literature (Figure 3). As a result, nine dental characters were included in the analyses.

FIGURE 5 PCA of dental characters across functional traits based on the museum data set. Each set of analysis is linked to a single functional trait as follows: (a) body size; (b) prey preference; and (c) feeding mechanism, with values for each trait defining convex hulls following Table 2. Arrows summarise how dental characters are correlated to each axis, based on their contributions recorded in Table 3. Density plots show the distribution of trait values along each axis. — Giant, — Large, — Medium, — Small, — High vertebrates, — Fishes, — Invertebrates, — Plankton, — Clutching, — Crushing, — Cutting, — Grasping, — Vestigial.

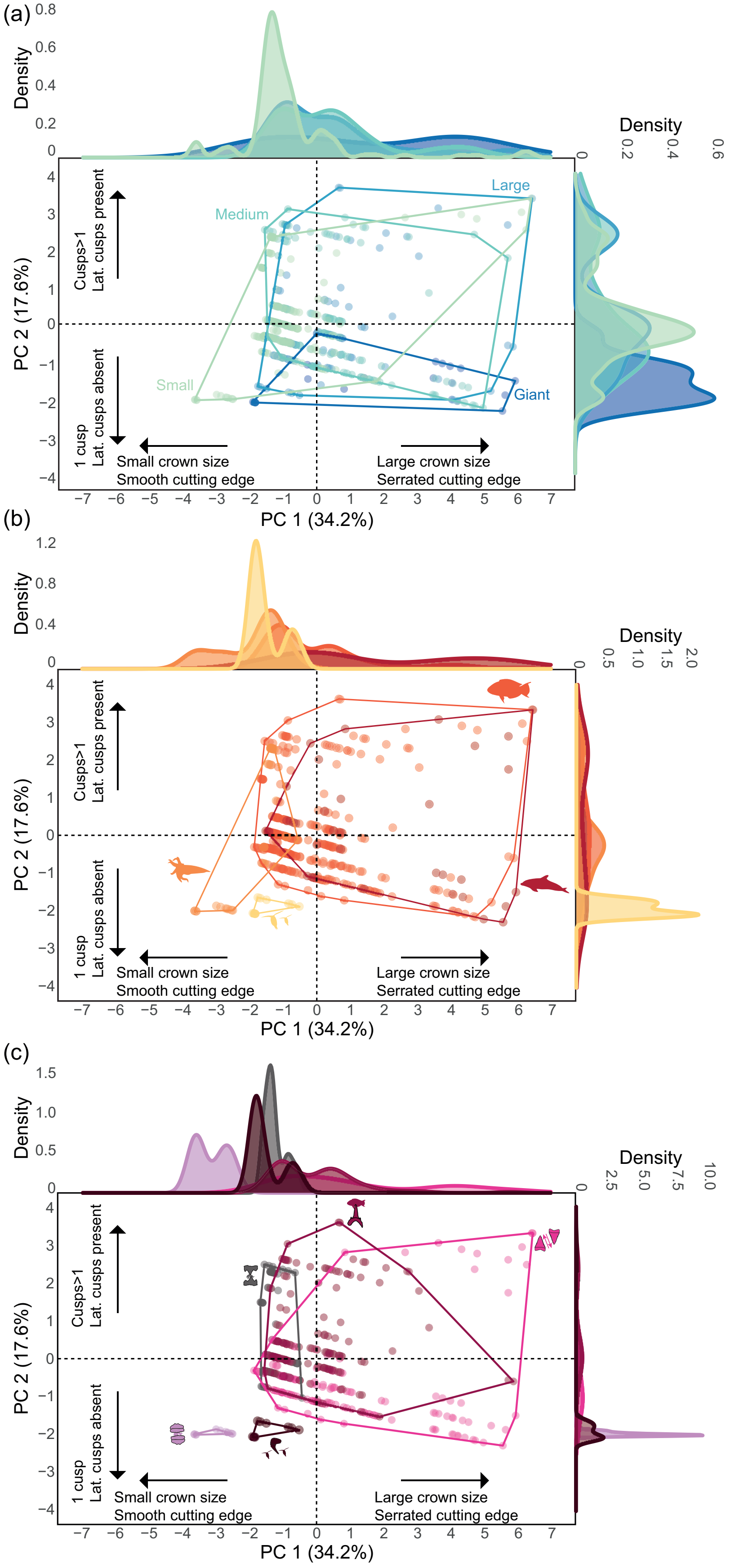


TABLE 3 Contribution of shark dental characters to morphospace variation in the first two axes of the PCA based on the museum data set and all tooth positions being considered

Character	Abbreviation	PC1 contribution	PC2 contribution
Crown height (numerical)	CH_num	**0.401**	−0.092
Crown height (categorical)	CH_cat	**0.379**	−0.061
Crown width (numerical)	CW_num	**0.475**	−0.117
Crown width (categorical)	CW_cat	**0.422**	−0.086
Cutting edge	CE	**0.362**	−0.091
Lateral cusplets	LC	−0.041	**0.534**
Curvature	Cur	−0.054	−0.291
Cross-section outline	XO	0.289	0.314
Longitudinal outline	LO	−0.140	0.289
Root lobes	RL	0.123	0.319
Number of cusps	NoC	0.184	**0.552**

Note: All results are accurate to three decimal places. Bold values denote highest contributions.

