JOURNAL OF **FISH** BIOLOGY

REGULAR ARTICLE

The rostral micro-tooth morphology of blue marlin, *Makaira nigricans*

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Numbers: GZ:HA 9403/1-1 AOBJ: 675842, 390523135

Abstract

Billfish rostra potentially have several functions; however, their role in feeding is unequivocal in some species. Recent work linked morphological variation in rostral micro-teeth to differences in feeding behavior in two billfish species, the striped marlin (*Kajikia audax*) and the sailfish (*Istiophorus platypterus*). Here, we present the rostral micro-tooth morphology for a third billfish species, the blue marlin (*Makaira nigricans*), for which the use of the rostrum in feeding behavior is still undocumented from systematic observations in the wild. We measured the micro-teeth on rostrum tips of

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blue marlin, striped marlin, and sailfish using a micro–computed tomography approach and compared the tooth morphology among the three species. This was done after an analysis of video-recorded hunting behavior of striped marlin and sailfish revealed that both species strike prey predominantly with the first third of the rostrum, which provided the justification to focus our analysis on the rostrum tips. In blue marlin, intact micro-teeth were longer compared to striped marlin but not to sailfish. Blue marlin had a higher fraction of broken teeth than both striped marlin and sailfish, and broken teeth were distributed more evenly on the rostrum. Micro-tooth regrowth was equally low in both marlin species but higher in sailfish. Based on the differences and similarities in the micro-tooth morphology between the billfish species, we discuss potential feeding-related rostrum use in blue marlin. We put forward the hypothesis that blue marlin might use their rostra in high-speed dashes as observed in striped marlin, rather than in the high-precision rostral strikes described for sailfish, possibly focusing on larger prey organisms.

1 | INTRODUCTION

Billfishes are a well-known, charismatic fish family that are widespread across the tropical and temperate oceans (Nakamura, 1985). Even though much of the attention has focused on their name-giving bill-like rostra (Atkins et al., 2014; Dhellemmes et al., 2020; Fierstine et al., 1996; Habegger et al., 2019, Habegger et al., 2015; Häge et al., 2022; Videler et al., 2016), we still know relatively little about the rostrum's function(s) in most billfish species. Exceptions to this are the sailfish, *Istiophorus platypterus* (Shaw 1792), and striped marlin, *Kajikia audax* (Philippi 1887). For both species, behavioral observations from the wild and detailed morphological analysis of their rostrums have (partly) revealed at least some of the structure's function (Hansen et al., 2020). Analysis of high-speed video recordings of both species preying on small schooling fish showed that sailfish used the rostrum more frequently when capturing fish compared to striped marlin. Sailfish often swim behind a fish school at about the same speed as the prey fish and then carry out either a targeted tap at individual prey or a powerful slash through the back of the school (Domenici et al., 2014), the latter of which typically injures many more fish than it kills (Herbert-Read et al., 2016; Krause et al., 2017). In contrast, striped marlin tend to accelerate before entering the fish school, dashing through it at high speed (Hansen et al., 2022). Prey contact with the rostrum often has the impression of being incidental to this attack strategy. This behavioral difference between both species was reflected by morphological differences in their rostral micro-teeth, a fine structure closely linked to the infliction of rostrum-mediated injuries in prey (Domenici et al., 2014; Krause et al., 2017). Hansen et al. (2020) successfully introduced the approach of relating micro-tooth morphology to differences in hunting behavior between billfish species. In comparison to striped marlin, sailfish, the species that uses its

rostrum more frequently when attacking prey, had more regrowth of micro-teeth and fewer broken teeth, which indicates more investment in micro-tooth maintenance (Hansen et al., 2020).

For other billfish species, direct behavioral observations are lacking; therefore, researchers have used indirect approaches to infer the function of the rostrum. Bill use for prey capture has, for instance, been predicted based on rostrum shape and its biomechanical properties. The characteristic flattened rostrum of the swordfish (*Xiphias gladius*, L. 1758) is predicted to be suited for horizontal slashing at prey, whereas the rounder rostrum of blue marlin is more suited for multiplane slashing (Habegger et al., 2015, 2019). Some evidence for potential rostrum use in prey capture by blue marlin has come from stomach content analysis, which provided cases of prey fish with characteristic slash wounds (Shimose et al., 2007).

