

# Theoretical calculations of bite force in billfishes

M. L. Habegger<sup>1,2,3</sup>, D. H. Huber<sup>4</sup>, M. J. Lajeunesse<sup>2</sup> & P. J. Motta<sup>2</sup>

<sup>1</sup> Department of Biology, Florida Southern College, Lakeland, FL, USA

<sup>2</sup> Department of Integrative Biology, University of South Florida, Tampa, FL, USA

<sup>3</sup> Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA

<sup>4</sup> Department of Biology, The University of Tampa, Tampa, FL, USA

## Keywords

bite force; feeding; billfishes; biomechanics; prey capture; rostrum.

## Correspondence

Maria Laura Habegger, Department of Biology, Florida Southern College, 111 Lake Hollingsworth Dr., Lakeland, FL 33801, USA.

Email: lhabegger@flsouthern.edu

Editor: Jean-Nicolas Volff

Received 9 May 2016; revised 12 March 2017; accepted 15 March 2017

doi:10.1111/jzo.12465

## Abstract

Bite force is one of the most utilized performance measures due to its association with feeding and consequently fitness. Due to their large size and the concomitant increase in the adductor muscles it is expected that apex predators may rely on high biting performance allowing for increased dietary breadth. Billfish are apex marine predators characterized by the extreme elongation of the upper jaw bones forming a rostrum. This structure has been shown to facilitate prey capture and processing, but little is known as to whether this elongated structure has had an effect on biting performance in this group of enigmatic fishes. The goal of this study was to investigate bite force among five billfish species differing in size and rostrum morphology, and to determine the relationship between bite force and cranial anatomy. Because prey processing is partially decoupled from the oral jaws in these fishes, we hypothesized that bite force will be relatively low in billfishes compared to other fish, and that mass specific bite force will be inversely proportional to rostrum length. Anterior and posterior values of bite force ranged from 29 to 330 N and 99 to 1361 N, respectively among billfish species. Although absolute bite forces reached high values, mass specific bite force was among the lowest recorded for cartilaginous and bony fishes. Contrary to our hypothesis, rostrum length was not a predictor of bite force. The evolution of this novel structure, however, has been demonstrated to have a role in feeding, and the relatively low bite force in billfishes may indicate a lack of dependence on this performance metric for prey capture and processing.

## Introduction

Bite force is a broadly utilized metric of feeding performance due to its perceived association to fitness. The investigation of bite force has significantly contributed to our overall understanding of organismal ecology since it is not only linked to feeding ecology, allowing the exploitation of differing dietary niches (Dumont *et al.*, 2012), but is also related to mating success (Lappin & Husak, 2005), intraspecific combat (Husak *et al.*, 2006), as well as burrowing efficiency (Van Daele, Herrel & Adriaens, 2009).

Bite force may be related to dietary specialization with high bite force found in durophagous species such as chameleon lizards (*Chamaeleolis*, Herrel & Holanova, 2008), the sheepshead *Archosargus probatocephalus* (Hernandez & Motta, 1997), and horn sharks *Heterodontus francisci* (Kolmann & Huber, 2009). High bite forces have been shown to affect prey processing (reduction in prey to edible size), since more forceful biters can reduce the amount of time utilized to subdue and reduce prey, perhaps increasing energy intake as shown in lizards (Verwajen, Van Damme & Herrel, 2002).

Biting performance has a strict association to size both within and among species. Within species, positive allometry of bite force is commonly observed over ontogeny owing to rapid increases in head and/or muscle size, and often in association with the consumption of hard and/or durable prey (Herrel *et al.*, 2005; Herrel & Gibb, 2006; Kolmann & Huber, 2009). Among species, size alone will be responsible for large absolute bite forces as seen in sharks and alligators (Erickson, Lappin & Van Vliet, 2003; Huber, Weggelaar & Motta, 2006; Erickson *et al.*, 2012).

In some cases for relative bite force, however, size may not be the driving factor, as some large predators have shown disproportionately lower biting performance than expected for their size. In these cases complementary feeding structures may replace the need for biting performance. In the komodo dragon (*Varanus komodoensis*) for example, it is suggested that venom glands are in part responsible for their predatory success since bite forces shown to be relatively small (Fry *et al.*, 2009). Alternatively, dentition, cranial architecture and feeding modes may also help to overcome bite force limitations. Sharp teeth and fast strikes by some bony fishes including king mackerel

(*Scomberomorus cavalla*) and great barracuda (*Sphyræna barracuda*) may override the necessity for high bite force as these apex predators have among the lowest mass specific bite forces of fishes (Habegger *et al.*, 2010; Ferguson *et al.*, 2015). In addition, biting species that feed on fast elusive prey may sacrifice powerful jaws for speed efficient ones such as the gharial (*Gavialis gangeticus*, Gavialidae) (Erickson *et al.*, 2012).

Given that patterns in biting performance may be related to size, dentition, and prey capture methodology, the billfishes represent an intriguing clade in which examine bite force, as they range considerably in size, in some cases edentulous, and utilize a truly unique prey capture methodology among aquatic vertebrates. Billfishes are fast pelagic fishes characterized by an extreme elongation of the upper jaw into a bill or rostrum, which varies in relative length, morphology, and presence of teeth. Swordfish (*Xiphias gladius*) possess a rostrum that may attain lengths up to 50% of its body length, is lenticular in cross-section, and lacks teeth along its length. Conversely, shortbill spearfish (*Tetrapturus angustirostris*) possess a rostrum that may only exceed lower jaw length by a few centimeters, is oval to round in cross-section, and has small villiform teeth (Nakamura, '83). Although the rostrum has been hypothesized to have several roles such as defense and drag reduction (Nakamura, 1983; Frazier *et al.*, 1994), recent biomechanical testing of the rostrum in several billfish species and kinematic analyses of the feeding behavior of Atlantic sailfish (*Istiophorus albicans*) evidenced the role of this structure during feeding (Atkins *et al.*, 2014; Domenici *et al.*, 2014; Habegger *et al.*, 2015; Herbert-Read *et al.*, 2016). In addition, examination of stomach contents of some istiophorids such as the blue marlin (*Makaria nigricans*), showed prey cut in half, punctured and lacerated. In many cases these injuries were attributed to the use of the rostrum while in others biting behavior was also suggested (Shimose *et al.*, 2007, 2008). Therefore, the ability of the rostrum to injure, immobilize or kill prey before ingestion, seemingly facilitates prey processing and capture (Gudger, 1940; Talbot & Penrh, 1964; Scott & Tibbo, 1968). Thus, billfishes's feeding anatomy and behavior seem to facilitate food acquisition for their specific pelagic lifestyle where other feeding modes such as suction feeding, commonly found in most fishes, seems not a feasible option (Berkovitz & Shellis, 2016).

Given that the billfish's most conspicuous attribute allows for pre-processing prey before ingestion, this structure may reduce the selective pressure for high bite forces common to other large predators. Furthermore, variability in rostral size may influence the extent to which this selective pressure is reduced such that species with a short rostrum may not use it to process prey, and therefore rely more heavily upon larger bite force than species with a longer rostrum. The goal of this study is therefore to investigate bite force and its possible predictors among five billfish species exhibiting different rostrum morphologies. Because prey processing is, in this case, partially decoupled from the oral jaw processing by the use of the rostrum, we hypothesize (1) that intraspecific variation in bite force will inversely proportional to rostrum length. (2) and because the role of the rostrum during feeding bite force will be relatively low in billfishes compared to other fish.

## Materials and methods

A total of 33 fish heads (five billfish species and one scombroid species) were collected from recreational fishing tournaments and commercial fisheries along the Gulf of Mexico, the Florida Keys, Ocean city, Maryland and Hawaii and kept frozen until dissections were performed. All five billfish species were selected to represent a wide range of rostrum morphologies and taxa according to the latest available phylogeny (Santini & Sorenson, 2013). Species collected include blue marlin (*Makaria nigricans*,  $N = 6$ ), swordfish (*Xiphias gladius*,  $N = 6$ ), white marlin (*Kajikia albida*  $N = 6$ ), shortbill spearfish (*Tetrapturus angustirostris*  $N = 5$ ) and sailfish (*Istiophorus albicans*  $N = 3$ ). In addition a non-billfish species, the wahoo (*Acanthocybium solandri*) was also collected ( $N = 6$ ) and assigned as the out-group for comparative purposes (Santini & Sorenson, 2013). Variables including body mass and rostrum length (from tip to orbit) were taken when possible (Table 1). In cases when mass was not available, extrapolations were performed from meristic regressions that include variables such as eye diameter and bill length available from the literature (sailfish: Prager, Prince & Lee, 1995; shortbill: Skillman & Yong, 1974; wahoo: Beerkircher, 2005).

