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Linking hunting weaponry to attack strategies in sailfish and striped marlin

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Linking morphological differences in foraging adaptations to prey choice and feeding strategies has provided major evolutionary insights across taxa. Here, we combine behavioural and morphological approaches to explore and compare the role of the rostrum (bill) and micro-teeth in the feeding behaviour of sailfish (*Istiophorus platypterus*) and striped marlin (*Kajikia audax*) when attacking schooling sardine prey. Behavioural results from high-speed videos showed that sailfish and striped marlin both regularly made rostrum contact with prey but displayed distinct strategies. Marlin used high-speed dashes, breaking schools apart, often contacting prey incidentally or tapping at isolated prey with their rostra; while sailfish used their rostra more frequently and tended to use a slower, less disruptive approach with more horizontal rostral slashes on cohesive prey schools. Capture success per attack was similar between species, but striped marlin had higher capture rates per minute. The rostra of both species are covered with micro-teeth, and micro-CT imaging showed that species did not differ in average micro-tooth length, but sailfish had a higher density of micro-teeth on the dorsal and ventral sides of their rostra and a higher amount of micro-teeth regrowth, suggesting a greater amount of rostrum use is associated with more investment in micro-teeth. Our analysis shows that the rostra of billfish are used in distinct ways and we discuss our results in the broader context of relationships between morphological and behavioural feeding adaptations across species.

1. Introduction

Comparative analyses of morphological and behavioural differences between species are a powerful tool in evolutionary and behavioural biology. Such an approach has led to landmark discoveries concerning the adaptive divergence of species. Most famously, differences in bill morphology between species of Darwin's finches (*Geospiza* sp.) have been related to feeding specializations where the shape and size of bills correspond to particular foods and feeding modes [1,2]. Differences between bill morphology and subsequent links to foraging behaviour and resource availability can also be found within a species [3,4]. The comparative exploration of morphological and behavioural feeding specializations is a robust and effectual method for gaining insights into biomechanics, speciation processes, the origin and maintenance of different feeding niches, and evolutionary arms races between predators and their prey.

Here, we use billfishes (Istiophoridae and Xiphiidae) for such an approach. This enigmatic group of fish are among the best-known fishes in the world owing to their popularity in sport-fishing and as a commercial fishery (mainly swordfish). The characteristic extended rostrum (bill) has been subject to morphological and biomechanical investigations [5–7] and linked with differences in foraging strategies [5,6,8,9]. While other potential functions for rostra, such as hydrodynamic benefits [10,11] or defence [12], have been suggested, there is morphological evidence [6] and clear behavioural evidence from field observations in sailfish, *Istiophorus platypterus* [5,8], that support its use for prey capture. Evidence for rostrum use in prey capture in billfish species other than sailfish is either anecdotal, or inferred from biomechanical tests [6,7,13], or stomach content analysis [9].

The rostra of billfishes appear superficially similar, but several differences exist and their implications for species-specific foraging ecology have been discussed [6,14]. The rostrum of the swordfish, for instance, is wide and dorso-ventrally flattened, making it suitable for horizontal movements, whereas the more rod-like rostrum of Istiophoridae, such as the blue marlin, *Makaira nigricans*, suggests it is more adapted for multi-plane strikes [6]. Another important aspect of the rostra of Istiophoridae (absent from Xiphiidae) is the presence of micro-teeth on the rostrum surface [14,15]. These micro-teeth are true teeth composed of an organic pulp cavity and enamel cap (see electronic supplementary material and figure 1 for more details) and play an important role in injuring prey during attacks prior to capture [5,8,15,16]. Fierstine & Voigt [14] concluded that sailfish have a larger area of dorsal micro-teeth than striped marlin, but no detailed investigations have been made to link their characteristics to differences in feeding strategies between species.

In this study, we collected behavioural and morphological data on two species of Istiophoridae, striped marlin (*Kajikia audax*) and sailfish. This included the first high-speed footage of striped marlin, providing a unique opportunity to compare both species at a fine behavioural and morphological scale. We chose the striped marlin for comparison with the sailfish for two main reasons. Firstly, while sailfish and striped marlin are closely related, with comparable body sizes and diet (see electronic supplementary material for more details) [17–20], their rostra are known to be shaped differently. Fierstine & Voigt [14] noted 26/32 rostral characteristics were significantly different in a pairwise comparison between sailfish and striped marlin. In general, sailfish have a more slender and rounder rostrum compared with the stouter and more dorso-ventrally flattened rostrum of striped marlin [14,19] (also see figure 1*f*,*g*). Secondly, while sailfish are known to be obligate rostrum users [5,8,15,16], striped marlin have been anecdotally reported to not use their rostra for feeding [21,22]. This is despite both species being observed group hunting schools of prey fish (even the same school of prey fish, M. J. Hansen 2018, personal observation).

In order to investigate the use of the rostrum in the context of the entire attack strategy, we used a Markovian classification task to test for behavioural differences between the two species. Sailfish have the lowest relative bite force among billfishes [11], suggesting a greater reliance on the rostrum (a complementary feeding structure) for prey capture in this species. Therefore, we hypothesized sailfish use their rostra more than striped marlin during attacks of sardine schools. Considering the known difference in shape of the two species' rostra, we also predicted that they would be employed differently when striking at prey fish. In addition to the behavioural observations, we performed micro-computed tomography (micro-CT) analyses of the micro-teeth on the rostral tip. Therefore, we also explore the potential coevolution of micro-tooth morphology and attack behaviour.