Here we adopt the approach of predicting feeding-related rostrum use based on detailed analysis of rostral micro-teeth. We investigated different characteristics of the rostral micro-teeth via micro–computed tomography (CT) analysis of the rostrum tips of blue marlin *Makaira nigricans* Lacepède 1802 from a dataset created for this study. Morphology of blue marlin micro-teeth is then compared to micro-CT images of sailfish and striped marlin. For this we extended the dataset published in Hansen et al. (2020) with additional individuals and a novel measurement approach. Although the study by Hansen et al. (2020) has investigated general differences in bill use frequency between striped marlin and sailfish, it was never quantified with which section of the rostrum both species predominantly make prey contact. To close this gap and to identify an area of focus for our morphological investigation, we analysed video recordings of hunting striped marlin and sailfish.

We derived our hypotheses for blue marlin micro-tooth structure on similarities and differences in general body morphology compared

to sailfish and striped marlin. Despite their close phylogenetic relationship (Collette et al., 2006; Williams et al., 2017), sailfish and blue marlin differ in their morphology, with sailfish exhibiting some unique morphological features among billfish (e.g., the name-giving sail-like first dorsal fin). Blue marlin share more morphological features with striped marlin such as a similar fin morphology and a less-compressed body shape (Nakamura, 1985). These similarities are consistent with previous biomechanical analyses of blue marlin rostra, which have predicted blue marlin's potential rostrum use and feeding behavior to be closer to the type observed in striped marlin than in sailfish, based on their slightly stouter and more dorsoventrally flattened shape (Fierstine et al., 1996; Hansen et al., 2020). Furthermore, Nakamura (1985) gave an anecdotal description of hunting behavior in blue marlin that resembles the characteristic high-speed dashes observed in striped marlin (Hansen et al., 2020, 2022). Given this observation and previous biomechanical analyses, we hypothesize that the micro-teeth of blue marlin more closely resemble those of striped marlin than those of sailfish. We hypothesize that the micro-teeth of blue marlin show a relatively high percentage of broken teeth and a low percentage of regrowing teeth. We tested these hypotheses and developed predictions regarding the potential hunting strategy of blue marlin by comparing their micro-tooth characteristics to those of sailfish and striped marlin.

2 | MATERIALS AND METHODS

To shed light on rostrum use in three species of billfish, we present newly acquired behavioral data on striped marlin and sailfish, as well as a combination of newly acquired and previously published morphological data on blue marlin, striped marlin, and sailfish (see Section 2.2. for details). We start by identifying the area of the rostrum that most predominantly comes into contact with prey. To the best of our knowledge, there is no systematically collected high-speed video footage of rostrum use in blue marlin; thus, we conducted this analysis using only video recordings of sailfish and striped marlin. Next, we focused on these identified areas of the rostrum by taking samples from this region to study micro-tooth differences across all three different species.

2.1 | Behavioral analysis of prey contact

To investigate the predominant rostrum area for prey contact, we analysed video recordings of sailfish and striped marlin hunting in the wild. Both species were filmed underwater while preying on small schooling fish by researchers snorkeling at c. 3–10 m distance. Sailfish were recorded (CASIO EX-FH100, 240 fps) 15–30 km offshore northern Quintana Roo in the Gulf of Mexico (21° 28.3–41.15′ N, 86° 38.41–41.30′ W) in 2012. We analysed 55 min of video footage of sailfish predating on six different schools of sardinellas (*Sardinella* sp.). Predation by striped marlin was filmed (GoPro HERO7, 60/120 fps) 10–30 km offshore Baja California, Mexico (24° 54.52–48.5′ N, 112°
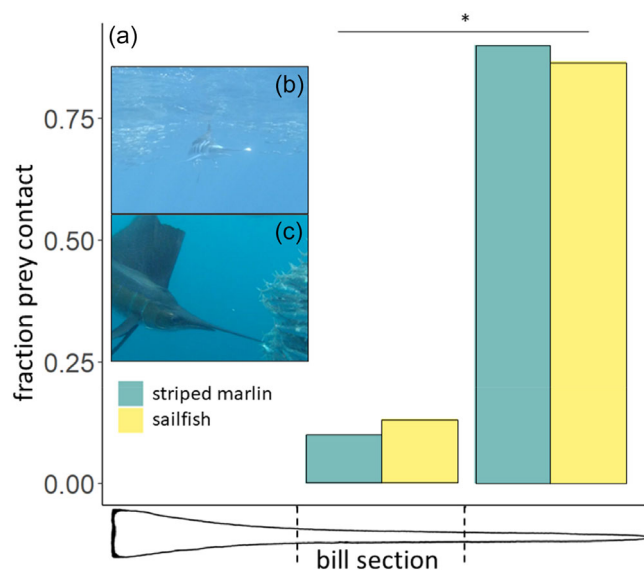

FIGURE 1 Behavioral analyses to determine the predominant rostrum section in prey contact for *Kajikia audax* and *Istiophorus platypterus*. (a) Both striped marlin (b, N = 30) and sailfish (c, N = 30) made prey contact significantly more often with the first third of their rostrum (*; X^2(2, N = 60) = 82.9, p < 0.05), with no difference between species.