## Anatomical descriptions

The anatomy of the muscles responsible for the adduction of the lower jaw was described. Dissections were performed on the left cheek of each specimen and identification of the adductor mandibulae complex was made following Winterbottom (1974), Davie (1990), Datovo & Vari (2013) and H. Fierstine (Pers. comm.).

## Theoretical calculations of bite force

Once the adductor mandibulae was identified for each species, each major subdivision was removed and bisected through its center of mass, perpendicular to the main fiber direction. Center of mass was estimated for each muscle subdivision by the point of intersection of two weighted lines that suspended each muscle. Muscles were bisected perpendicular to the main fiber direction at the center of mass. Since all muscles were parallel fibered, anatomical cross-sectional area (CSA,  $\text{mm}^2$ ) were traced from digital pictures (Canon Power Shot A710is, Canon Inc., NY, USA) using Sigma Scan Pro version 4 (SYSTAT Software Inc., Point Richmond, CA, USA). Previous modeling studies have verified this method (Huber & Motta, 2004), however for some muscles results may be underestimated, in addition this model did not incorporated length tension effects associated to each muscle. Theoretical maximum tetanic force ( $P_0$ ) for each subdivision was determined by multiplying the CSA by the specific tension of fish muscle (TS) ( $20 \text{ N/cm}^2$ , Altringham & Johnston, 1982) following Powell *et al.* (1984).

$$P_0 = \text{CSA} \times \text{TS}$$

After the muscles were dissected from the skulls, three-dimensional coordinates of origin and insertion of each adductor subdivision, jaw joint, and two bite points along the lower

**Table 1** Raw mean values  $\pm$ SD of bite force and biomechanical variables for billfishes and wahoo

Species	Bite force		Species information		Biomechanical variables							
	N	ABF (N)	PBF (N)	Mass (kg)	BL (cm)	AMA	PMA	IL (cm)	AOL (cm)	POL (cm)	R+M <sub>CSA</sub> (cm <sup>2</sup> )	S <sub>CSA</sub> (cm <sup>2</sup> )
<i>Acanthocybium solandri</i>	6	29.18 $\pm$ 10.16	98.97 $\pm$ 38.32	18.22 $\pm$ 6.52	15.6 $\pm$ 1.73	0.25 $\pm$ 0.02	0.67 $\pm$ 0.06	4.54 $\pm$ 0.48	18.1 $\pm$ 2.03	6.71 $\pm$ 0.74	2.56 $\pm$ 0.92	1.68 $\pm$ 0.69
<i>Xiphias gladius</i>	7	56.84 $\pm$ 16.55	158.83 $\pm$ 48.5	41.7 $\pm$ 14.73	80.44 $\pm$ 7.46	0.24 $\pm$ 0.02	0.68 $\pm$ 0.14	5.76 $\pm$ 0.64	24.09 $\pm$ 2.15	8.84 $\pm$ 1.77	4.43 $\pm$ 1.09	3.26 $\pm$ 0.95
<i>Istiophorus albicans</i>	3	60.57 $\pm$ 2.67	331.43 $\pm$ 31.1	20.43 $\pm$ 4.46	48.37 $\pm$ 3.21	0.27 $\pm$ 0.01	1.33 $\pm$ 0.15	6.97 $\pm$ 0.06	25.97 $\pm$ 0.59	5.17 $\pm$ 0.5	6.6 $\pm$ 0.44	2.3 $\pm$ 0.87
<i>Makaira nigricans</i>	6	329.97 $\pm$ 40.6	1361 $\pm$ 184.0	218.52 $\pm$ 40.4	72.35 $\pm$ 7.32	0.27 $\pm$ 0.0	1.05 $\pm$ 0.1	10.45 $\pm$ 0.3	38.38 $\pm$ 1.29	10 $\pm$ 0.96	29.13 $\pm$ 3.92	9.93 $\pm$ 0.85
<i>Kajikia albida</i>	7	78.73 $\pm$ 10.78	405.23 $\pm$ 62.9	29.34 $\pm$ 1.76	49.9 $\pm$ 1.39	0.26 $\pm$ 0.01	1.25 $\pm$ 0.09	7.74 $\pm$ 0.54	29.84 $\pm$ 1.6	6.2 $\pm$ 0.39	8.86 $\pm$ 1.21	3.79 $\pm$ 0.94
<i>Tetrapturus angustirostris</i>	5	37.62 $\pm$ 3.53	205.98 $\pm$ 19.5	15.05 $\pm$ 2.28	22.9 $\pm$ 1.47	0.26 $\pm$ 0.0	1.33 $\pm$ 0.12	6.05 $\pm$ 0.17	23.12 $\pm$ 0.8	4.57 $\pm$ 0.46	4.62 $\pm$ 0.61	1.66 $\pm$ 0.24

ABF, anterior bite force, PBF, posterior bite force, BL, bill length, AMA, anterior mechanical advantage, PMA, posterior mechanical advantage, IL, in lever, AOL, anterior out lever, POL, posterior out lever, R + M<sub>CSA</sub>, cross-sectional area of the pars rectalis and pars malaris subdivision of the adductor muscles, S<sub>CSA</sub>, cross-sectional area of the pars stegalis subdivision of the adductor muscles.

jaw were gathered for each individual of each species using a three dimensional digitizer (PATRIOT™ digitizer, Polhemus, Colchester, VT, USA). The most distal point of the lower jaw was designated as the anterior bite force point (ABF), and the most proximal margin of the teeth was designated as the posterior bite force point (PBF). As swordfish teeth were not visible the posterior bite point was traced by hand until the ridged surface of the jaw disappeared. Weighted in-lever (IL) and out-lever (OL) distances to these points were measured and mechanical advantage (MA) calculated.

The theoretical tetanic force and 3D position for each muscle was used to calculate three dimensional force vectors produced for each adductor mandibulae subdivision in specimens with adducted jaws, however, utilizing a single gape angle may underestimate bite force due to not all muscles may be at their peak length-tension curve at once. Theoretical maximum bite forces produced along the lower jaw were calculated via summation of moments about the jaw joint with a 3D static equilibrium model in Mathcad 13 (Material S1, Mathsoft, Inc., Cambridge, MA, USA), following Huber *et al.* (2005):

$$F_{LJ} = F_{JR} + F_{AM1+2} + F_{AM3} + F_B = 0$$

$F_{LJ}$ : forces acting on the lower jaw

$F_{JR}$ : jaw joint reaction

$F_{AM1+2}$ ,  $F_{AM3}$ : forces generated by each adductive muscle subdivision

$F_B$ : bite reaction force from the prey item

### Bite force predictors and best fit models

All data were log-transformed to account for some skewness in trait measurements (Zar, 2010). Since the traits from each species do not represent phylogenetically independent information in a regression framework (Felsenstein, 1985), and because animal mass is related to bite force, all data were size-corrected by weight using the phylogenetically corrected method outlined by Revell (2009) and implemented in the *R* package *phyTools* (Revell, 2012). Size-corrected trait values were then analyzed with both ordinary least squares (OLS) and phylogenetic generalized least-squares (PGLS) regressions assuming trait evolution via Brownian motion (Grafen, 1989; Rohlf, 2001). A full Brownian motion model of evolution was assumed for all PGLS analyses because there were too few species ( $N = 6$ ) to confidently estimate lambda-fitted (phylogenetic signal) models (Lajeunesse & Fox, 2015). Both the OLS and PGLS analyses were fitted using the *gls()* function from the *nlme* package (Pinheiro *et al.*, 2007) assuming a maximum likelihood estimator (ML), and the PGLS models had an additional Brownian correlation structure defined by the *corBrownian()* function from the *ape* R package (Paradis *et al.*, 2004). The phylogenetic tree used in size-corrections and phylogenetic analyses had a topology based on Santini & Sorenson (2013) and internode divergence times based on Santini & Sorenson (2013) and Hedges, Dudley & Kumar (2006) (Fig. S1).