The PCA revealed which of the nine remaining dental characters contributed most to variation across tooth morphology and associated trait values (Figure 5; Figure S7). PC1 explained 34% of shark tooth morphology variation, whereas PC2 explained 18% when considering all teeth and anteriors only (Table 3; Table S3). Morphological variation in PC1 was mostly related to crown height and crown width and to a lesser extent to cutting edge (Figure 2; Table 3; Table S3). This is the case when considering all teeth and anteriors only (Figure S7). As such, positive PC1 values were occupied primarily by large crowns and serrated cutting edges, and negative values were occupied by smaller crowns and smooth or no cutting edges. Numerical and categorical crown height and crown width were found to make very similar contributions to morphospace variation (Table 3; Table S3), suggesting that the nature of these variables has negligible effect on interpretation. The contributions of dental characters to PC2 differed when considering all teeth *vs*. anteriors only. When all teeth were included, PC2 was mostly related to the presence of lateral cusplets and number of cusps (Figure 2; Table 3), with positive values occupied by teeth with multiple cusps, including lateral cusplets, and negative values occupied by single-cusp teeth with no lateral cusplets (Table 3). Nonetheless, when only anterior teeth were considered, PC2 was mostly related to longitudinal outline (Figure 2c; Table S3). As such, positive PC2 values were occupied by triangular longitudinal outlines, whereas negative PC2 values were occupied by teeth with a "piercing" longitudinal outline (Table 1). Overall, the PCA results indicate that tooth size (crown height and crown width), cutting edge and lateral cusplets are drivers of variation in shark tooth morphology, with longitudinal outline also driving variation in anterior teeth.

3.2.1 | Body size

The PCA revealed great overlap between body size classes across tooth morphologies when considering both all teeth (Figure 5a) and only anterior teeth (Figure S7a). This likely reflects how similar-sized sharks can have different ecologies. For example, the dental morphospace of giant sharks (>6 m; Table 2; darkest blue polygon in Figure 5a) included both large and serrated teeth (*e.g*., *C. carcharias*; maximum body size = 7 m) and minute and smooth teeth (*e.g*., *R. typus*; maximum body size = 18 m; McClain *et al*., 2015). Nevertheless, unlike the morphospace of mid-body sizes, the smallest and largest morphospaces (*i.e*., small and giant body size classes; Table 2) showed clear peaks in PC values. For instance, the small body size morphospace (light-green curve in Figure 5a) showed a distinct single peak between −2 and −1 along PC1, suggesting small tooth sizes. This morphospace also diverged from the main cluster that encompasses all other body sizes along the most negative PC1 values (Figure 5a). This was the case when considering both all teeth and anteriors only (light-green polygon diverging between −4 and −2 along PC1; Figure 5a; Figure S7a). These divergent, extreme morphologies include the smallest tooth sizes (*i.e*., crown height <5 mm; crown width <10 mm) and the absence of a cutting edge (Table 1), suggesting that plate-like teeth (*i.e*., flat crowns) are associated with some of the smallest body sizes. Also notably, the giant morphospace was mostly restricted to positive PC1 values when considering all teeth and anteriors only (darkest blue polygon in Figure 5a and Figure S7a), suggesting a general association between giant sharks and large tooth sizes. Along PC2, the giant morphospace was associated with a single-cusp morphology with no lateral cusplets. This is evidenced by the concentration of negative values along PC2 (darkest blue curve peaks around −2 in Figure 5a) when all teeth are considered and of positive PC2 values (darkest blue curve peaks around 2 in Figure S7a) when only anterior teeth are considered. Overall, these results suggest that even though there is great overlap between body size classes across tooth morphologies, the morphospace of small body sizes is generally associated with small crowns and smooth cutting edges (PC1), and the giant morphospace is associated with large, single-cusp teeth (PC2).

The body size classification tree indicated that crown height was the main predictor of body size (Figure 6a; Table S4). Cross-validation analyses aimed to assess tree reliability produced an accuracy of 53.1% on the test set. Repeating the analysis on only anterior teeth produced a near-identical tree (Figure S8a) but with a test set