2. Methods

(a) Behavioural analysis

Research was conducted on sailfish (*I. platypterus*) [17] and striped marlin (*K. audax*) using video recordings of wild predation events upon schools of sardines (*Sardinella aurita* and *Sardinops sagax caerula*, respectively) (see electronic supplementary material for details). We assessed behaviour from this video footage using two complementary approaches. All research was conducted in line with the laws and legislation of Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), Mexico, and with consideration given to the treatment of animals in behavioural research [23].

(i) Analysis of attack dynamics

A Markov chain analysis was performed on the video footage collected from both sailfish ($n = 7$ schools) and striped marlin ($n = 3$ schools) to identify the most important states of an attack sequence and to compare attack behaviour between the two species. Markov chain analysis is a common approach for classification tasks including behaviour pattern analysis [24,25]. We described attacks as sequences of actions, which formed the states of our Markov chains. We distinguished the following seven actions (states): *approach*, *dash*, *bill use*, *prey contact*, *open mouth*, *ingest* and *leave* (see electronic supplementary material for definitions). All sequences used for our analysis describe complete attacks, i.e. they start with *approach* and end with *leave*. Between *approach* and *leave* the states *dash*, *bill use*, *prey contact*, *open mouth* and *ingest* may (potentially) occur in any order and number (figure 2). Sailfish data consist of 150 attack sequences with a mean length of 3.6 ± 0.14 (s.e.) actions (median length = 3 actions). Striped marlin data consist of 665 attack sequences with a mean length of 4.2 ± 0.07 (s.e.) actions (median length = 4 actions).

To determine differences in the attack sequences between species we constructed first-order Markov chains (see electronic supplementary material, Methods and table S1 for details on model selection) for each species and calculated the percentage of attack sequences that were correctly classified by the model

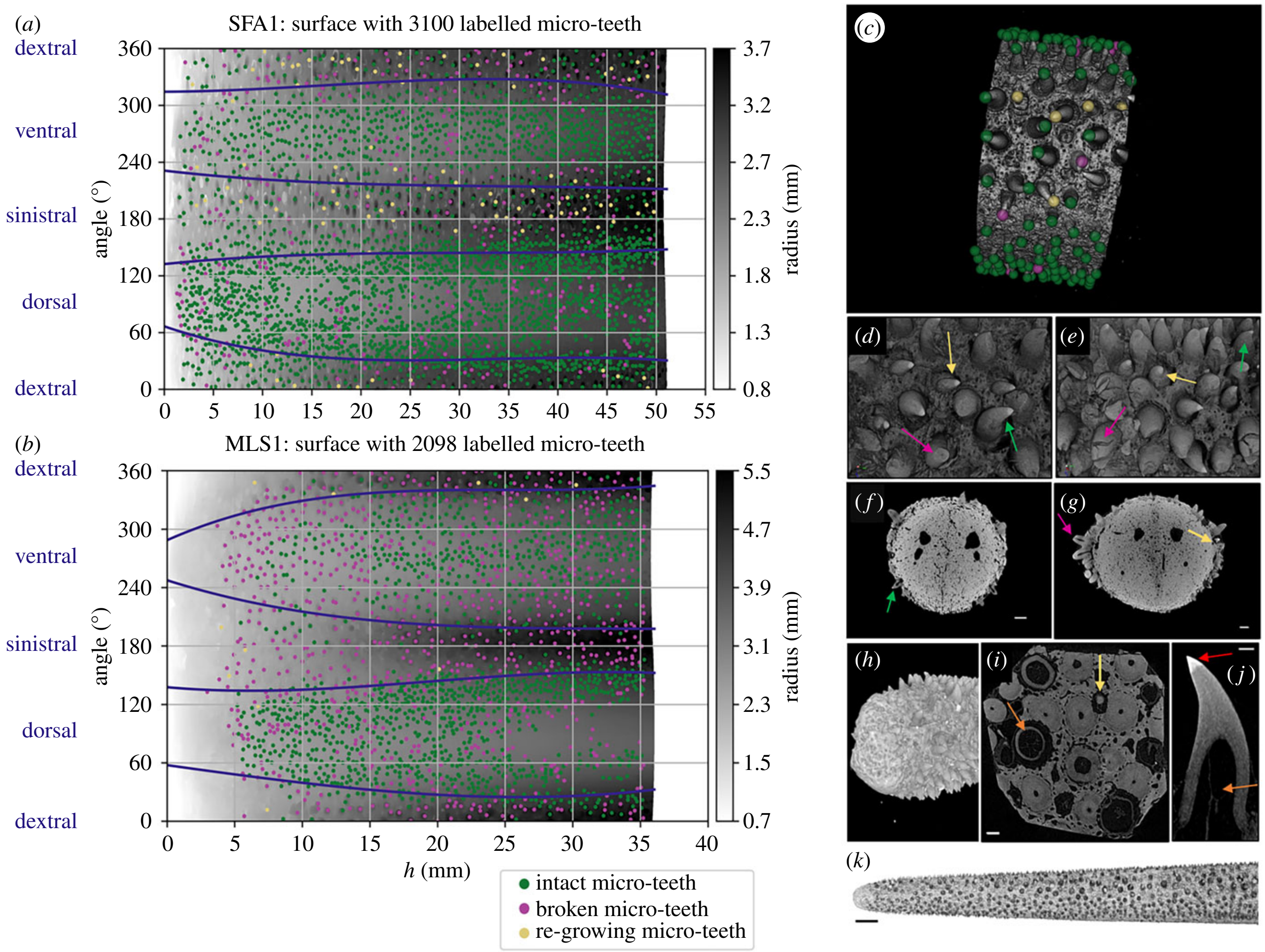
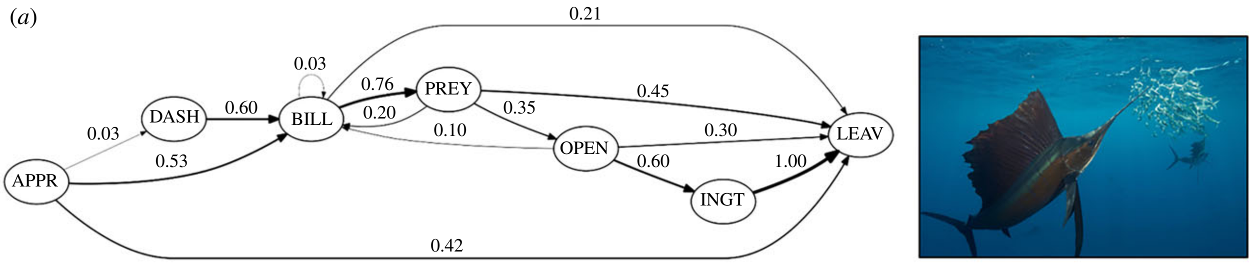