We employed an information theoretic framework to compete all possible predictors of bite force (Johnson & Omland, 2004). To identify the best predictors of bite force, we compared all

candidate OLS and PGLS models fitted with combinations of main effects without interactions using up to two predictors of bite force. We limited the complexity of these candidate models to up to two simultaneous predictors (and intercept) to avoid regression overfitting relative to our small sample size (Zar, 2010). In total, 37 candidate models were compared; these models were constructed using the following pool of predictors: bill length (BL), anterior mechanical advantage (AMA), posterior mechanical advantage (PMA), in lever (IL), anterior out lever (AOL), posterior out lever (POL), cross-sectional area of the segmentus facialis, pars malaris and pars rectalis ( $R+M_{csa}$ ), and cross-sectional area of the segmentus facialis, pars stegalis ( $S_{csa}$ ). Model comparisons were designed to distinguish between fit and parsimony among candidate models based on Akaike's information criterion corrected for small-sample bias (AICc; Anderson, 2008). These were estimated for all OLS and PGLS candidate models using the *glmulti R* package (Calcagno & de Mazancourt, 2010). Following Burnham & Anderson (2002), we determined the top candidate models to those fitting a substantial support criteria of  $\Delta AICc < 2.0$ , but for comparison purposes, we also present all models that provided considerably less support based on  $\Delta AICc < 7.0$ . We also assigned an AICc weight to these models; this is the probability of each model being the most parsimonious.

### Bite force within billfishes

Raw values of anterior bite force were log transformed, and OLS and PGLS regressions were performed with the average for each species against body mass to obtain size-removed bite force residuals. These raw and phylogenetically corrected residual values were compared and ranked among all billfish species and the wahoo (out-group). For the comparison of bite force among billfishes and other non-billfish species, only ABF is considered further because this position is anatomically determined by the anterior margin of the mandible, whereas the position of the most posterior teeth varies greatly. In addition, ABF is most commonly used for comparative purposes since it can be measured in the field and theoretically.

### Bite force among fishes

In order to assess how billfishes' bite force ranked among other fish species (bony fishes and elasmobranchs), OLS regressions were used. Only species with similar feeding ecology, such as feeding in open water or dietary similarities were included (i.e. bite forces from durophagous fish and suction feeders were excluded from the analysis). Anterior values of bite force were gathered for the blacktip shark (*Carcharhinus limbatus*, Huber *et al.*, 2006), lemon shark (*Negaprion brevirostris*, Huber *et al.*, 2005), the great barracuda (*Sphyrna barracuda*, Habegger *et al.*, 2010), bull shark (*Carcharhinus leucas*, Habegger *et al.*, 2012) and kingfish mackerel (*Scomberomerus Cavalla*, Ferguson *et al.*, 2015). Mass specific anterior bite force was obtained from residuals and compared among species. Due to the wide phylogenetic range of the species, a phylogenetic correction was not performed.

## Results

### Anatomy

The adductor mandibulae is described following the most recent nomenclature proposed by Datovo & Vari (2013). The adductor mandibulae complex in billfishes and wahoo is comprised by the segmentus facialis and segmentus mandibularis (Datovo & Vari, 2013), (former adductor mandibulae subdivisions A1 + A2, A3 and Aw, Winterbottom, 1974). The most superficial area of the cheek is occupied by two subdivisions of the segmentus facialis, the pars malaris (M) and the pars rictalis (R), however separation was not possible and this section was treated as one in our calculations (R + M). Points of origin for the most superficial portion of the adductor muscles ranged from the hyomandibula, preoperculum, metapterygoid attaching partially to the maxilla but with the majority inserting on the segmentus mandibularis (SM), which in turn fills the Meckelian fossa of the lower jaw. The point of insertion on the segmentus mandibularis is not clearly defined; most of the connection is made by a sheath of connective tissue enveloping the segmentus mandibularis. Since this insertion is broad and not specific, for the purpose of bite force calculations the insertion point was determined as the center of mass of the segmentus mandibularis.

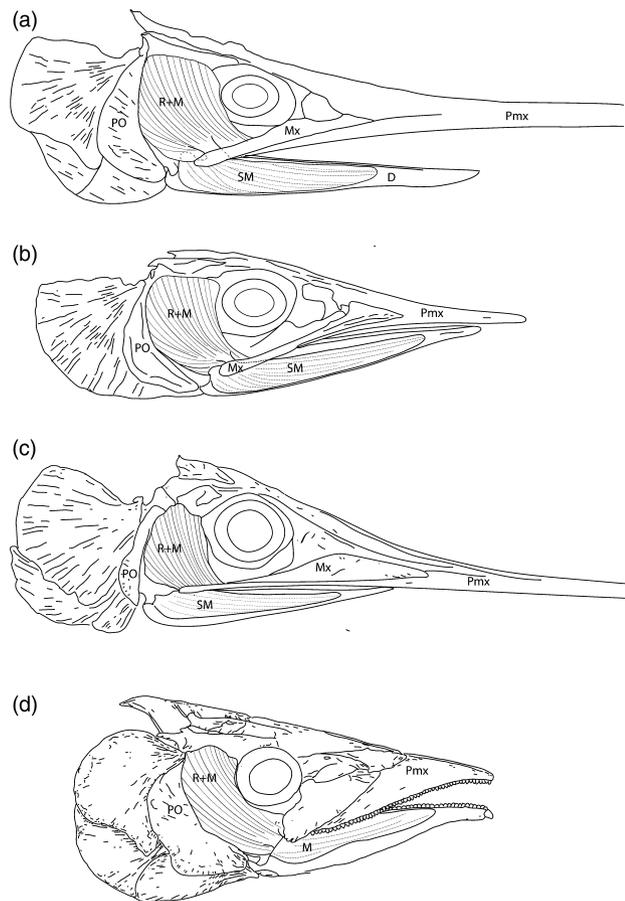
The deepest subdivision pars stegalis (S) originates mostly on the hyomandibula but also on the preopercle and metapterygoid and inserts by a tendonous insertion on the sesamoid bone of the articular. The anatomy of the adductor mandibulae, including general origin, insertion and patterns of muscles size appeared conserved among all species examined (Figs 1 and 2).

### Bite force and biomechanical parameters

Anterior values of bite force ranged from  $29.2 \pm 10.2$  to  $330.0 \pm 40.6$  N (wahoo and blue marlin respectively; mean  $\pm$  SD). Posterior values ranged from  $99.0 \pm 38.3$  to  $1361 \pm 184.0$  N (wahoo and blue marlin, respectively). In-lever lengths varied from  $4.5 \pm 0.5$  to  $10.5 \pm 0.3$  cm (wahoo and blue marlin, respectively). Anterior out-lever varied from  $18.1 \pm 2.0$  to  $38.1 \pm 1.3$  cm and posterior out-lever ranged from  $4.6 \pm 0.5$  to  $10 \pm 1.0$  cm (shortbill and blue marlin, respectively). Anterior mechanical advantage ranged from  $0.2 \pm 0.0$  to  $0.3 \pm 0.0$  (swordfish and blue marlin, respectively) and posterior mechanical advantage ranged from  $0.7 \pm 0.1$  to  $1.3 \pm 0.2$  (wahoo and white marlin, respectively). Muscle cross-sectional area was larger for the most superficial subdivisions, (R + M) in all studied species, and ranged from  $2.6 \pm 0.9$  to  $29.1 \pm 3.9$  cm<sup>2</sup> (wahoo and blue marlin, respectively) the CSA of the deepest subdivision (S) ranged from  $1.7 \pm 0.2$  to  $9.9 \pm 0.9$  (shortbill and blue marlin, respectively). All results are also summarized in Table 1.