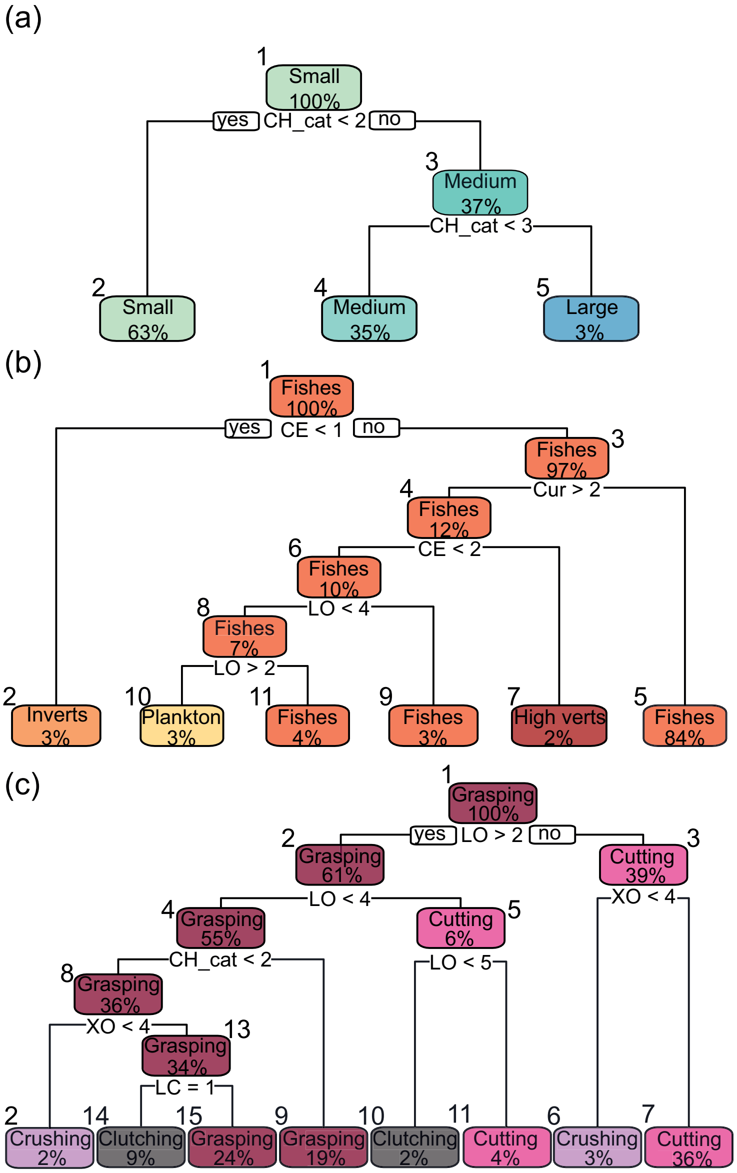


FIGURE 6 Classification tree analyses on dental characters recorded from the museum data set. Each tree is related to a single functional trait as follows: (a) body size, (b) prey preference and (c) feeding mechanism. Nodes are produced by splitting the data based on the presence of the dental character states recorded as predictors. The proportional node contributions to the entire data set are included alongside the most common trait value making up each node (Tables S4–S6). Abbreviations are as follows: CH_cat, categorical crown height; CE, cutting edge; Cur, curvature; LO, longitudinal outline; XO, cross-section outline; and LC, lateral cusplets (Table 1). 🟦 Large, 🟩 Medium, 🟩 Small, 🟥 High vertebrates, 🟥 Fishes, 🟧 Invertebrates, 🟨 Plankton, ⬛ Clutching, 🟪 Crushing, 🟪 Cutting, 🟥 Grasping.

accuracy of 68.2%. The difference in accuracy is likely due to the purported more direct association between crown height and body size in anterior teeth (Condamine *et al.*, 2019; Shimada *et al.*, 2020). Nevertheless, this accuracy difference is only modest (*i.e.*, 15.1%) given that tooth position was not returned as an important predictor of body size (Figure 6a; Figure S8). These findings differ from those obtained from the linear regressions based on data from the literature review, in which crown width was found to be more strongly correlated to body size than crown height across tooth positions (Figure 3a; Figure S5). This difference could be explained by the broader categorical nature of the classification tree's variables (De'ath & Fabricius, 2000) compared to the numerical nature of the linear regressions. Nevertheless, the classification tree (Figure 6a) supports the authors' general findings that large crown sizes are associated with large bodies in sharks (Figures 3a, 4a,b and 5a; Figures S4 and S5). Overall, their analyses suggest that crown height and crown width are the most common and best proxies for body size in sharks.

3.2.2 | Prey preference

The PCA showed some overlap in prey preference across tooth morphologies (Figure 5b; Figure S7b), likely representing the generalist diets of most shark species (Wetherbee & Cortés, 2004). A fish prey preference occupied the largest extent of the dental morphospace when considering both all teeth and only anterior teeth (orange polygon in Figure 5b; Figure S7b), reflecting diversity of shark tooth morphologies linked to piscivory. In both sets of analyses, the morphospace for high vertebrates (red polygon in Figure 5b; Figure S7b) was contained inside the fish morphospace, likely due to the fact that (a) sharks that prey upon large organisms such as high vertebrates tend to feed on a wide range of prey (Lucifora *et al.*, 2009) and (b) sharks such as *C. carcharias* that consume high vertebrates as adults specialise in fishes as juveniles (Estrada *et al.*, 2006), this dietary shift likely reflected in ontogenetic heterodonty where crowns get wider as the shark grows (French *et al.*, 2017). The authors' analyses further showed that the high vertebrates' and the fishes' morphospaces mostly extended along positive PC values, indicating an association with large crown sizes, serrated cutting edges and the presence of cusplets. Nonetheless, unlike the high vertebrate morphospace, which largely extended along most PC1 values (red curve in Figure 5b), the fish morphospace concentrated at mid-PC1 values (orange curve peaks mostly at −1 and to a lesser degree at 1; Figure 5b), reflecting mid-tooth sizes (*i.e.*, 5–20 mm crown height) and both smooth and serrated cutting edges. Furthermore, the fishes' morphospace of anterior teeth extended into the most negative PC2 values, reflecting piercing longitudinal outlines and lateral cusplets, whereas the high vertebrates' morphospace is restricted to more positive values representing triangular longitudinal outlines lacking lateral cusplets (Figure S7b).