Figure 1. Examples of micro-CT overview images displaying the positions of all micro-teeth measured on the rostrum, coloured by micro-teeth type, for (*a*) one sailfish and (*b*) one striped marlin specimen. Green dots/arrows represent intact micro-teeth, pink dots/arrows represent broken micro-teeth and yellow dots/arrows represent re-growing micro-teeth in all images. The *x*-axis (*h*, mm) represents the distance from bill tip (0 on the far left) to the head (50 on the far right). The *y*-axis and purple lines show the angular position of the micro-teeth in degrees from the roll-axis of the rostrum. 0° is the dextral side, 90° is the dorsal side, 180° is the sinistral side and 270° is the ventral side. (*c*) 3D computer visualization with volume rendering of a random section of rostral surface displaying micro-teeth, (*d*) 3D surface of sailfish rostrum showing micro-teeth, (*e*) 3D surface of marlin rostrum showing micro-teeth, (*f*) sailfish rostrum cross-section (21.26 mm from tip) (scale bar, 500 µm), (*g*) marlin rostrum cross-section (21.26 mm from tip) (scale bar, 500 µm), (*h*) 3D perspective of the tip of sailfish rostrum, (*i*) slice of sailfish rostrum showing (yellow arrow) re-growing micro-tooth encroaching on broken dead micro-teeth, and (orange arrow) pulp of healthy tooth (scale bar, 200 µm), (*j*) micro-CT of a single intact micro-tooth showing enamel cap (red arrow) and organic pulp cavity (orange arrow) (scale bar, 100 µm), (*k*) micro-CT image of entire sailfish rostrum tip (scale bar, 2 mm). (Online version in colour.)

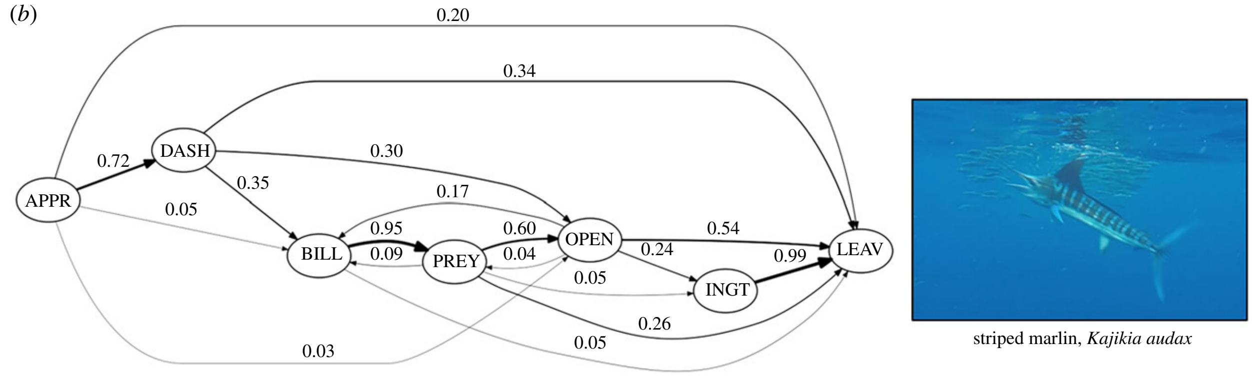
(i.e. where the model correctly recognized the species). We randomly selected a subset of the striped marlin data that had the same number of attack sequences as the sailfish data ($n = 150$ attack sequences) and randomly split the striped marlin and sailfish data into two subsets, respectively, one for the parameter estimation of the models ('training': M_{train}, consisting of 120 attack sequences) and one for the evaluation ('test': M_{test}, consisting of 30 attack sequences). The predictive power of the trained models was tested on the 'unseen' test data. This process was repeated 1000 times. The classification decision was made by choosing the species whose Markov chain model maximized the likelihood of this sequence (using the Bayesian information criterion (BIC)).