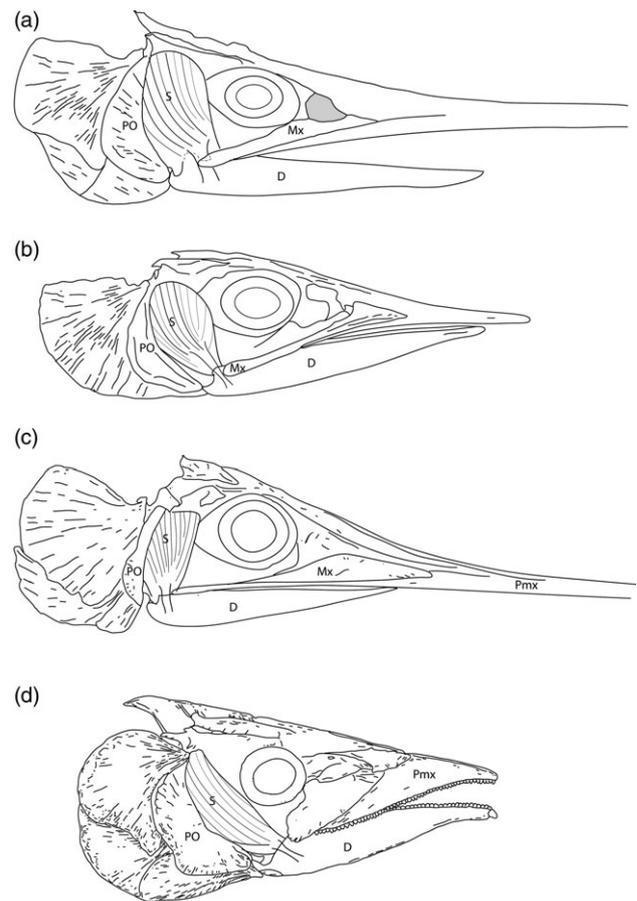
### Bite force predictors

Based on our model selection criteria using AICc scores (Akaike's information criterion corrected for small-sample bias), two OLS regression models emerged as having equally good



**Figure 1** Outline of the adductor mandibulae complex (superficial subdivision of the segmentus facialis,) pars rictalis (R) and pars malaris (M) and the segmentum mandibularis (SM) in three representative billfishes (complete rostrum not shown) and non-billfish species. (a) blue marlin (*Makaira nigricans*), (b) shortbill spearfish (*Tetrapturus angustirostris*), (c) swordfish (*Xiphias gladius*), (d) wahoo (*Acanthocybium solandri*). Outlines were modified from Bloomer (1986) for blue marlin, Gregory & Conrad (1937) for swordfish and Conrad (1938) for wahoo. OP, opercle; PO, preopercle; Mx, maxilla; PMx, premaxilla; D, dentary.

predictive power of anterior bite force (ABF): a model with CSA of the pars malaris and the pars rictalis as a predictor and a model that contained no predictors (i.e. the intercept-only model). The high AICc ranking of the intercept-only model (i.e. the most basic model that can be fitted to the data) indicates that none of the predictors (with the exception of CSA of the pars malaris and the pars rictalis subdivisions) were helpful in explaining variation in anterior bite force. When phylogenetic relationships were taken into account using PGLS, only the regression model that included the CSA of these muscles emerged as the best fit (Table 2). Similar results were observed for posterior bite force (PBF) for the non-phylogenetically corrected (OLS) regressions; however, with PGLS regressions three models emerged as having strong predictive power of PBF: a



**Figure 2** Outline of the adductor mandibulae complex (deeper subdivision of the segmentus facialis, pars stegalis) in three representative billfishes (complete rostrum not shown) and wahoo. (a) blue marlin (*Makaira nigricans*), (b) shortbill spearfish (*Tetrapturus angustirostris*), (c) swordfish (*Xiphias gladius*), (d) wahoo (*Acanthocybium solandri*). Superficial subdivision of the segmentus facialis, pars rictalis (R) and pars malaris (M) and segmentum mandibularis (SM) not shown. Outlines were modified from Bloomer (1986) for blue marlin, Gregory & Conrad (1937) for swordfish and Conrad (1938) for wahoo. OP, opercle; PO, preopercle; Mx, maxilla; PMx, premaxilla; D, dentary.

model with only the CSA the pars malaris and the pars rictalis subdivisions, a second with only anterior out-lever (AOL), and again a model with no predictors (i.e. intercept-only model; see Table 2). For all compared regression models, rostrum length (BL) was not a predictor of bite force in billfishes.

### Bite force among billfishes

The raw value of anterior bite force (ABF) was highest for the blue marlin and lowest for wahoo (Table 1). However, when the rankings were based on size-corrected ABF, or based on size- and phylogenetically corrected ABF, anterior bite force was largest for white marlin and lowest for sailfish (Table 3, Fig. 3).

**Table 2** The best predictors of anterior bite force (ABF) and posterior bite force (PBF) for billfishes and wahoo based on a model selection competition using  $\Delta$  AICc scores to rank regression models. All biomechanical variables described in Table 1 were treated as possible predictors in this model competition

Regression model	Best fit rankings	Best fit models	AICc	$\Delta$ AICc	AICc weights	Cumulative AICc weights	$F$ (d.f. = 1)	$P$
Anterior bite force								
<b>PGLS</b>	<b>1</b>	<b>ABF ~ 1 + (R+M<sub>CSA</sub>)</b>	<b>17.73</b>	<b>0.00</b>	<b>0.76</b>	<b>0.76</b>	<b>69.41</b>	<b>0.0011</b>
PGLS	2	ABF ~ 1 + IL	21.22	3.49	0.13	0.89	37.62	0.0036
PGLS	3	ABF ~ 1 + AOL	21.79	4.06	0.10	0.99	33.99	0.0043
<b>OLS</b>	<b>1</b>	<b>ABF ~ 1</b>	<b>19.13</b>	<b>0.00</b>	<b>0.43</b>	<b>0.43</b>	<b>NA</b>	<b>NA</b>
<b>OLS</b>	<b>2</b>	<b>ABF ~ 1 + (R+M<sub>CSA</sub>)</b>	<b>19.25</b>	<b>0.13</b>	<b>0.40</b>	<b>0.53</b>	<b>11.16</b>	<b>0.0288</b>
OLS	3	ABF ~ 1 + IL	21.74	2.61	0.12	0.95	6.47	0.0638
OLS	4	ABF ~ 1 AOL	24.71	5.59	0.03	0.98	2.89	0.1640
Posterior bite force								
<b>PGLS</b>	<b>1</b>	<b>PBF ~ 1</b>	<b>25.30</b>	<b>0.00</b>	<b>0.35</b>	<b>0.35</b>	<b>NA</b>	<b>NA</b>
<b>PGLS</b>	<b>2</b>	<b>PBF ~ 1 + (R+M<sub>CSA</sub>)</b>	<b>25.65</b>	<b>0.35</b>	<b>0.30</b>	<b>0.65</b>	<b>10.66</b>	<b>0.0310</b>
<b>PGLS</b>	<b>3</b>	<b>PBF ~ 1 + AOL</b>	<b>27.24</b>	<b>1.94</b>	<b>0.13</b>	<b>0.78</b>	<b>7.56</b>	<b>0.0514</b>
PGLS	4	PBF ~ 1 + PMA	27.97	2.67	0.09	0.87	6.34	0.0649
PGLS	5	PBF ~ 1 + (S <sub>CSA</sub> )	28.88	3.57	0.06	0.93	5.11	0.0865
PGLS	6	PBF ~ 1 + IL	28.97	3.67	0.06	0.99	4.99	0.0892
<b>OLS</b>	<b>1</b>	<b>PBF ~ 1</b>	<b>16.67</b>	<b>0.00</b>	<b>0.61</b>	<b>0.35</b>	<b>NA</b>	<b>NA</b>
<b>OLS</b>	<b>2</b>	<b>PBF ~ 1 + (R+M<sub>CSA</sub>)</b>	<b>17.81</b>	<b>1.14</b>	<b>0.34</b>	<b>0.95</b>	<b>9.01</b>	<b>0.0399</b>

Following Burnham & Anderson (2002), regression models with  $\Delta$  AICc equal or lower than 2.0 were identified as the best fitted regression models (here emphasized in bold). Also presented are models with 'minimal support' with  $\Delta$  AICc values <7.0. Phylogenetically corrected regressions were based on PGLS analyses assuming a full Brownian motion model of evolution, and conventional linear regressions were based of GLS models without phylogenetic correlations. All models include the intercept (described here as '1'). Intercept-only models (i.e. ABF ~ 1) contain no predictors, and when they are identified as top ranking models, this indicates that none of the predictors included in the model competition were useful for predicting bite force. The statistical significance of the predictors included in regressions are also presented ( $F$ -tests); the results of these significance tests were not used during the model selection analyses. Finally, 37 regression models were compared.

**Table 3** Mass specific bite force (mean  $\pm$  SD) within billfishes

Species	$N$	Mass (Kg)	Absolute ABF (N)	Size corrected residulas	Phylogenetically corrected residuals
<i>Istiophorus albicans</i>	3	20.43	60.57 $\pm$ 2.67	-1.03	-0.98
<i>Tetrapturus angustirostris</i>	5	15.05	37.62 $\pm$ 3.53	-0.32	-0.2
<i>Xiphias gladius</i>	7	41.70	56.84 $\pm$ 16.55	0.03	-0.05
<i>Acanthocybium solandri</i>	6	18.22	29.18 $\pm$ 10.16	0.07	0.07
<i>Makaira nigricans</i>	6	218.52	329.97 $\pm$ 40.6	0.28	0.1
<i>Kajikia albida</i>	7	29.34	78.73 $\pm$ 10.78	0.96	1.1

All values are from anterior bite points, ABF = absolute bite forces for each species, residuals are mass specific bite forces and phylogenetically corrected residuals are relative values of bite force corrected for the lack of independence among species (see Revell *et al.*, 2008). Species are ranked from smallest to largest size-corrected bite force.