The invertebrates' morphospace overlapped with the fishes' morphospace on negative PC1 values, with a main peak around −1.5 (light-orange polygon and curve in Figure 5b) reflecting small crowns and smooth cutting edges associated with both prey preferences. Nonetheless, the invertebrates' morphospace diverged further into the most negative PC1 and PC2 values (extending across values of −3 to −4 in PC1 and around −2 in PC2), reflecting even smaller crowns, no cutting edge and no cusp (*i.e.*, the unique plate-like morphology, especially useful to consume invertebrates). This was also the case when only anterior teeth are analysed (Figure S7b). Nonetheless, in anterior teeth, the diverging invertebrates' morphospace occupied a PC2 value of around 0, reflecting the semi-circular longitudinal outlines of these teeth. The plankton morphospace completely diverged from all others, exclusively occupying negative values along PC1 and PC2, with a peak around −2 in both PCs (yellow polygon and curves in Figure 5b). This area of the morphospace was associated with small (<5 mm crown height; <10 mm crown width) single-cusped teeth with smooth cutting edges. A similarly distinct divergence was observed in anterior teeth (Figure S7b). As such, this divergence likely indicates a dietary specialisation. Overall, the authors' results suggest that (a) the dietary preferences for high vertebrates and fishes are associated with large- to mid-sized crowns, and serrated cutting edges, though may be distinguished by lateral cusplets and longitudinal outline; (b) the dietary preferences for invertebrates and plankton are associated with small crown sizes, a lack of lateral cusplets and smooth or no cutting edges; and (c) crown size and cutting edge are the dental characters that drive most of the observed variation in prey preference.

The classification tree analysis revealed cutting edge to be the main predictor of prey preference at the root node (Figure 6b), in line with the authors' findings from the literature where the lack of a cutting edge was linked to invertebrate specialisation, smooth cutting edges were associated with multiple prey preferences and serrated cutting edges were linked to preferences for high vertebrates (Figure 4c–e). Curvature and longitudinal outline were also predictors at subsequent decision nodes, indicating their use to distinguish teeth associated with planktivory (Figure 6b; Table S5). Cross-validation analyses indicated an accuracy of 83.9% on the test set, suggesting that the dental characters used in the tree are strong predictors of prey preference. When only anterior teeth were analysed, cross-section outline was the main predictor at the root node, albeit primarily to distinguish teeth linked to planktivory from the rest of the subset (Figure S8b). Of the remaining sample, the tree indicated that crown width, lateral cusplets and crown height could be used to distinguish prey preferences of fishes from invertebrates. In particular, larger crown sizes were associated with piscivory, and smaller crown sizes were associated with a dietary preference for invertebrates (Figure S8b; Table S5). The resulting tree's test set had an accuracy of 78.8%. Tooth position was not returned as a predictor of prey preference by either tree, suggesting lesser importance compared to the returned dental characters (Figure 6b; Figure S8b). The classification trees therefore indicate that cutting edge is the most important predictor of prey preference but that crown size and shape (*i.e.*, longitudinal and cross-section outline), as well as curvature and lateral cusplets, can be subsequently used in combination to distinguish specific prey preferences. Overall, the authors' results collectively suggest that cutting edge and crown size are the most common and best dental character proxies for prey preference.

3.2.3 | Feeding mechanism

The PCA showed morphospace overlap between clutching, cutting and grasping feeding when considering both all teeth and anterior teeth only (Figure 5c; Figure S7c). This could be reflective of a lack of functional difference between these mechanisms previously suggested by biomechanical studies (Whitenack *et al.*, 2011; Whitenack & Motta, 2010). Nonetheless, some variation between the tooth morphologies of these feeding mechanisms was detected. The clutching morphospace concentrated at negative PC1 values when considering both all teeth and anteriors only, peaking at around −1.5 (grey polygon and curve in Figure 5c and Figure S7c) and reflecting small crowns and smooth cutting edges. Some of this morphospace overlapped with the grasping morphospace, suggesting some similar tooth morphology, a result also obtained from the literature review (Figure 4f–i). For example, both morphospaces occupied both positive and negative PC2 values due to variation in number of cusps or the presence of lateral cusplets (Figure 5c). Nonetheless, the grasping morphospace extended along mid- to positive PC1 values (purple polygon in Figure 5c), suggesting that this mechanism is also associated with larger tooth sizes (*i.e.*, medium crown heights of 5–20 mm). The cutting morphospace extended across even more positive PC1 values (pink polygon in Figure 5c). This suggests that cutting feeding is primarily associated with large crowns and serrated cutting edges. Across PC2 when considering all teeth, the cutting morphospace mostly occupied negative values, reflecting single-cusped and no lateral cusplet morphologies. Nonetheless, some divergence into positive PC2 values represented the unique lower-tooth morphologies of Hexanchiformes, known for having multiple cusps (*i.e.*, >5; Figure 5c; Adnet, 2006). In anterior teeth, the cutting and grasping morphospaces diverged into positive and negative PC2 values, respectively. This suggests that cutting feeding is linked to teeth with triangular longitudinal outlines and no lateral cusplets, whereas grasping mechanism teeth are associated with piercing longitudinal outlines and the presence of lateral cusplets.