34.46–23.51′ W). We analysed 62 min of video footage of striped marlin predating on three different schools of Pacific sardine (*Sardinops sagax*). As both species show variation in the frequencies, with which they use their rostrum during hunting (Hansen et al., 2020), video recordings were screened by a human observer for attacks in which an actual rostrum–prey contact was observable. We identified 30 different attacks per species and extracted the still frame of the initial prey contact (see Figure 1). We used these frames to determine our area of interest, defined as the relative third of the rostrum with which initial rostrum–prey contact is made during rostrum use in sailfish and striped marlin, respectively.

2.2 | Analysis of micro-tooth morphology

Based on our behavioral observations, we selected the rostrum tip for a micro-CT analysis of micro-teeth in blue marlin (N = 5, lower jar fork length [LJFL]: 204–256 cm, rostrum length [RL]: 53.6–71.3 cm), striped marlin (N = 6, LJFL: 167–203 cm, RL: 43.2–58.4 cm), and sailfish (N = 6, LJFL: 183–242 cm, RL: 53.6–60.0 cm). All specimens were collected by commercial fishermen in Reunion, France. Further details on collection site, size of analysed specimens, and the relationship between animal size and micro-tooth length are given in Table S1 and Figure S1. Micro-teeth were therefore exclusively measured on the first 55 mm of the rostrum. Segments of this length represented the maximum size of a single object measurable, while simultaneously maintaining a sufficient resolution with our selected micro-CT methodology. Scans were performed at the Julius-Wolf Institute, Charité Berlin (three striped marlin rostral tips in 2019, Micro-CT Skyscan
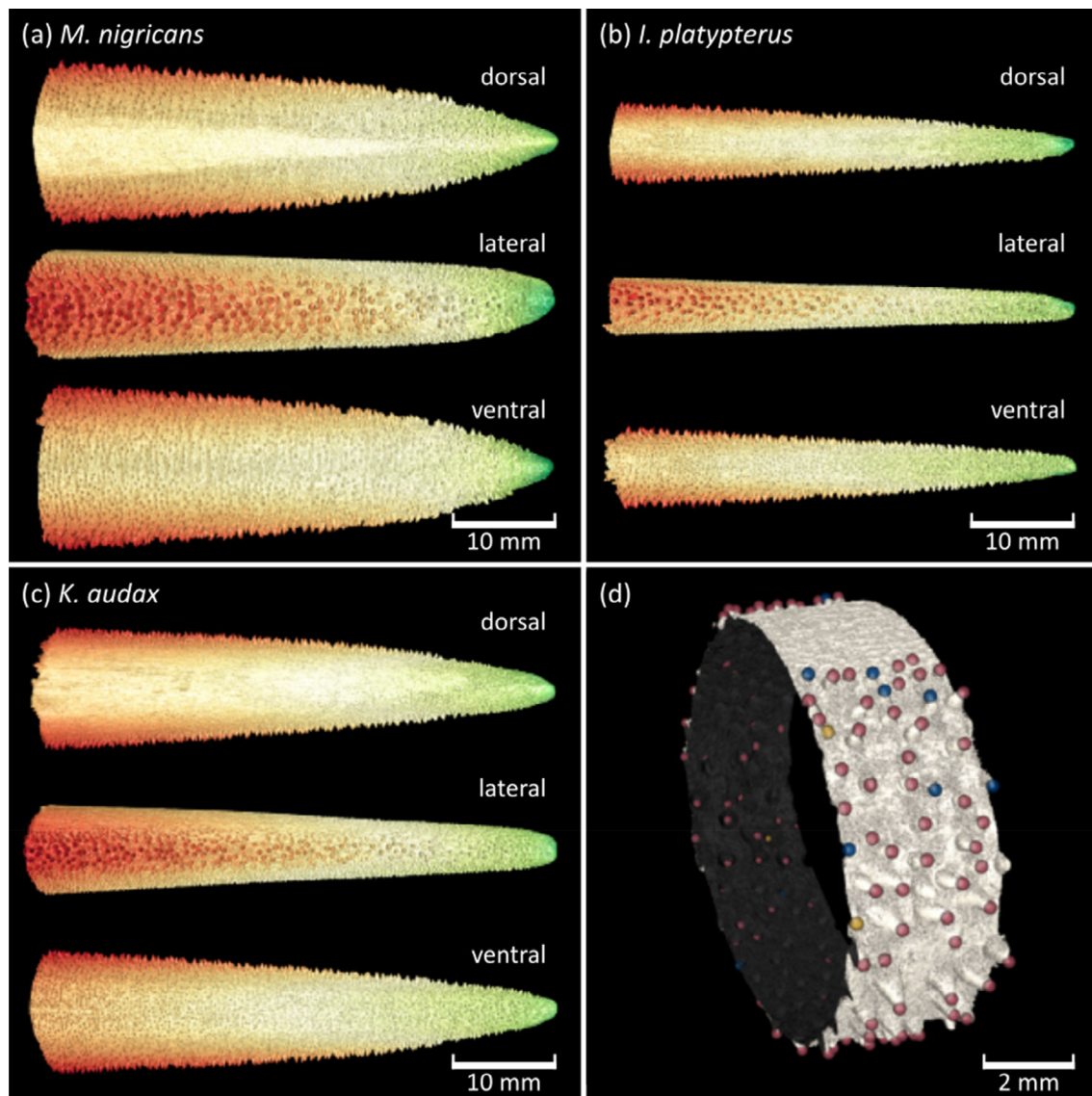
FIGURE 2 Micro-CT (computed tomography) images of rostrum tips of (a) *Makaira nigricans*, (b) *Istiophorus platypterus*, and (c) *Kajikia audax*. (d) State of micro-teeth was determined by a visual inspection of individual micro-teeth on 1.5–2.0 mm rostral segments (example image is of a blue marlin rostral segment). The state (i.e., broken, intact, and growing) was assessed by a human observer.