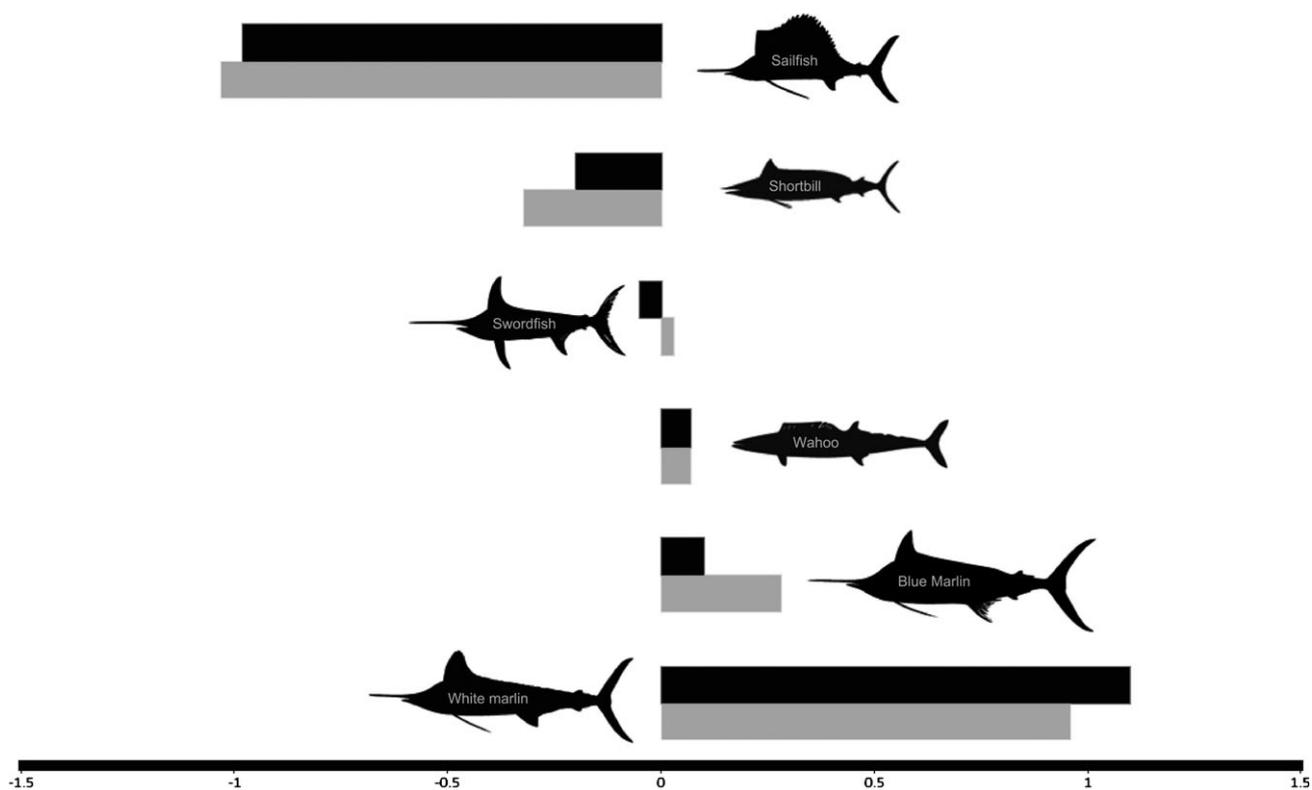
## Bite force among fishes

Compared to other fish species with similar feeding ecology or diet, the mass-specific bite force of billfishes was relatively small (Table 4). Sharks typically ranked the highest, with the bull shark showing the largest value of relative bite force. Although billfish typically occupied the lowest ranks, some non-billfish species including the wahoo and king mackerel were often nested among the billfishes; however the blue marlin had the lowest mass specific bite force of all species compared (Table 4).

## Discussion

### Bite force in billfishes

Absolute values of anterior bite force (ABF) ranged widely in billfishes, with blue marlin showing the highest (ABF = 329.97  $\pm$  40.6 N) and shortbill spearfish the lowest bite forces (ABF=37.62  $\pm$  3.53 N) (mean  $\pm$  SD). Since larger animals will bite harder owing to an increase in their muscle CSA (Herrel *et al.*, 2005), this variation is intuitive by virtue of the large range in sizes of the species examined (15 to



**Figure 3** Relative bite force within billfish and outgroup wahoo. Black bars show residual values of bite force performed in a linear regression. Gray bars show phylogenetically corrected residuals generated following Revell, Harmon & Collar (2008). From top to bottom (lowest to highest relative bite force): sailfish (*Istiophorus albicans*), shortbill spearfish (*Tetrapturus angustirostris*), swordfish (*Xiphias gladius*), wahoo (*Acanthocybium solandri*), blue marlin (*Makaira nigricans*) and white marlin (*Kajikia albida*). Residuals values range from negative (lowest) on the left to positive (largest) to the right.

**Table 4** Mass specific bite force in billfish versus 'non-billfish'

Common name	Scientific name	N	MASS	ABF	Residuals
Blue marlin	<i>Makaira nigricans</i>	6	218.5	330.0	-2.39
Swordfish	<i>Xiphias gladius</i>	7	41.7	56.8	-0.51
Wahoo	<i>Acanthocybium solandri</i>	6	18.2	29.2	-0.42
Shortbill spearfish	<i>Tetrapturus angustirostris</i>	5	15.1	37.6	-0.36
Kingfish mackerel <sup>a</sup>	<i>Scomberomorus cavalla</i>	7	5.7	19.3	-0.35
White marlin	<i>Kajikia albida</i>	7	29.3	78.7	-0.30
Sailfish	<i>Istiophorus albicans</i>	3	20.4	60.6	-0.30
Great barracuda <sup>b</sup>	<i>Sphyrna barracuda</i>	4	14.5	81	-0.16
Lemon shark <sup>c</sup>	<i>Negaprion brevirostris</i>	4	1.3	68.6	-0.09
Blacktip shark <sup>d</sup>	<i>Carcharhinus limbatus</i>	4	7.7	247.5	0.65
Bull shark <sup>e</sup>	<i>Carcharhinus leucas</i>	4	91.1	907.5	2.87

All values are from anterior bite points, ABF = absolute bite forces for each species, residuals are mass specific bite force. Non-billfish species except for wahoo, were gathered from the literature cited below. Species with similar feeding ecology were only included in the comparison, durophagous taxa or suction feeders were not included.

<sup>a</sup>Ferguson *et al.* (2015).

<sup>b</sup>Habegger *et al.* (2010).

<sup>c</sup>Huber (2006).

<sup>d</sup>Huber *et al.* (2006).

<sup>e</sup>Habegger *et al.* (2012).

219 kg, respectively). Considering absolute bite force as a measure of predator's maximal performance, blue marlin and white marlin stand out among billfishes. Posterior bite force was 1359 N in the 2.6 m TL blue marlin; this magnitude is similar to other top predators such as a 2.5 m TL white shark *Carcharodon carcharias* (Wroe *et al.*, 2008).

When comparing anterior bite force among species, rankings can vary substantially with regards to relative or absolute values as seen in other studies where small often durophagous species are compared (Huber, Dean & Summers, 2008; Grubich *et al.*, 2012). In billfishes, however, the rankings of absolute (raw) versus relative bite force did not differ greatly (Table 3 and Fig. 3). Relative bite force was largest in the white marlin and the blue marlin whereas swordfish, sailfish and shortbill spearfish showed the smallest values. Furthermore, the phylogenetic correction did not seem to influence these rankings, suggesting these patterns of bite force are not due to phylogenetic relatedness. Although a phylogenetic framework is necessary in any comparative study due to the few number of species compared (with  $N = 6$  species ranked), conclusions based on phylogenetic-corrections should be treated with caution as they may not have sufficient power to effectively model the phylogenetic correlations among related taxa (Lajeunesse & Fox, 2015).