(ii) Capture rates and rostrum use

To investigate in detail possible differences in rostrum use, we used 990 attack sequences (sailfish $n = 325$, striped marlin $n = 665$ attack sequences) recorded from 10 prey schools (sailfish $n = 7$, striped marlin $n = 3$ schools). For each sequence, we noted the following five variables: (i) capture success—whether the attack eventuated in a prey fish being ingested, (ii) rostrum use—whether the rostrum was used, (iii) the type of rostrum use: tap (a short-range movement of the rostrum), or slash (a forceful horizontal movement of the rostrum) [5], (iv) location of rostrum use—whether the rostrum was used on an isolated prey fish or whether it was directed at a school of prey fish (see electronic supplementary material). Furthermore, we assessed, (v), the direction in which the rostrum was used (horizontal or vertical). The latter was done for a subset of attack sequences in which this was possible to determine (sailfish $n = 28$, striped marlin $n = 28$ attack sequences; see electronic supplementary material, videos for examples of each—video S1: horizontal slash, video S2: vertical tap). To test for a difference between species in each of these five behaviours, we ran Bayesian multilevel regression models, using the R package 'brms' [17]. We ran separate models for each behaviour, fitting 'species' as population-level and prey school as group-level effect, using the binary distribution (family Bernoulli). We ran three chains of 2000 iterations, discarding the first 1000 as warm-up. For statistical inference, we determined whether the 95% credibility interval of the population-level effect (i.e. species) overlapped



sailfish, *Istiophorus platypterus*



striped marlin, *Kajikia audax*

Figure 2. Attack sequences for (*a*) sailfish and (*b*) striped marlin in the form of a Markov chain with state transitions. Only those transitions that were observed at least three times are shown. In order to make the figures comparable, the counts of the transitions for the striped marlin data were scaled, such that their sum equalled the sum of the transition counts for the sailfish data. States (*approach, dash, bill use, prey contact, open, ingest, leave*) are shown within ellipses and transitional probabilities are represented by the weighted arrows linking states. Photo credit: Rodrigo Friscione Wyssmann. (Online version in colour.)

with zero or not. Finally, we calculated the mean capture rate per minute for each prey school and tested for a difference between species with an unpaired Student's *t*-test.

(b) Morphological analysis

We used sailfish rostra ($n = 6$, lower jaw fork length (LJFL): 183–242 cm, rostrum length (RL): 48.8–73.2 cm) and striped marlin rostra ($n = 4$, LJFL: 167–205 cm, RL: 38.5–71.3 cm) for micro-CT analysis of the micro-teeth (see electronic supplementary material for collection details).

(i) Micro-teeth length, type, position and density

We used high-resolution computed tomography to characterize the length, type, position and density of all micro-teeth on the rostra tips (up to the first 55 mm of the rostra) (figure 1; electronic supplementary material, figure S1 and details of micro-CT, and also for details on micro-teeth chemical composition). Rostral tips were selected because 90% of contact with prey is made with the first third of the rostrum (J. Krause 2014, unpublished data). For each micro-tooth we measured its (i) length: distance from base of the root to apex, (ii) type: intact, broken or re-growing, (iii) distance: distance away from the tip of the rostrum, and (iv) angle: position of the micro-tooth in degrees from the roll-axis of the bill (figure 1; electronic supplementary material, figure S2). Not every micro-tooth detected could be measured. The mean percentage of failed micro-tooth measurements per rostrum was 1.9 ± 0.4 (s.e.)%.

To determine whether species differed in mean tooth length, we ran a series of Bayesian multilevel regression models [26]. As response variable we used tooth length, as population-level effects we fitted 'species', 'angle' and 'distance'. Distance was included as a linear term and angle as a circular spline, to reflect the circular nature of this measure (see also figure 1; electronic supplementary material, figure S2). We also fitted interactions between 'species + angle', and 'species + distance'. 'Individual bill' was used as a group-level effect. We used an ex-Gaussian distribution as this distribution best approximated actual tooth length distribution. We ran 11 different models, which included either both interactions, one of the interactions, or a variation of main predictors only (i.e. without interactions). For each model, we ran three chains with 2000 samples, discarding the first 1000 as warm-up. To evaluate the effect of our main predictor of interest (i.e. 'species'), we selected the best performing model (in terms of widely applicable information criterion (WAIC) score) and checked whether the 95% credibility interval of 'species' overlapped with zero or not (full model details are presented in the electronic supplementary material). For splines, we evaluated their importance by comparing WAIC weights between models including and excluding the splines.

To determine whether species differed in the percentage of teeth broken, or re-growing, we used 'broken' (yes/no) and 're-growing' (yes/no), as response variables in separate models. Group- and population-level effects were the same as above, with the exception that distance was included as a spline, as this provided a better fit than using a linear relationship (see also figure 4*f*,*i*). We used a Bernoulli distribution as both response variables were binary.