The PCA further revealed that crushing and vestigial feeding mechanisms were associated with unique tooth morphologies, as both morphospaces diverged from the main cluster when considering all teeth and anteriors only (light-pink and darkest purple polygons, respectively, in Figure 5c and Figure S7c). Crushing feeding was linked to small crowns with no cutting edge (*e.g.*, plate-like teeth typically observed in *Mustelus canis*, *Heterodontus francisci* and *S. tiburo*; Kent, 1994; Cappetta, 2012). Meanwhile, vestigial feeding was linked to the small non-functional teeth of planktivorous sharks (*e.g.*, *M. pelagios*, *C. maximus* and *R. typus*; Kent, 1994). Indeed, the vestigial morphospace mirrored the morphospace for plankton prey preference (Figure 5b; Figure S7b), suggesting a one-to-one correspondence in tooth morphology between these two trait values. When considering all teeth, the crushing and vestigial morphospaces both concentrated at the most negative PC1 and PC2 values, overlapping in density along PC2 (curves peaking around −2) due to the absence of lateral cusplets. The crushing morphospace peaked at more negative PC1 values (between −4 and −3) than the vestigial morphospace (peaking at −2). This reflects that, despite both morphologies including the smallest teeth (*i.e.*, <5 mm crown height; Figure 5c), the (plate-like) crushing morphology lacks a cutting edge, whereas the vestigial morphology displays a smooth cutting edge. When analysing anterior teeth, crushing feeding was represented by just two teeth from a single species (*M. canis*; Supporting Information Data S3), thus constituting outliers that caused large density peaks along both PC1 and PC2 (Figure S7c). Despite this, the crushing morphospace occupied PC2 values of around 0 due to a semi-circular longitudinal outline and the absence of lateral cusplets. The vestigial morphospace displayed more positive PC2 values (1–2; darkest purple polygon in Figure S7c), associated with more triangular outlines than crushing morphologies in anterior teeth.

Overall, the PCAs on feeding mechanism suggest that (a) despite overlap between the clutching, grasping and cutting morphospaces, these dentitions can be distinguished by crown size (small-, medium- and large crown heights, respectively), cutting edge (serrated in cutting feeding and smooth in clutching and grasping feeding) and lateral cusplets (absent in cutting feeding and present in clutching and grasping feeding); (b) there are unique tooth morphologies associated to specific mechanisms [*i.e.*, no cutting edge (=plate-like) and semi-circular longitudinal outline represent the crushing mechanism, and the smallest crowns and triangular longitudinal outlines represent the vestigial mechanism]; and (c) crown size, cutting edge, lateral cusplets and longitudinal outline are the dental characters that drive the most observed variation in feeding mechanisms.

The classification tree analysis found the longitudinal outline to be the main predictor of feeding mechanism, both in the root node and in subsequent decision nodes (Figure 6c). Cross-section outline, crown height and lateral cusplets were also predictors at subsequent decision nodes, used to predict specific feeding mechanisms from smaller subsamples (Figure 6c; Table S6). Tree accuracy was found to be 74.4% for the test set during cross-validation analyses. Longitudinal outline was also the main predictor at the root node when the classification tree used only anterior teeth, with crown height and curvature being predictors of subsequent decision nodes (Figure S8c), producing a test set of 74.4% accuracy. Tooth position was not returned as a predictor of feeding mechanism by either tree (Figure 6c; Figure S8c). The trees thus suggest that longitudinal outline is an important predictor of feeding mechanism in sharks. For example, the cutting morphology typically includes a triangular longitudinal outline, whereas the grasping morphology typically has a piercing longitudinal outline (Figure 6c; Ciampaglio *et al*., 2005), something also supported by the PCA on anterior teeth (Figure S7c). Moreover, crushing morphology was associated with unique plate-like tooth morphologies (*i.e.*, no cutting edge; Figure 6c; Kent, 1994; Cappetta, 2012). Overall, the authors' analyses collectively suggest that tooth size (crown height and width), cutting edge and lateral cusplets are the most commonly used and among the best proxies for feeding mechanism, with tooth shape (longitudinal outline) being less widely used in the literature, but also showing strong associations with feeding mechanisms.