1172, Skyscan, Kontich, Belgium), and the Natural History Museum, Berlin (six sailfish rostral tips in 2019, three striped marlin, and five blue marlin rostral tips in 2022, Phoenix Nanotom, General Electric, Wunstorf).

We followed a framework previously applied by Hansen et al. (2020) for micro-tooth comparison of sailfish and striped marlin. Rostrum tips of all three species were analysed using high-resolution CT (Figure 2). Micro-CT data were processed and visualized in a previously developed software to automatically identify, label, and measure parameters of rostral micro-teeth. For each micro-tooth we determined four variables: (1) length, measured as distance from the base of the tooth on the rostrum to its apex; (2) state, distinguishing between intact, broken, or regrowing; (3) distance of an individual tooth to rostrum tip; and (4) angle, measured as its angular position in degrees from the roll axis of the rostrum (from a frontal view: 0°/360°

dextral side, 90 dorsal side, 180° sinistral side, and 270° ventral side; see Figure S5). This analysis was done for all rostra of blue marlin and two rostra of striped marlin. For the remaining rostra (four striped marlin, six sailfish) we partly used a previously published dataset of Hansen et al. (2020) from which we used the original micro-CT scans and the designation of micro-tooth state.

To perform measurements, we used the following novel semiautomated approach. Due to the large volume of raw micro-CT data, we needed to process it such that we could examine and evaluate them. For some steps no human intervention was required, and they could be performed automatically, whereas other steps needed human monitoring. We converted the original form of the data (image series, volume data) into 3D objects. The conversion process, including filtering, segmentation, and surface extraction, was done automatically by the software. This reduced the human workload and ensured uniform and

repeatable processing of the data with consistent quality. To be able to compare the rostra, the software aligned them to a standardized coordinate system, and a human observer verified correct alignment. In the next step micro-teeth were identified and classified. To do this, we developed an automatic feature detection system. A two-dimensional regular grid was created by ray casting the 3D surface data. The software identified local maxima on the grid and labeled the micro-teeth found with color marks (see Figure 2d). We then manually inspected the labeled micro-teeth to remove artifacts and assess the state of each tooth. To keep the examination manageable, only 1.5–2.0 mm rostral segments of the labeled micro-teeth were visually inspected (see Figure 2d) at a time. Automatic pre-labeling and partitioning speeded up the process considerably and still ensured high reliability of micro-teeth identification. In the final step the lengths of all verified micro-teeth were automatically measured. Further details can be found in Data S1.