Finally, we were interested in potential differences in micro-teeth density between species. For this, we calculated micro-teeth density for each individual, for each section of 5 mm ($n = 11$ sections) to capture the distance parameter, and for the four 'sides' of the bill (i.e. dextral, ventral, sinistral and dorsal) to capture the angle parameter. Density was calculated by dividing the total number of teeth measured in each subsection by the surface area of this subsection. We used an ex-Gaussian distribution as this best approximated density distribution.

3. Results

(a) Behavioural analysis

Both species were found to hunt in groups. Sailfish group size ranged from approximately 6 to 40 individuals and sailfish

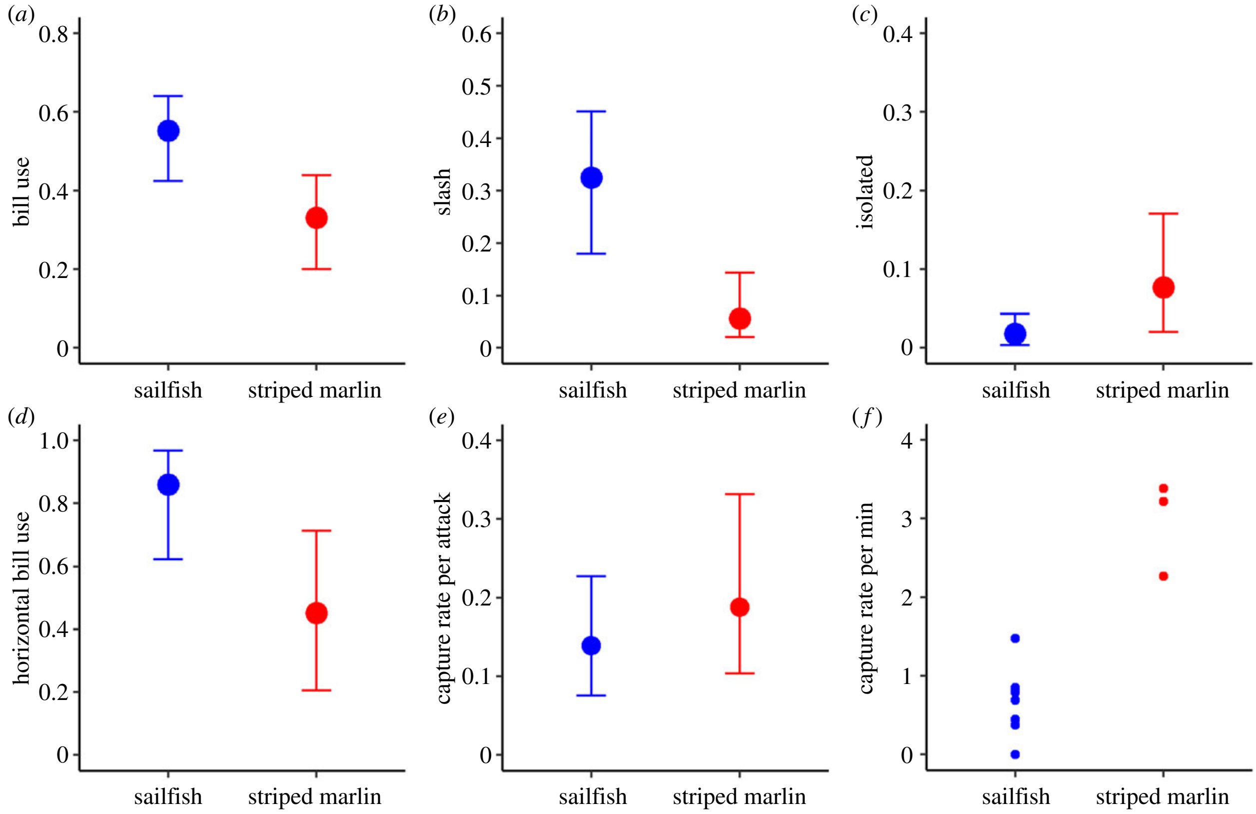


Figure 3. Rostrum use, and capture success for sailfish and striped marlin. (*a*) The likelihood of bill use during an attack sequence, (*b*) the likelihood the type of bill use was a slash, (*c*) the likelihood that bill was used on isolated prey, (*d*) the likelihood that the bill was used in a horizontal motion. (*e*) The likelihood that an attack sequence resulted in a successful capture, and (*f*) the mean capture rate per minute per group. (*a–e*) The marginal effects of the brms, with the dots showing the posterior median and the errors bars the 95% credibility intervals. (Online version in colour.)

fed on sardine schools size ranging from approximately 25 to 150 fish. Striped marlin group size was approximately 12–40 individuals and fed on sardine schools ranging in size from approximately 50 to 200 fish. Both sailfish and striped marlin attacked each sardine school one at a time.