4 | CONCLUSIONS

Based on a literature review of 56 studies, the authors identified 12 dental characters from extant shark teeth that have been used as proxies for three functional traits: body size, prey preference and feeding mechanism (Table 1). Following two separate sets of analyses on an independent data set of jaw specimens from museum collections, they determined that tooth size (crown height and crown width) and cutting edge contributed the most to the variation they observed in tooth morphology (Table 3; Figure 5; Figure S7). They further found that seven dental characters – crown height, crown width, cutting edge, lateral cusplets, curvature, cross-section outline and longitudinal outline – were suggested to be predictors of functional trait values based on the classification trees (Figure 6; Figure S8). Importantly, they found that tooth position was not a predictor of any functional trait, suggesting that heterodonty, although important to acknowledge, has little influence on the relationship between functional traits and dental characters in isolated teeth. Overall, their results suggest that tooth size is a key and commonly used proxy for body size; tooth size and cutting edge are the dental characters most used and best suited to predict prey preference; and that tooth size, cutting edge, lateral cusplets and overall shape (*i.e.*, longitudinal outline) are the most common and useful proxies for feeding mechanism (Figures 3–6). The key implication of these findings is that the proposed dental character proxies can be applied to extinct sharks whose fossil records are primarily composed of isolated teeth. This would thus provide insights into the ecological roles sharks played in marine systems millions of years ago and their ecological responses to environmental changes.

AUTHOR CONTRIBUTIONS

C.P. conceived the project. J.A.C., C.P. and J.N.G. designed the research work. J.A.C. collected the data. R.K. provided data from his collection and corresponding inventory numbers. J.A.C. performed all analyses with guidance from C.P. and J.N.G. J.A.C. led the writing with input from C.P. All authors contributed to manuscript preparation.

ACKNOWLEDGEMENTS

The authors thank C. Ciampaglio for providing data from his earlier work. Jack A. Cooper thanks K. Brandt, L. Cappelatti and B. MacFadden for advice and support. For access to jaw specimens in museum collections used in this study, the authors thank E. Bernard and J. Maclaine (NHM); C. Klug (PIMUZ); O. Pauwels and J. Venderickx (RBINS); S. Godfrey, J. Nance and V. Perez (CMM); and G. Hubbell (GHC). Finally, the authors thank two anonymous reviewers for their constructive feedback, which substantially improved this paper. Jack A. Cooper was funded by a PhD studentship from the Fisheries Society of the British Isles and an international travel grant from the University of Florida. Catalina Pimiento was funded by a PRIMA grant (no.: 185798) from the Swiss National Science Foundation.

DATA AVAILABILITY STATEMENT

Images of all specimens used for validation analyses are available on Figshare: https://figshare.com/articles/media/Are_shark_teeth_proxies_for_functional_traits_/20518716.

ORCID

Jack A. Cooper https://orcid.org/0000-0003-2252-4983
John N. Griffin https://orcid.org/0000-0003-3295-6480
Catalina Pimiento https://orcid.org/0000-0002-5320-7246

REFERENCES

Abràmoff, M. D., Magalhães, P. J., & Ram, S. J. (2004). Image processing with ImageJ. *Biophotonics International*, *11*, 36–42.

Adnet, S. (2006). Biometric analysis of the teeth of fossil and recent hexanchid sharks and its taxonomic implications. *Acta Palaeontologica Polonica*, *51*, 477–488.

Adnet, S., & Martin, R. A. (2007). Increase of body size in sixgill sharks with change in diet as a possible background of their evolution. *Historical Biology*, *19*, 279–289.

Baremore, I. E., Murie, D. J., & Carlson, J. K. (2010). Seasonal and size-related differences in diet of the Atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. *Aquatic Biology*, *8*, 125–136.

Barley, S. C., Clark, T. D., & Meeuwig, J. J. (2019). Ecological redundancy between coral reef sharks and predatory teleosts. *Reviews in Fish Biology and Fisheries*, *30*, 153–172.

Bazzi, M., Campione, N. E., Kear, B. P., Pimiento, C., & Ahlberg, P. E. (2021). Feeding ecology has shaped the evolution of modern sharks. *Current Biology*, *31*, 1–11.

Bemis, W. E., Moyer, J. K., & Riccio, M. L. (2015). Homology of lateral cusplets in the teeth of lamnid sharks (Lamniformes: Lamnidae). *Copeia*, *103*, 961–972.

Berio, F., Evin, A., Goudemand, N., & Debiais-Thibaud, M. (2020). The intraspecific diversity of tooth morphology in the large-spotted catshark *Scyliorhinus stellaris*: Insights into the ontogenetic cues driving sexual dimorphism. *Journal of Anatomy*, *237*, 960–978.

Bonfil, R., Meÿer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., … Paterson, M. (2005). Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science*, *310*, 100–103.

Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A., & Dill, L. M. (2013). Patterns of top-down control in a seagrass ecosystem: Could a roving apex predator induce a behaviour-mediated trophic cascade? *Journal of Animal Ecology*, *82*, 1192–1202.

Cappetta, H. (2012). Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In H.-P. Schultze (Ed.), *Handbook of paleoichthyology. Volume 3 E* (pp. 1–512). Munich: Verlag Dr. Friedrich Pfeil.

Chavez, S., Zufan, S., Kim, S. H., & Shimada, K. (2012). Tooth sizes as a proxy for estimating body lengths in the porbeagle shark, *Lamna nasus*. *Journal of Fossil Research*, *45*, 1–5.

Ciampaglio, C., Wray, G., & Corliss, B. (2005). A toothy tale of evolution: Convergence in tooth morphology among marine Mesozoic–Cenozoic sharks, reptiles, and mammals. *The Sedimentary Record*, *3*, 4–8.