To ensure our classification of tooth state was accurate, a small sub-sample of micro-teeth was counterchecked for accuracy regarding the classification of tooth state using additional imaging methods. First, we used high-definition light microscopic images of whole bill tips (Keyence VHX-5000 digital microscope, Keyence Corporation, Osaka, Japan, 50× magnification) and compared 21 teeth per species between light microscopy and micro-CT renderings to find possible artifacts and differences, which could influence tooth state classification (see Figures S6 and S7). Second, we acquired scanning electron microscopic images (Phenon XL G2, Thermo Fisher Scientific, Waltham, MA, USA, 600× magnification, chamber pressure: 60 kPa, accelerating voltage: 15 kV) of 10 lateral micro-teeth of blue marlin and compared their state with the same teeth on our micro-CT renderings (see Figure S8). Neither our comparisons of micro-tooth state between micro-CT renderings and light microscopy nor comparisons between micro-CT renderings and scanning electron microscopy revealed differences that would have justified a different classification of tooth state.

2.3 | Statistical analysis

All statistical analyses were carried out in R (v4.2.2, R Core Team 2023). To investigate how micro-tooth length differed between species, we fitted a series of Bayesian multilevel regression models using the brms library (Bürkner, 2017) in which the length of intact micro-teeth was set as a response variable. Species, distance to the rostrum tip, and angle were fitted as population-level effects. To account for the unique properties of our population-level effects, distance was included as a linear term, whereas angle was included as a circular spline (see Supplementary Materials for details on model specification). In addition, we fitted models in which interaction terms among "species and distance" and "species and angle" were included. To account for repeated measurements, we included rostrum ID as a group-level effect. We used an ex-Gaussian distribution as this approximated best-intact tooth length distribution. We fitted a series of seven models in which both interactions, one interaction and a variation in the predictors, were included. We ran three chains per model,

all with 5000 samples of which the first 2500 were discarded as warmup. To estimate the effect of species on the length of intact micro-teeth, we selected the best-performing model of a series by comparing WAIC (Widely Applicable Information Criterion) score and checked the 95% credibility interval for species overlapping with zero. For circular splines we compared the WAIC weight of models in which the term was included and excluded.

To gain insight into how the fraction of broken and regrowing micro-teeth differed among our analysed species, we fitted a series of separate models in which tooth broken (yes/no) or tooth growing (yes/no) was fitted as binary variables. We fitted a series of seven models per response variable with the same specifications regarding group and population-level effects. As our response variables were binary, we used Bernoulli distributions. We ran three chains with 3000 iterations per model in which the first 1500 were discarded as warmup.

3 | RESULTS

3.1 | Behavioral analysis

Analysis of video recordings of hunting striped marlin and sailfish showed that significantly more prey contact was made with the first third of the rostrum (X^2(2, $N = 60$) = 82.9, $p < 0.05$), with no difference between the striped marlin and sailfish (Fisher's exact test, $p = 1$, two sided, Figure 1). Based on these findings we focused our analysis of micro-tooth morphology on the tip of the rostrum.

3.2 | Morphological analysis

We measured 42,507 individual micro-teeth. Intact micro-teeth in blue marlin were significantly longer than intact micro-teeth in striped marlin, but not longer than those in sailfish (Figure 3a; species-striped marlin: estimated = −0.09; 95% C.I. [−0.17–0.01]; species sailfish: estimated = −0.07; 95% C.I. [−0.14–0.01]). In addition, the circular position (i.e., angle) strongly correlated with the length of rostral micro-teeth as its exclusion notably worsened model fit. Lateral micro-teeth, indicated by an angle of 0/360° (dextral) and 180° sinistral), were longest in all three species (Figure 3b). Distance from the tip had no effect on length in all three species (Figure 3c).

The fraction of broken teeth was significantly different among all three species, with blue marlin having the highest proportion and both striped marlin and sailfish having fewer broken micro-teeth (Figure 3d; species-striped marlin: estimated = −1.37; 95% C.I. [−2.31–0.43]; species sailfish: estimated = −2.94; 95% C.I. [−3.90–1.99]). Both striped marlin and sailfish showed variation in the fraction of broken teeth, with more teeth broken on the lateral rostrum sides, whereas notably this effect was absent for blue marlin (Figure 3e).