### Bite force predictors

Bite force predictors provide a window into the determinants, and perhaps even the evolution, of biting performance (Habegger *et al.*, 2012). Measurements of cranial morphology such as head length, head width, and head depth are good proxies for biting performance in some fishes (Carothers, 1984; Wainwright, 1987; Huber *et al.*, 2006; Habegger *et al.*, 2012), and knowledge of these predictors can facilitate rapid assessments of organismal performance in lieu of complex biomechanical modeling. Contrary to our expectations, bill length (BL) was not a good predictor of biting performance among billfishes. Although the shortbill spearfish (the species with the shortest rostrum) had one of the lowest relative values of relative bite force, swordfish (the species with the largest rostrum) also had low values.

Although rostrum length was not a predictor of bite force among billfishes, the adductor muscles CSA repeatedly emerged in both OLS and PGLS regressions as having strong predictive power of bite force (see Table 2). Based on our anatomical descriptions, these results are intuitive as the pars rictalis and the pars malaris subdivisions of the segmentus facialis were consistently the largest CSA, whereas the pars stegalis was the smallest and most variable subdivision in all species investigated (Figs 1 and 2; Table 1). Adductor muscle CSA has been shown to be one of the most common predictors of bite force in sharks and clariid catfishes (Herrel, O'Reilly & Richmond, 2002a; Herrel *et al.*, 2002b; Habegger *et al.*, 2012).

Clear predictors for posterior bite force (PBF) were not detected in our analyses. The fact that the intercept-only model (with no predictors) ranked above all other models indicates that none of the variables explored may be a particularly useful

for predicting PBF. Although the lack of clear predictors has been described for other taxa including alligators (Erickson *et al.*, 2012), a possible reason for these results could be the large variability associated with measuring the most posterior tooth position. In swordfish, the teeth are reduced to almost absent, making the most posterior position difficult to determine. However, this variability does not prevent further comparisons in overall biting performance, given that most comparative analyses in fishes, both theoretically and experimentally, are more likely to use ABF over PBF due to its accessibility (Huber *et al.*, 2005; Huber *et al.*, 2009; Wroe, McHenry & Thomason, 2005; Wroe *et al.*, 2008; Mara, Motta & Huber, 2010; Grubich *et al.*, 2012).

Mechanical advantage (MA), a variable used to characterize closing performance of the lower jaw can also influence bite force, as it represents the proportion of muscular force transmitted to a prey item via the jaw lever system, and is indicative of the trade-off between force and velocity in lever systems in general (Westneat, 2004). High MA results in the amplification of biting performance in the chimaera (PBF = 190 N) (*Hydrolagus colliei*) (Huber *et al.*, 2008), horn shark (ABF = 382 N) (*Heterodontus francisci*) (Kolmann & Huber, 2009) and is an important predictor of size specific bite force throughout shark evolution (Habegger *et al.*, 2012). The low AMA in billfishes and the wahoo (0.25–0.27) is characteristic of fishes reported as having a speed efficient, rather than force efficient jaw (Westneat, 2004).

### Bite force comparison

Billfish exhibited low values of mass-specific bite force compared to 'non-billfish' species of similar ecology (large piscivores predators), supporting the hypothesis that the presence of the rostrum, and subsequent decoupling of the oral jaws from prey processing, has resulted in decreased biting performance of the oral jaws (Table 4). High bite force does not appear to be crucial for billfish predatory success, although evidence from stomach contents suggest biting may be used to some extent (Shimose *et al.*, 2007). Although the rostrum cannot be definitively categorized as an adaptation for feeding, its use has been shown to enhance prey pre-processing (Domenici *et al.*, 2014; Herbert-Read *et al.*, 2016), perhaps reducing the need for strong bite force relative to other 'non-billfish' species. In fact, a variety of top predators have been shown not to rely on large bite force for prey capture and processing. For example, the great barracuda (*Sphyraena barracuda*) and the king mackerel (*Scomberomorus cavalla*), appear to rely on a combination of high pursuit acceleration, fast closing jaws and sharp teeth to capture and subdue their prey (Porter & Motta, 2004; Grubich, Rice & Westneat, 2008; Habegger *et al.*, 2010; Ferguson *et al.*, 2015).

Results from this comparative analysis positioned sharks on the top of the hierarchy, this could be explained by the wide differences in dietary breath (see below), prey manipulation and feeding behavior, for example bull sharks that primarily prey in murky waters may use extremely large bite forces to hold struggling prey, preventing prey escapes to low water visibility (Habegger *et al.*, 2012).

Bite force is often related to prey properties; for example, turtles (*Chelydra* and *Staurotypus*) and lizards (*Anolis sp.*) that eat harder prey show high biting performance (Herrel, De Grauw & Lemos-Espinal, 2001; Herrel *et al.*, 2002a,b). However, dietary preferences are highly conserved among billfishes; and their diets are composed mostly of teleost fish including scombrids and carangids, as well as cephalopods, mostly squid (Nakamura, 1985; Shimose *et al.*, 2007). In addition, the force needed for shark teeth to puncture fish prey is surprisingly low (5 N) (Whitenack & Motta, 2010), whereas processing of hard prey such as turtle shells may reach significantly larger values (up to 3000 N) (Magwene & Socha, 2012) suggesting that high values of bite force in billfish may not be essential.

Low values of bite force in billfish could be attributed to functional trade-offs between feeding and sensory structures such as the eyes in billfishes. The heating organ, a sensory adaptation that characterizes this group and may augment visual acuity (Block, 1986; Block *et al.*, 1993; De Metrio, Ditrich & Palmieri, 1997) indicate the importance of vision in these predators. A large amount of adipose tissue found surrounding the eyes in several species examined (M.L. Habegger pers. comm.), may facilitate heat conservation in this area resulting in limiting space available for the jaw adductor muscles, perhaps decreasing biting performance. This type spatial constraints have been shown in other fish species where eye size reduction resulted in a concomitant increase in jaw adductor muscle size (i.e. *Petrotilapia*, Barel, 1984).

### The rostrum and its role in feeding

Although the adaptive value of the rostrum in billfishes cannot be assured, feeding has been shown repeatedly as its main role (Fierstine, 2006). Recent field observations and mechanical testing support the idea that this novel structure acts as a feeding weapon and that rostral morphology may influence feeding behavior (Domenici *et al.*, 2014; Habegger *et al.*, 2015; Herbert-Read *et al.*, 2016). Contrary to many other predators with long jaws, such as gar (*Lepisosteus platyrhincus*) and needlefish (*Strongula notata*) that capture elusive prey with rapid jaw adduction (Porter & Motta, 2004), billfish only have their upper jaw elongated. However, this was not the case for most of the extinct billfish species, such as *Aglyptorhynchus*, *Paleorhynchus* and *Xiphiorhynchus*, where both lower and upper jaws were elongated (Fierstine, 2006). Evolutionary changes toward the current rostrum morphology seem to support a more efficient role of the rostrum during feeding since stunning prey with both jaws could limit breathing, by constraining flow into the mouth and through the gills of these ram ventilation based species. In addition, breakage of both jaws during prey striking or defensive behavior could have resulted in total incapacitation for prey capture (Fierstine, 2006).

Rostrum morphology may favor a decrease in drag in different feeding behaviors. Theoretical models indicate drag is lowest during lateral striking as compared to dorsoventral striking in swordfish, and striking in any plane for the blue marlin (Habegger *et al.*, 2015). In addition, it may reduce the chances of early detection and fleeing by prey when approached head on as the rate of angle change in a predator's frontal profile,

the 'looming threshold', has been shown to trigger prey awareness (Dill, 1974; Webb, 1982). Long and narrow rostra or jaws result in a less abrupt change in frontal profile of a predator as they approach a prey delaying their fleeing until the predator is within striking distance.

In summary, bite force performance within billfishes was predicted by adductor muscles CSA and was not related to rostrum length. Even though there was no association between rostrum length and bite force production among billfishes, it is clear that billfishes do not rely on extreme bite force as apex predators. Although the rostrum of billfishes cannot be proved to be an adaptation for feeding, our results suggest that rostral elongation may relax the selective pressures toward high biting performance. Similar to other apex predators, their predatory success may be due to a combination of many variables including elongation of the rostrum to capture and process prey.

### Acknowledgments

We are extremely grateful to many people that made this study possible. This study could not be done without Anna Avrigian, Jim Franks, Ann Barse, Dave Itano and Geoff Walker generous help that made the specimen collection possible. Eric Prince allowed us to collect in many fishing tournaments. Rick Stanczyk, J. Gardiner, A. Ferguson, J. Morris, R. Hueter and Mote Marine laboratory provided samples. Many thanks to M. Montocchio for sharing his beautiful artwork. Thank you to S. Mulvany for helping in multiple collecting trips. Special thanks go to M. Berdugo for his continuous assistance in every step of the process. We are extremely grateful to H. Fierstine for providing insightful answers to all our billfish related questions and for his endless support and encouragement. This research was supported by the University of South Florida, the Guy Harvey Ocean Foundation, and the Porter Family Foundation.