Condamine, F. L., Romieu, J., & Guinot, G. (2019). Climate cooling and clade competition likely drove the decline of lamniform sharks. *Proceedings of the National Academy of Sciences*, *116*, 20584–20590.

Cortés, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science*, *56*, 707–117.

Cullen, J. A., & Marshall, C. D. (2019). Do sharks exhibit heterodonty by tooth position and over ontogeny? A comparison using elliptic Fourier analysis. *Journal of Morphology*, *280*, 687–700.

De'ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, *81*, 3178–3192.

Dicken, M. L., Hussey, N. E., Christiansen, H. M., Smale, M. J., Nkabi, N., Cliff, G., & Wintner, S. P. (2017). Diet and trophic ecology of the tiger shark (*Galeocerdo cuvier*) from south African waters. *PLoS One*, *12*, e0177897.

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.

Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., … Svenning, J. C. (2016). Global nutrient transport in a world of giants. *Proceedings of the National Academy of Sciences*, *113*, 868–873.

Ebert, D. A., Dando, M., & Fowler, S. (2021). *Sharks of the world: A complete guide*. Plymouth: Princeton University Press.

Estrada, J. A., Rice, A. N., Natanson, L. J., & Skomal, G. B. (2006). Use of isotopic analysis of vertebrae in reconstructing ontogenetic feeding ecology in white sharks. *Ecology*, *87*, 829–834.

Estupiñán-Montaño, C., Tamburin, E., & Delgado-Huertas, A. (2021). Stable isotope evidence for movements of hammerhead sharks *Sphyrna lewini*, connecting two natural protected areas in the Colombian Pacific. *Marine Biodiversity*, *51*, 74.

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.

Frazzetta, T. H. (1988). The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology*, *108*, 93–107.

French, G. C. A., Sturup, M., Rizzuto, S., van Wyk, J. H., Edwards, D., Dolan, R. W., … Hughes, W. O. H. (2017). The tooth, the whole tooth and nothing but the tooth: Tooth shape and ontogenetic shift dynamics in the white shark *Carcharodon carcharias*. *Journal of Fish Biology*, *91*, 1032–1047.

Frisch, A. J., Ireland, M., Rizzari, J. R., Lönnstedt, O. M., Magnenat, K. A., Mirbach, C. E., & Hobbs, J.-P. A. (2016). Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs*, *35*, 459–472.

Hammerschlag, N., Schmitz, O. J., Flecker, A. S., Lafferty, K. D., Sih, A., Atwood, T. B., … Cooke, S. J. (2019). Ecosystem function and services of aquatic predators in the Anthropocene. *Trends in Ecology and Evolution*, *34*, 369–383.

Heupel, M. R., Knip, D. M., Simpfendorfer, C. A., & Dulvy, N. K. (2014). Sizing up the ecological role of sharks as predators. *Marine Ecology Progress Series*, *495*, 291–298.

Hubbell, G. (1996). Using tooth structure to determine the evolutionary history of the white shark. In A. P. Klimley & D. G. Ainley (Eds.), *Great white sharks: The biology of Carcharodon carcharias* (pp. 9–18). San Diego: Academic Press.

Kent, B. W. (1994). *Fossil sharks of the Chesapeake Bay region*. Columbia, Maryland: Egan Rees & Boyer, Inc.

Leigh, S. C., Papastamatiou, Y. P., & German, D. P. (2018). Seagrass digestion by a notorious 'carnivore'. *Proceedings of the Royal Society B*, *285*, 20181583.

Litvinov, F., Agapov, S., Katalimov, V., & Mironov, S. (1983). Rate of tooth replacement in blue shark, *Prionace glauca* (Carcharhinidae), in relation to feeding. *Journal of Ichthyology*, *23*, 143–145.

Lucifora, L. O., García, V. B., Menni, R. C., Escalante, A. H., & Hozbor, N. M. (2009). Effects of body size, age and maturity stage on diet in a large shark: Ecological and applied implications. *Ecological Research*, *24*, 109–118.

MacNeil, M. A., Skomal, G. B., & Fisk, A. T. (2005). Stable isotopes from multiple tissues reveal diet switching in sharks. *Marine Ecology Progress Series*, *302*, 199–206.

Mara, K. R., Motta, P. J., & Huber, D. R. (2010). Bite force and performance in the durophagous bonnethead shark, *Sphyrna tiburo*. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *313*, 95–105.

McClain, C. R., Balk, M. A., Benfield, M. C., Branch, T. A., Chen, C., Cosgrove, J., … Thaler, A. D. (2015). Sizing Ocean giants: Patterns of intraspecific size variation in marine megafauna. *PeerJ*, *3*, e715.

Meekan, M., Virtue, P., Marcus, L., Clements, K., Nichols, P., & Revill, A. (2022). The world's largest omnivore is a fish. *Ecology*, *103*, e3818.

Motta, P. J. (2004). Prey capture behavior and feeding mechanics of elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (pp. 165–202). Boca Raton: CRC Press.

Mouillot, D., Graham, N. A., Villeger, S., Mason, N. W., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, *28*, 167–177.