(i) Analysis of attack dynamics

The attack sequences of sailfish and striped marlin significantly differed in terms of the actions performed and their ordering (figure 2). The Markov chain models on average correctly classified 85.2% (81.7 and 88.3% lower and upper quartiles) attack sequences (binomial test, $p < 0.001$ in a two-sided test). The main behavioural difference between the two species was the state *dash*, where the predator rapidly accelerates directly at the prey school and disperses it (electronic supplementary material, video S2). This was very common in striped marlin attack sequences but rare in sailfish. To investigate whether this state alone could explain the significant differences between species, all *dash* states were removed and the test repeated. Classification accuracy decreased, but was still significant (binomial test, $p = 0.013$ in a two-sided test). On average, 66.2% of the attack sequences were correctly classified (63.3 and 70.0% lower and upper quartiles).

(ii) Capture rates and rostrum use

Rostrum use occurred regularly in both species of billfish during hunting (see also figure 2). However, sailfish were more likely to use their rostra in an attack sequence (185/325) compared with striped marlins (233/665) (estimate = −0.93 (95% credibility interval [−1.66, −0.27]); figure 3*a*). Sailfish showed more rostrum use in the form of slashing (125/185) than striped marlin (35/233) (estimate = −2.05 (95% credibility interval [−3.20, −0.68]); figure 3*b*). Striped marlin used their rostra more on isolated prey fish (63/233) compared with sailfish (7/185) (estimate = 1.50 (95% credibility interval [0.03, 3.04]); figure 3*c*). Sailfish used a horizontal motion more often (40/47) than striped marlin (14/31) (estimate = −2.05 (95% credibility interval [−4.15, −0.23]) (figure 3*d*, see also electronic supplementary material, figure S3 for raw data).

When looking at capture success, we found no difference in the success rate per attack sequence between sailfish (53/325) and striped marlin (100/665) (estimate = 0.38, (95% credibility interval [−0.54, 1.45]); figure 3*e*). However, capture rate per minute was significantly higher in striped marlin groups (mean: 2.96 ± 0.35s.e., $n = 3$) than sailfish groups (mean: 0.66 ± 0.17 s.e., $n = 7$) (t-test: $t = -5.913$, d.f. = 3.0815, $p = 0.009$; figure 3*f*).

(b) Morphological analysis

In both species, micro-teeth showed tips (figure 1*f,j*) that had a dense mineralized composition of mainly phosphorus and calcium (see electronic supplementary material for details). Micro-teeth were interspaced with tubules and had a large pulp cavity filled with organic material (figure 1*j*). Furthermore, the micro-teeth were found to be in different maturation states (figure 1*c–g*), with new micro-teeth growing out of the holes of formerly exfoliated micro-teeth. In the process of growing, new micro-teeth also dissolved adjacent broken ones (figure 1*i*).