Finally, the fraction of regrowing teeth was not different between blue marlin and striped marlin, whereas sailfish had a greater proportion of growing teeth (Figure 3g; species sailfish: estimated = 0.64; 95% C.I. [0.54 3.04]), especially in the lateral rostrum region (Figure 3h).
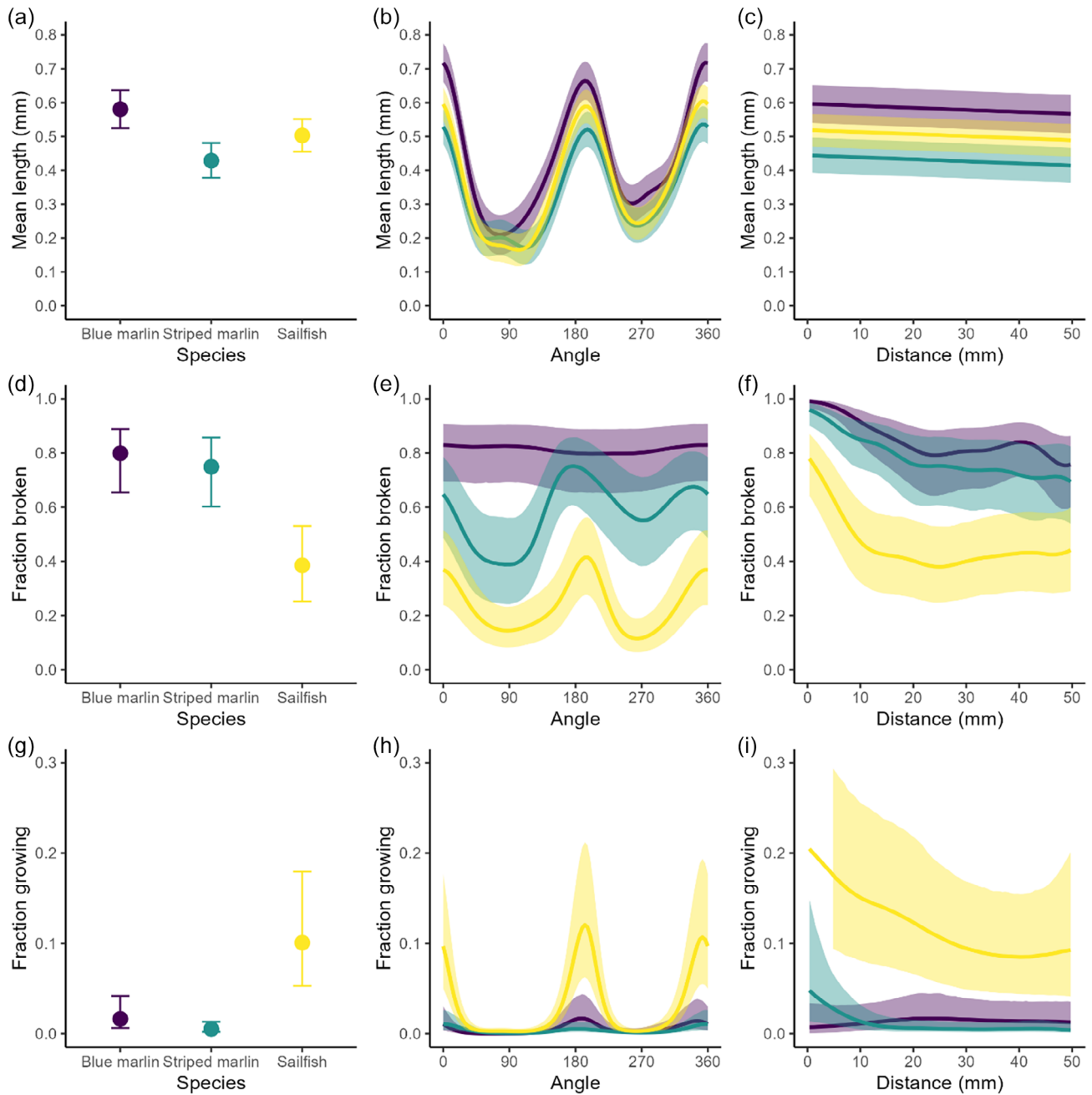
FIGURE 3 Analysis of micro-tooth variables from micro-CT (computed tomography) measurements for *Makaira nigricans*, *Istiophorus platypterus*, and *Kajikia audax*. Shown are results for blue marlin (*M. nigricans* in purple; N = 5), striped marlin (*K. audax* in turquoise, N = 6), and sailfish (*I. platypterus* in yellow, N = 6) rostral tips of 55 mm length. Plotted are the effect of "species," "angle (with 0°, 90°, 180°, and 270°, corresponding to dextral, dorsal, sinistral, and ventral, respectively)," and "distance from tip (mm)" on (a–c) mean length of intact micro-teeth, (d–f) fraction of broken micro-teeth, and (g–i) fraction of growing micro-teeth. Plots show the marginal effects of Bayesian multilevel regression models, with solid dots/lines representing the posterior median and error bars/shaded lines 95% c.ɪ..