Moyer, J. K., & Bemis, W. E. (2017). Shark teeth as edged weapons: Serrated teeth of three species of selachians. *Zoology*, *120*, 101–109.

Munroe, S. E. M., Simpfendorfer, C. A., & Heupel, M. R. (2013). Defining shark ecological specialisation: Concepts, context, and examples. *Reviews in Fish Biology and Fisheries*, *24*, 317–331.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*, 1846–1850.

Paillard, A., Shimada, K., & Pimiento, C. (2020). The fossil record of extant elasmobranchs. *Journal of Fish Biology*, *98*, 445–455.

Papastamatiou, Y. P., Wetherbee, B. M., Lowe, C. G., & Crow, G. L. (2006). Distribution and diet of four species of carcharhinid shark in the Hawaiian islands: Evidence for resource partitioning and competitive exclusion. *Marine Ecology Progress Series*, *320*, 239–251.

Perez, V. J., Leder, R. M., & Badaut, T. (2021). Body length estimations of Neogene lamniform sharks (*Carcharocles* and *Otodus*) derived from associated dentitions. *Palaeontologia Electronica*, *24*, a09.

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*, 741–758.

Pimiento, C., & Balk, M. A. (2015). Body-size trends of the extinct giant shark *Carcharocles megalodon*: A deep-time perspective on marine apex predators. *Paleobiology*, *41*, 479–490.

Pimiento, C., & Benton, M. J. (2020). The impact of the pull of the recent on extant elasmobranchs. *Palaeontology*, *63*, 369–374.

Pimiento, C., Ehret, D. J., MacFadden, B. J., & Hubbell, G. (2010). Ancient nursery area for the extinct giant shark megalodon from the Miocene of Panama. *PLoS One*, *5*, e10552.

Pimiento, C., Leprieur, F., Silvestro, D., Lefcheck, J., Albouy, C., Rasher, D., … Griffin, J. (2020). Functional diversity of marine megafauna in the Anthropocene. *Science Advances*, *6*, eaay7650.

R Development Core Team. (2017). *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

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*, 395–407.

Shimada, K. (2002). Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). *Journal of Morphology*, *251*, 38–72.

Shimada, K. (2003). The relationship between the tooth size and total body length in the white shark. *Journal of Fossil Research*, *35*, 28–33.

Shimada, K. (2019). The size of the megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), revisited. *Historical Biology*, *33*, 904–911.

Shimada, K., Becker, M. A., & Griffiths, M. L. (2020). Body, jaw, and dentition lengths of macrophagous lamniform sharks, and body size evolution in Lamniformes with special reference to 'off-the-scale' gigantism of the megatooth shark, *Otodus megalodon*. *Historical Biology*, *33*, 2543–2559.

Strasburg, D. W. (1963). The diet and dentition of *Isistius brasiliensis*, with remarks on tooth replacement in other sharks. *Copeia*, *1963*, 33–40.

Straube, N., & Pollerspöck, J. (2020). Intraspecific dental variations in the deep-sea shark *Etmopterus spinax* and their significance in the fossil record. *Zoomorphology*, *139*, 483–491.

Tavares, D. C., Moura, J. F., Acevedo-Trejos, E., & Merico, A. (2019). Traits shared by marine megafauna and their relationships with ecosystem functions and services. *Frontiers in Marine Science*, *6*, 262.

Therneau, T., Atkinson, B., & Ripley, M. B. (2015). Package 'rpart'. The Comprehensive R Archive Network.

Turtscher, J., Jambura, P. L., Lopez-Romero, F. A., Kindlimann, R., Sato, K., Tomita, T., & Kriwet, J. (2022). Heterodonty and ontogenetic shift dynamics in the dentition of the tiger shark *Galeocerdo cuvier* (Chondrichthyes, Galeocerdidae). *Journal of Anatomy*, *241*, 372–392.

Weigmann, S. (2016). Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity. *Journal of Fish Biology*, *88*, 837–1037.

Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A., & Block, B. A. (2007). Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology*, *152*, 877–894.

Wetherbee, B. M., & Cortés, E. (2004). Food consumption and feeding habits. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (pp. 225–246). Boca Raton: CRC Press.

Whitenack, L. B., & Motta, P. J. (2010). Performance of shark teeth during puncture and draw: Implications for the mechanics of cutting. *Biological Journal of the Linnean Society*, *100*, 271–286.

Whitenack, L. B., Simkins, D. C., Jr., & Motta, P. J. (2011). Biology meets engineering: The structural mechanics of fossil and extant shark teeth. *Journal of Morphology*, *272*, 169–179.

Williams, J. J., Papastamatiou, Y. P., Caselle, J. E., Bradley, D., & Jacoby, D. M. P. (2018). Mobile marine predators: An understudied source of nutrients to coral reefs in an unfished atoll. *Proceedings of the Royal Society B*, *285*, 20172456.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cooper, J. A., Griffin, J. N., Kindlimann, R., & Pimiento, C. (2023). Are shark teeth proxies for functional traits? A framework to infer ecology from the fossil record. *Journal of Fish Biology*, 1–17. https://doi.org/10.1111/jfb.15326