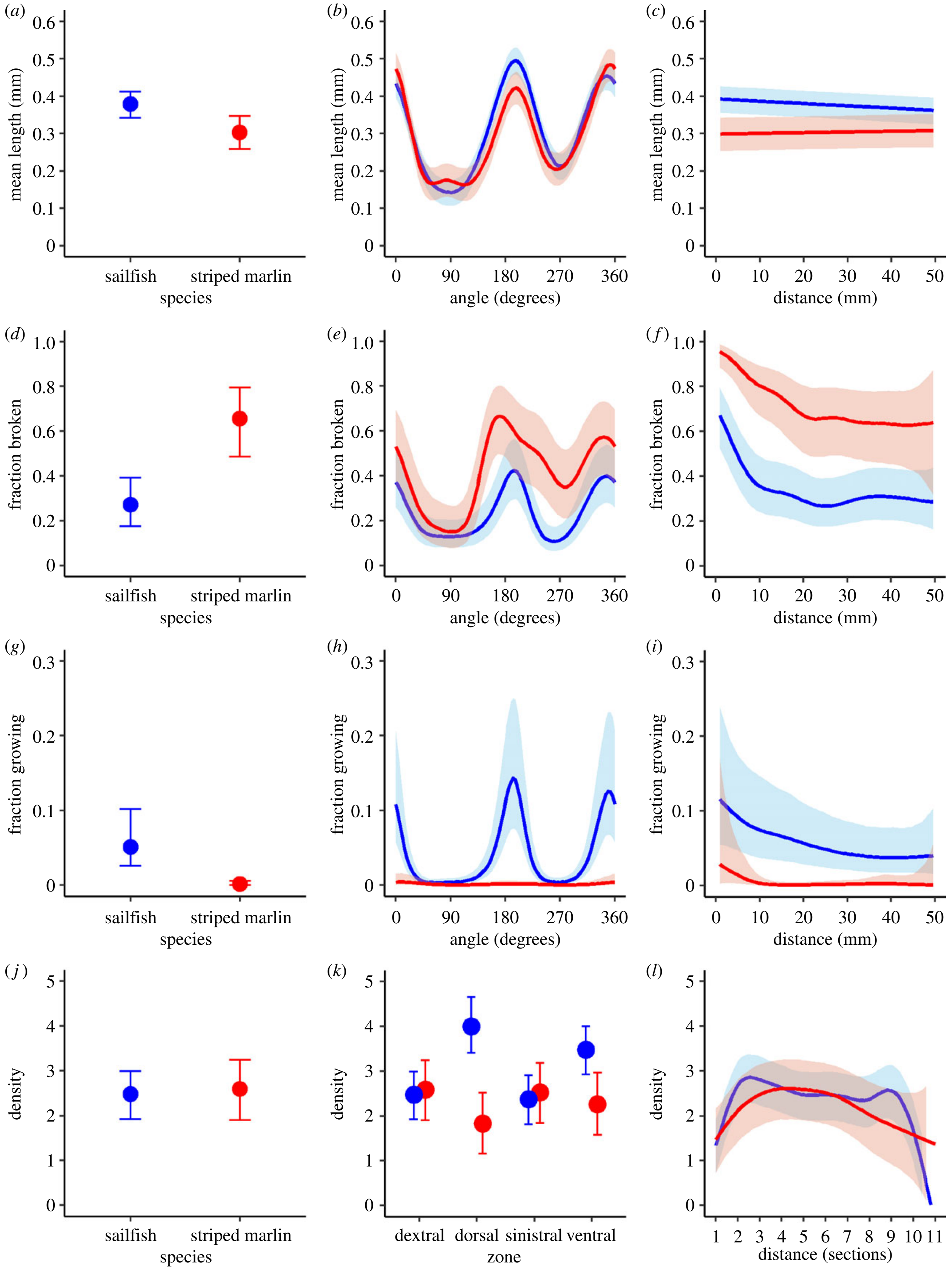


Figure 4. Micro-teeth analysis from micro-CT for sailfish ($n = 6$, blue) and striped marlin ($n = 4$, red) rostral tips (ranging from 0 to 55 mm). Shown are the effect of 'species', 'angle' and 'distance from tip' on (*a–c*) mean tooth length, (*d–f*) fraction of broken teeth, (*g–i*) fraction of growing teeth, and (*j–l*) tooth density. Shown are the marginal effects of the brms, with the solid lines/dots showing the posterior median; and the shaded areas/error bars the 95% credibility intervals. (Online version in colour.)

We did not find a difference in micro-tooth length between the two species (estimate = −0.04 (95% credibility interval [−0.09, 0.02]), electronic supplementary material, table S2 and figure 4*a*). Angle had a strong effect on tooth length—as removing angle substantially worsened model performance—and tooth length peaked at 0/360° (dextral side) and 180° (sinistral side) in both species (figure 4*b*). There was no effect of distance from the bill tip on tooth length (figure 4*c*).

Regarding the fraction of broken micro-teeth, we found an effect of species, with striped marlin having a larger fraction of broken teeth than sailfish (estimate = 0.90 (95% credibility interval [0.04, 1.78]), electronic supplementary material, table S3 and figure 4*d*). Also, in the second-best model—which was almost as good as the best model—we found this effect. In both species, most teeth were broken at 0/360° (dextral side) and 180° (sinistral side) (figure 4*e*), and at the tip of the bill (figure 4*f*).

Regarding the fraction of re-growing micro-teeth, we found an effect of species, with sailfish having a larger fraction of re-growing teeth than striped marlin (estimate = −2.23 (95% credibility interval [−3.71, −0.98]), electronic supplementary material, table S4 and figure 4*g*). For sailfish, most regrowth occurred at 0/360° (dextral side) and 180° (sinistral side) (figure 4*h*).

We found no credible difference in micro-tooth density between sailfish and striped marlins (estimate = −0.11 (95% credibility interval [−0.85, 0.64]), electronic supplementary material, table S5 and figure 4*j*). The best-performing model did, however, include the interaction between 'species' and 'zone', and sailfish had a higher density of teeth on the dorsal and ventral sides than striped marlin (figure 4*k*).

4. Discussion

Rostrum morphology in striped marlin and sailfish was largely consistent with the differences found in the attack strategies of the two species. Sailfish, which show more rostrum use overall, had fewer broken teeth at the tip of their rostra compared with striped marlin; however, they had more re-growing teeth than striped marlin. These trends suggest sailfish invest more in micro-tooth maintenance and that micro-teeth are of greater importance to prey capture in sailfish than they are in striped marlin.

Previous comparative work on fishes with toothed rostra (common sawshark (*Pristiophorus cirratus*), largetooth sawfish (*Pristis pristis*) and knifetooth sawfish (*Anoxypristis cuspidata*)) examined rostrum function through an analysis of rostral tooth microwear and stomach analysis [27], and related research explored the feeding strategy of captive sawfish via examination of the transitional probabilities between behavioural states [28]. Our study builds upon this illuminating work and suggests that matching the physical properties of rostra to behavioural strategies in the wild is a productive methodology, especially when capture success can be quantified. This methodology allows us to understand links between morphological adaptations and behavioural hunting strategies in large marine predators such as billfishes.

New micro-teeth grow out of the holes of old micro-teeth, and intact teeth also dissolve the dead material around them, indicating a remodelling of the rostrum (figure 1*e,f,j*; see also [13]). Remodelling of feeding structures has also been observed in other species. Oystercatcher (*Haematopus ostralegus*) bills re-shape in response to differences in prey type availability and it is thought that the food type chosen by oystercatchers and the shape of the bill positively reinforce each other, facilitating specialization [3,4]. Abrasion of the horny rhamphotheca (keratin sheet covering the bill) is greatest at the tip of the bill (where it makes contact with food and sediment) in the same way that more breakage and regrowth happen at the tip of billfish rostra (where there is greater prey contact). Across bird species, rhamphotheca regrowth and the rate of wear are thought to co-evolve, as there are greater differences between species than within [29]. A similar phenomenon may be occurring in billfish. Rostrum use is most pronounced in sailfish, and correspondingly there are greater regrowth rates in this species. Within species, there may even be different rates of wear and regrowth depending on spatial and seasonal distribution of prey types.