### References

- Altringham, J.D. & Johnston, I.A. (1982). The pCa-tension and force-velocity characteristics of skinned fibers isolated from fish fast and slow muscle. *J. Physiol.* **333**, 421–449.
- Anderson, D. R. (2008). *Model based inference in the life sciences*, New York: Springer-Verlag.
- Atkins, A., Dean, M.N., Habegger, M.L., Motta, P.J., Ofer, L., Repp, F., Shipov, A., Weiner, S., Currey, J.D. & Shahar, R. (2014). Remodeling in bone without osteocytes: billfish challenge bone structure–function paradigms. *Proc. Nat. Acad. Sci. USA* **111**, 16047–16052.
- Barel, C.D.N. (1984). Form-relations in the context of constructional morphology: the eye and 575 suspensorium of lacustrine Cichlidae (Pisces, Teleostei): with a discussion on the 576 implications for phylogenetic and allometric form-interactions. *Neth. J. Zool.* **34**, 439–577.
- Beerkircher, L.R. (2005). Length to weight conversions for wahoo, *Acanthocybium solandri*, in the Northwest Atlantic. *Col. Vol. Sci. Pap. ICCAT* **58**, 1616–1619.
- Berkovitz, B. & Shellis, P. (2016). *The tooth of non-mammalian vertebrates*. Academic Press.

- Block, B.A. (1986). Structure of the brain and eye heater tissue in marlins, sailfish and spearfishes. *J. Morph.* **190**, 169–189.
- Block, B.A., Finnerty, J.R., Stewart, A.F.R. & Kidd, J. (1993). Evolution of endothermy in fish: mapping physiological traits on a molecular phylogeny. *Science* **260**, 210–216.
- Bloomer, C. (1986). *An illustrated study of the feeding mechanism of the Blue Marlin (Makaira nigricans)*. (Unpublished senior project). California Polytechnic State University, San Luis Obispo.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*. New York: Springer-Verlag.
- Calcagno, V. & de Mazancourt, C. (2010). glmulti: an R package for easy automated model selection with (generalized) linear models. *J. Stat. Softw.* **34**, i12.
- Carothers, J.H. (1984). Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.* **124**, 244–254.
- Conrad, G.M. (1938). The osteology and relationships of the wahoo (*Acanthocybium solandri*), a scombroid fish. *Am. Mus. Novit.* **1000**, 1–32.
- Datovo, A. & Vari, R.P. (2013). The jaw adductor muscle complex in teleostean fishes: evolution, homologies and revised nomenclature (Osteichthyes: Actinopterygii). *PLoS One* **8**, e60846.
- Davie, P. (1990). *Pacific marlins: anatomy and physiology*. Palmerston North: New Zealand Massey University Press.
- De Metrio, G., Ditrich, H. & Palmieri, G. (1997). Heat-producing organ of the swordfish (*Xiphias gladius*): a modified eye muscle. *J. Morph.* **234**, 89–96.
- Dill, L.M. (1974). The escape response of zebra danio (*Brachydanio rerio*). The stimulus for escape. *Anim. Behav.* **22**, 710–721.
- Domenici, P., Wilson, A.D.M., Kurvers, R.H.J.M., Marras, S., Herbert-Read, J.E., Steffensen, S., Krause, S., Viblanc, P.E., Couillaud, P. & Krause, J. (2014). How sailfish use their bills to capture schooling prey. *Proc. Biol. Sci.* **281**, 20140444.
- Dumont, E.R., D'avalos, L.M., Goldberg, A., Voigt, C.C., Rex, K. and Santana, S.E. (2012). Morphological innovation, diversification and the invasion of a new adaptive zone. *Proc. Biol. Sci.* **279**, 1797–1805.
- Erickson, G.M., Lappin, A.K. & Van Vliet, K.A. (2003). The ontogeny of bite-force performance in American alligator (*Alligator mississippiensis*). *J. Zool. Lond.* **260**, 317–327.
- Erickson, G.M., Gignac, P.M., Steppan, S.J., Lappin, A.K., Vliet, K.A., Brueggen, J.D., Inouye, B.D., Kledzik, D. & Webb, G.J.W. (2012). Insights into the ecology and evolutionary success of crocodylians revealed through bite-force and tooth-pressure experimentation. *PLoS One* **7**, e31781.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Ferguson, A.R., Huber, D.R., Lajeunesse, M.J. & Motta, P.J. (2015). Feeding performance of king mackerel, *Scoromorus Cavalla*. *J. Exp. Zool.* **323A**, 399–413.
- Fierstine, H.L. (2006). Fossil history of billfishes (Xiphoidei). *Bull. Mar. Sci.* **79**, 433–453.
- Frazier, J.G., Fierstine, H.L., Beavers, S.C., Achaval, F., Hiroyuki, S., Pitman, R.L., Yamaguchi, Y. & Prigioni, C.M. (1994). Impalement of marine turtles (Reptilia, Chelonia: Cheloniidae and Dermochelyidae) by billfishes (Osteichthyes, Perciformes: Istiophoridae and Xiphiidae). *Env. Biol. Fish.* **39**, 85–96.
- Fry, B.G., Wroe, S., Teeuwisse, W., van Osch, M.J., Moreno, K., Ingle, J., McHenry, C., Ferrara, T., Clausen, P., Scheib, H., Winter, K.L., Greisman, L., Roelants, K., van der Weerd, L., Clemente, C.J., Giannakis, E., Hodgson, W.C., Luz, S., Martelli, P., Krishnasamy, K., Kochva, E., Kwok, H.F., Scanlon, D., Karas, J., Citron, D.M., Goldstein, E.J., McNaughtan, J.E. & Norman, J.A. (2009). A central role for predation by *Varanus komodoensis* (Komodo Dragon) and the extinct giant *Varanus (Megalania) priscus*. *PNAS* **106**, 8969–8974.
- Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **326**, 119–157.
- Gregory, W.K. & Conrad, G.M. (1937). The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). *Am. Mus. Novitates* **952**, 7–25.
- Grubich, J.R., Rice, A.N. & Westneat, M.W. (2008). Functional morphology of bite mechanics in the great barracuda (*Sphyræna barracuda*). *Zoology* **111**, 16–29.
- Grubich, J.R., Huskey, S., Crofts, S., Orti, G. & Porto, J. (2012). Mega-bites: extreme jaw forces of living and extinct piranhas (Serrasalminidae). *Sci. Rep.* **2**, 1009.
- Gudger, E.W. (1940). The alleged pugnacity of the swordfish and the spearfishes as shown by their attacks on vessels. *Roy. Asiatic. Soc. Bengal* **2**, 215–231.
- Habegger, M.L., Motta, P.J., Huber, D.R. & Deban, S. (2010). Feeding biomechanics in the great barracuda (*Sphyræna barracuda*) during ontogeny. *J. Zool. Lond.* **283**, 63–72.
- Habegger, M.L., Motta, P.J., Huber, D.R. & Dean, M.N. (2012). Feeding biomechanics and theoretical calculations of bite force in bull sharks (*Carcharhinus leucas*) during ontogeny. *Zoology* **115**, 354–364.
- Habegger, M.L., Motta, P.J., Dean, M., Huber, D., Dunlop, J., Mullins, G., Stokes, M.J. & Winters, D. (2015). Feeding biomechanics in billfish: inferring the role of the rostrum during feeding in two billfish species. *J. Exp. Biol.* **218**, 824–836.
- Hedges, S.B., Dudley, J. & Kumar, S. (2006). TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* **22**, 2971–2972.
- Herbert-Read, J.E., Romanczuk, P., Krause, S., Strömbom, D., Couillaud, P., Domenici, P., Kurvers, R., Marras, S., Steffensen, J.F., Wilson, A.D.M. & Krause, J. (2016). Proto-cooperation: group hunting sailfish improve hunting success by alternating attacks on grouping prey. *Proc. Biol. Sci.* **283**, 20161671.
- Hernandez, L.P. & Motta, P.J. (1997). Trophic consequences of differential performance, ontogeny of oral jaw-crushing performance in the sheepshead, *Archorsargus probatocephalus* (Teleostei, Sparidae). *J. Zool. Lond.* **243**, 737–756.