4 | DISCUSSION

The micro-tooth morphology of blue marlin rostral tips was in accordance with our predictions; compared to other billfish species, it was more similar to that of striped marlin than sailfish, with a relatively high percentage of broken micro-teeth and a low regrowth rate. A comparative approach has previously been successful in identifying

feeding-related functions of morphological structures in a variety of different taxa, such as birds (Olsen, 2017), marine mammals (Franco-Moreno et al., 2021), elasmobranchs (Nevatte et al., 2017; Wueringer et al., 2012), and other species of billfishes (Dhellemmes et al., 2020; Habegger et al., 2015; Hansen et al., 2020). Notably, Hansen et al. (2020) have linked lower percentages of broken teeth and an increased regrowth rate on the sailfish rostrum to a higher investment

into the maintenance of these structures. The morphological differences in sailfish are associated with a unique hunting strategy in which they use their rostra for precision strikes on prey in contrast to the more sporadic rostrum use observed in striped marlin. Biomechanical investigations of bite force across billfish species found the lowest relative bite force in sailfish compared to other billfish species (or other similar-sized piscivorous teleosts), which was seen as an indication that sailfish rely more on their rostrum (than on bite force) for feeding (Habegger et al., 2017). Blue marlin was reported as second highest among the analysed billfish species (striped marlin bite force was not investigated), which by implication should result in a lower dependence on the rostrum throughout feeding and is in line with differences in micro-tooth regrowth observed in our study.

We found lateral micro-teeth to be the longest in all three billfish species. Even though the multifunctionality of the billfish rostrum is under discussion (Dhellemmes et al., 2020; Häge et al., 2022; Videler et al., 2016), inflicting physical damage on prey is regarded as the main purpose of rostral teeth (Domenici et al., 2014; Hansen et al., 2020; Nevatte et al., 2017). This is well documented in sailfish, which are known to swim in close proximity to schooling prey and repeatedly injure fish with precise rostrum strikes, thus negatively affecting the prey's swimming performance and increasing the predators' hunting success (Herbert-Read et al., ; Krause et al., 2017; Kurvers et al., 2017). As these rostrum strikes are mostly performed on the horizontal plane, the long lateral micro-teeth should predominantly make contact and increase damage in prey organisms. Even though rostrum use is regularly observed, behavioral studies have not provided clear evidence of a preference for horizontal rostrum strikes in striped marlin, which would explain the greatest micro-tooth length on the lateral rostrum. In blue marlin, no video recordings of their hunting behavior are available, but a hunting technique similar to that of sailfish is an unlikely explanation for the greater length of lateral micro-teeth found in our study. Sailfish hunting behavior is directly associated with the unique body morphology of the species, such as a compressed body shape and dorsal fin size. The large dorsal fin (i.e., the sail) has been linked to its stabilizing properties on extension, thus enabling the execution of precise movement during high swimming speeds (Marras et al., 2015), whereas a laterally compressed body shape is predicted to provide the sailfish with the needed flexibility to carry out its precise maneuverers during hunting (Domenici, 2001; Marras et al., 2015; Nakamura, 1985). Neither striped- nor blue marlin share these morphological features with sailfish. Both species exhibit a body morphology indicated by a less-compressed cross-section and no posterior dorsal-fin extension (Nakamura, 1985).

Noticeably, striped marlin have a lower fraction of broken teeth than sailfish (Hansen et al., 2020). Blue marlin show the highest fraction of broken teeth across the three species, and this occurs at all angles around the rostrum, unlike sailfish that show broken teeth mainly in lateral positions, as a result of their slashes directed sideways. With regard to these morphological and behavioral differences in sailfish and striped marlin, rostrum use and hunting in blue marlin might therefore more closely resemble the high-speed dashes of striped marlin, rather than the high-precision sideway rostral strike strategy described for sailfish.