In both species, micro-tooth length on the lateral sides was greater than on the dorsal and ventral sides of rostra, and sailfish had a higher density of micro-teeth on the dorsal and ventral sides compared with striped marlin. The lateral micro-teeth are those that would primarily contact prey during horizontal movement of the rostrum, which was more frequent movement in sailfish than in striped marlin. Striped marlin have a slightly more dorso-ventrally flattened rostrum compared with sailfish, which could arguably be more suited biomechanically for lateral movements [6] (figure 1*f,g*). However, sailfish had more lateral movements, and differences in rostrum flatness are small between these two species. Hypotheses that do not rely on the biomechanics of flattened rostra should also be considered.

There are several potential hypotheses as to how body design differences between the two species are in accordance with the differences in attack strategy, that is, sailfish seemed to position themselves around the school (with the school remaining cohesive) and effected extensive rostral use (including many lateral swipes) on the prey, whereas striped marlins' general strategy was to *dash* in-line through the school in a 'rush and grab' movement, dispersing the prey fish (see electronic supplementary material, videos). The thinner, rounder shape of the sailfish rostrum [14,19] may be related to visual or tactile camouflage, allowing it to be inserted into the sardine shoal without the prey dispersing [5], and followed by a slash. Sailfish also have a larger dorsal fin [19], which is extended during foraging manoeuvring [5]. Large vertical surfaces such as this can provide control surfaces that maximize manoeuvrability [30] and minimize the yaw of the rostra and disturbance prior to slashing [5,31]. This larger dorsal fin would not be advantageous to in-line dashing of the striped marlin owing to drag. Finally, sailfish are more laterally compressed than striped marlin (max. depth/width ratio at origin of first anal fin: 1.45 and 2.16 for striped marlin and sailfish, respectively, calculated based on [19]), which is associated with high lateral flexibility [32] and thus potentially higher manoeuvrability (in terms of turning radius and turning rate [33]).

The 'rush and grab' strategy of striped marlin appears to be a strategy of many large marine piscivore predators that feed on schooling fish [34,35]. This repeated *dashing* led to higher prey capture rates per minute in striped marlin compared with sailfish, and future work should assess the energetics of this fast pace strategy in comparison with the attack strategy used by sailfish.

Striped marlin would often *open* their mouths after a *dash* (30%) before *prey contact* (17%) regardless of whether they subsequently ingested a fish or not. This suggests this attack strategy could be relatively opportunistic and less targeted than that of sailfish. Sailfish would only *open* their mouths after *prey contact*, and *open mouth* was a strong predictor of whether a fish was caught (*ingest* would follow *open mouth* 60% of the time). This difference in how the two species used their mouths within the attack sequence is intriguing in light of the result from Habegger *et al*. [7] that sailfish have the lowest relative bite force of the billfishes that were tested, and white marlin (*Kajikia albida*) the greatest (striped marlin, *K. audax,* were not analysed). The use of a rostrum is a form of food handling, and it may be viewed as a compensatory feeding structure. If sailfish use their rostra more for food capture, they will be on average mouthing already damaged prey and therefore weaker prey. Striped marlin, however, would require a stronger relative bite force if they more often handle uninjured and relatively stronger prey. Overall, our behavioural analysis shows that, while Markov chains for classifications are commonly used in other research fields, their application to predator attack strategies has considerable potential because it goes beyond simple binary tests (e.g. rostra use in sailfish and striped marlin) and facilitates the comparison of complex, dynamic behaviour patterns.

We found that the two species of billfish have evolved different feeding strategies and associated differences in morphology despite feeding on similar resources (schooling prey). This seems in juxtaposition to work on other comparative studies looking at adaptive divergence of feeding specialization, where resource differentiation is a driving factor [2,4]. Specialization of rostrum use could be an interesting example of behavioural and morphological coevolution; however, more research on the behavioural ecology of other billfish species is required. While prey type was similar in this study, billfishes are known to be opportunistic feeders [36] and there is likely differentiation in the species' diets at other times of the year, or other selective factors unaccounted for, which require further exploration. Comparative research into other physiological or morphological traits potentially involved in attack dynamics, such as vision, the vibrant lateral markings in striped marlin, and the larger dorsal sail of the sailfish, are warranted [5,37,38].

Ethics. All research was conducted in line with the laws and legislation of Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), Mexico and complied to the guidelines regarding the treatment of animals in behavioural research [23].

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contribution. M.J.H., F.D. and J.K. collected the striped marlin data, A.D.M.W., J.E.H.-R., R.H.J.M.K., K.B., P.D., J.F.S., P.E.V. and J.K. the sailfish data, and P.B. and P.S.S. provided the rostra. P.Z., J.M. C.M., T.B.H., P.E.V. and G.F. carried out the CT scanning and M.B. and S.K. the automated analysis of the CT-data. S.K, M.J.H. and R.H.J.M.K. performed the statistical analysis. M.J.H., J.K. and S.K. wrote the paper with substantial input from all co-authors. All authors gave final approval for publication.

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