Franco-Moreno et al. (2021) classified specialization within three species of pinnipeds by analysing morphological skull characteristics and relative bite force. The study provided evidence for three different feeding strategies in closely related marine predators occurring within the same habitat. Similarly, variation in micro-tooth morphology may hint at resource specialization among the billfish species analysed in our study. Blue marlin are known to hunt during the night in the epi- and mesopelagic zones, occasionally performing deep vertical migrations (Hoolihan et al., 2011), where they feed on cephalopods (Abitia-Cardenas et al., 1999). This behavior is similar to swordfish, which is the billfish species widely associated with adaptions for hunting in deep oceanic habitats (Hoolihan, 2005; Potier et al., 2007; Prince et al., 2010). Sailfish, in contrast, are the billfish species most known for their preference for near-surface habitats and a completely diurnal activity pattern (Hoolihan, 2005). The ecology and morphology of sailfish and swordfish may therefore serve as two opposite ends of specialization within the billfishes. Swordfish are solitary predators, exhibiting a rounded torpedo-like body shape, and are known for their physiological adaptions for hunting at great depths, such as large eyes and endothermal properties in the respective body region to maintain visual function at low water temperatures (Braun et al., 2015; Carey & Carey, 1982; Nakamura, 1985; Videler et al., 2016). Whereas rostrum use in swordfish is yet undocumented, indirect evidence from gut analyses suggests the swordfish uses its sword for regularly killing and severing the bodies of larger prey organisms (Habegger et al., 2019; Scott & Tibbo, 1968). Sailfish, on the contrary, are known to form large aggregations near the surface, where they utilize their unique morphological adaptions (e.g., compressed body shape, extended dorsal fin) to effectively overcome defensive measures by small schooling prey (Domenici et al., 2014; Hansen et al., 2020; Marras et al., 2015). Additional evidence for these feeding strategies can be derived from Dhellemmes et al. (2020), where swordfish, blue marlin, striped marlin, and sailfish were analysed for their rostral oil pore morphology. The study found swordfish and sailfish to represent two extremes in oil pore extension along the rostrum, with the lowest extension in swordfish and the highest in sailfish, respectively. Interestingly, pore morphology of blue marlin was found to be closer to swordfish, whereas striped marlin differed only slightly from sailfish. Placing micro-tooth morphology within the broader context of the ecology and morphology of swordfish and sailfish provides a potential explanation for differences found in the present study.

Rostrum use in blue marlin might somewhat resemble the hunting strategy predicted for swordfish, namely that larger prey organisms are attacked at greater depths, where they are severely incapacitated, killed, and dismembered before ingestion. There are reports of severely damaged prey organisms retrieved from stomachs of blue marlin (Shimose et al., 2007). As sustained swimming speeds scale up with body size (Videler, 1993), blue marlin and swordfish could rely on this strategy to avoid costly pursuits of larger individual prey (instead of using the rostrum to injure and isolate smaller prey items from a school). However, whereas swordfish seem specialized to inflict injury

through mostly horizontal rostral strikes (Habegger et al., 2015, 2019), blue marlin were the only species in our study with broken micro-teeth at all orientations on the rostrum. This suggests prey contact is made more uniformly around the rostrum tip and, therefore, we predict they either utilize a greater range of rostral motion to strike at prey compared to other species or they are less purposeful with their rostral use, focusing more on fast dashes and incidental prey contact—more similar to striped marlin. In either case, their long micro-teeth could aid in inflicting maximum damage to larger and faster prey (compared to prey of other billfish species) with the first contact. Sailfish rostra are, in contrast, specialized for predating on small schooling prey organisms near the surface, where the main challenge is overcoming the prey's high maneuverability (Domenici et al., 2014). Following this approach, a more opportunistic feeding strategy is predicted for striped marlin, which is known for occasionally preying on schooling prey in surface-near layers, while lacking the distinctive features in body and rostrum morphology, indicating a high level of specialization on this prey type. This assumption is supported by long-term tagging data and gut analysis, both predicting a high flexibility in habitat and dietary preferences for striped marlin (Lam et al., 2015; Torres Rojas et al., 2013).

5 | CONCLUSION

In conclusion, the present study on blue marlin found high percentages of broken teeth and low levels of tooth regrowth, similar to striped marlin, and indicates a lower reliance on precise rostrum use, as observed in sailfish. Further morphological variation among blue- and striped marlin, namely longer teeth and a more uniform distribution of broken micro-teeth in blue marlin, may be the result of different levels of specialization. Notably, the reported morphological differences in this study are derived from billfish populations from the Indian Ocean in which hunting behavior has not yet been observed. And although differences in tooth morphology in sailfish and striped marlin are consistent with variation in hunting behavior observed in the Atlantic and Pacific populations, an interpopulation comparison within the same species would be all the more intriguing. This could present a promising approach for further research to unravel additional functions of the rostrum in different species of billfish and provide in-depth knowledge of an enigmatic group of pelagic teleost predators.

AUTHOR CONTRIBUTIONS

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