- Herrel, A. & Gibb, A.C. (2006). Ontogeny of performance in vertebrates. *Physiol. Biochem. Zool.* **79**, 1–6.
- Herrel, A. & Holanova, V. (2008). Cranial morphology and bite force in *Chamaeleolis* lizards – adaptations to molluscivory? *Zoology* **111**, 467–475.
- Herrel, A., De Grauw, E. & Lemos-Espinal, J.A. (2001). Head shape and bite performance in Xenosaurid lizards. *J. Exp. Zool.* **290**, 101–107.
- Herrel, A., O'Reilly, J.C. & Richmond, A.M. (2002a). Evolution of bite performance in turtles. *J. Evol. Biol.* **15**, 1083–1094.
- Herrel, A., Adriaens, D., Verraes, W. & Aerts, P. (2002b). Bite performance in clariid fishes with hypertrophied jaw adductors as deduced by bite modeling. *J. Morphol.* **253**, 196–205.
- Herrel, A., Podos, J., Huber, S.K. & Hendry, A.P. (2005). Evolution of bite force in Darwin's finches: a key role for head width. *Evol. Biol.* **18**, 669–675.
- Huber, D.R. (2006). *Cranial biomechanics and feeding performance of sharks*. Ph.D. Thesis, University of South Florida, Tampa.
- Huber, D.R. & Motta, P.J. (2004). Comparative analysis of methods for determining bite force in the spiny dogfish *Squalus acanthias*. *J. Exp. Zool.* **301A**, 26–37.
- Huber, D.R., Eason, T.G., Hueter, R.E. & Motta, P.J. (2005). Analysis of bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci*. *J. Exp. Biol.* **208**, 3553–3571.
- Huber, D.R., Weggelaar, C.L. & Motta, P.J. (2006). Scaling of bite force in the blacktip shark *Carcharhinus limbatus*. *Zoology* **109**, 109–119.
- Huber, D.R., Dean, M.N. & Summers, A.P. (2008). Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish *Hydrolagus colliei*. *J. R. Soc. Interface* **5**, 1–12.
- Huber, D.R., Claes, J.M., Mallefet, J. & Herrel, A. (2009). Is extreme biting performance associated with extreme morphologies in sharks? *Physiol. Biochem. Zool.* **82**, 20–28.
- Husak, J.F., Lappin, K., Fox, S.F. & Lemos-Espinal, J.A. (2006). Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* **2006**, 301–306.
- Johnson, J.B. & Omland, K.S. (2004). Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**, 101–108.
- Kolmann, M.A. & Huber, D.R. (2009). Scaling of feeding biomechanics in the horn shark *Heterodontus francisci*: ontogenetic constraints on durophagy. *Zoology* **112**, 351–361.
- Lajeunesse, M.J. & Fox, G.A. (2015). Statistical approaches to the problem of phylogenetically correlated data. In *Ecological statistics: contemporary theory and application*: 261–283. Fox, G.A., Negrete-Yankelevitch, S. & Sosa, V.J. (Eds). Oxford: Oxford University Press.
- Lappin, A.K. & Husak, J.F. (2005). Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard. *Am. Nat.* **166**, 426–436.
- Magwene, P.M. & Socha, J.J. (2012). Biomechanics of turtle shells: how whole shells fail in compression. *J. Exp. Zool.* **319A**, 86–98.
- Mara, K.R., Motta, P.J. & Huber, D.R. (2010). Bite force and performance in the durophagous bonnethead shark, *Sphyrna tiburo*. *J. Exp. Zool. A Ecol. Genet. Physiol.* **313**, 95–105.
- Nakamura, I. (1983). Systematics of the billfishes (Xiphiidae and Istiophoridae). *Publ. Seto Mar. Biol. Lab.* **28**, 255–396.
- Nakamura, I. (1985). Billfishes of the world. FAO species catalogue. *FAO Fish. Synop.* **5**, 1–65.
- Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution. *Bioinformatics* **20**, 289–290.
- Pinheiro, J., Bates, B., DebRoy, S. and Sarkar, D., & the R Core team. (2007). nlme: linear and nonlinear mixed effects models. R package version 3.1-86. (<http://cran.r-project.org/web/packages/nlme/index.html>)
- Porter, H.T. & Motta, P.J. (2004). A comparison of strike and prey capture kinematics of three species of piscivorous fishes: florida gar (*Lepisosteus platyrhincus*), redfin needlefish (*Strongylura notata*), and great barracuda (*Sphyrna barracuda*). *Mar. Biol.* **145**, 989–1000.
- Powell, P.L., Roy, R.R., Kanim, P., Bello, M.A. & Egerton, V.R. (1984). Predictability of skeletal muscle tension from architectural determinations in guinea pigs. *J. Appl. Physiol.* **57**, 1715–1721.
- Prager, M.H., Prince, E.D. & Lee, D.W. (1995). Empirical length and weight conversion equations for blue marlin, white marlin, and sailfish from the North Atlantic Ocean. *Bull. Mar. Sci.* **56**, 201–210.
- Revell, L.J. (2009). Size-correction and principal components for interspecific comparative studies. *Evolution* **63**, 3258–3268.
- Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Meth. Ecol. Evol.* **3**, 217–223.
- Revell, L.J., Harmon, L.J. & Collar, D.C. (2008). Phylogenetic signal, evolutionary process and rate. *Sys. Biol.* **57**, 591–601.
- Rohlf, F.J. (2001). Comparative methods for the analysis of continuous variables: geometric interpretations. *Evolution* **55**, 2143–2160.
- Santini, F. & Sorenson, L. (2013). First molecular timetree of billfishes (Istiophoriformes: Acanthomorpha) shows a Late Miocene radiation of marlins and allies. *Ital. J. Zool.* **80**, 481–489.
- Scott, W.B. & Tibbo, S.N. (1968). Food and feeding habits of swordfish, *Xiphias gladius*, in the Western North Atlantic. *J. Fish. Res. Bd. Can.* **25**, 903–972.
- Shimose, T., Yokawa, K., Saito, M. & Tachihara, K. (2007). Evidence for the use of the bill by blue marlin (*Makaira nigricans*), during feeding. *Ichthyol. Res.* **54**, 420–422.
- Shimose, T., Yokawa, K., Saito, M. & Tachihara, K. (2008). Seasonal occurrence and feeding habits of black marlin (*Istiompax indica*), around Yonaguni Island, southwestern Japan. *Ichthyol. Res.* **55**, 90–94.
- Skillman, R.A. and Yong, M.A. (1974). *Length-weight relationships for six species of billfishes in the Central Pacific Ocean*. In: Shomura, R.S. and Williams, F. (eds). Proceedings of the International Billfish Symposium, Kailua-Kona, Hawaii, 9–12 August 1972, Pt. 2. Review and

- Contributed Papers. NOAA Tech. Rep. NMFS SSRF-675: 126–137.
- Talbot, F.H. & Penrh, J.J. (1964). Spearing behavior in feeding in the black marlin, *Istiompax marlina*. *Copeia* **1964**, 468.
- Van Daele, P.A.A.G., Herrel, A. & Adriaens, D. (2009). Biting performance in teeth-digging African mole-rats (*Fukomys*, Bath-yergidae, Rodentia). *Phys. Bioch. Zool.* **82**, 40–50.
- Verwajen, D., Van Damme, R. & Herrel, A. (2002). Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Funct. Ecol.* **16**, 842–850.
- Wainwright, P.C. (1987). Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool. Lond.* **213**, 283–297.
- Webb, P.W. (1982). Avoidance responses of fathead minnow to strikes by four teleost predators. *J. Comp. Physiol.* **147**, 371–378.
- Westneat, M.W. (2004). Evolution of levers and linkages in the feeding mechanics of fishes. *Int. Comp. Biol.* **44**, 378–389.
- Whitenack, L.B. & Motta, P.J. (2010). Performance of shark teeth during puncture and draw; implications for the mechanics of cutting. *Biol. J. Linn. Soc.* **100**, 271–286.
- Winterbottom, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phil.* **125**, 225–317.
- Wroe, S., McHenry, C. & Thomason, J. (2005). Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proc. Biol. Sci.* **272**, 619–625.
- Wroe, S., Huber, D.R., Lowry, M., McHenry, C., Moreno, K., Clausen, P., Ferrara, T., Cunningham, E., Dean, M.N. & Summers, A.P. (2008). Three-dimensional computer analysis of white shark jaw mechanics: how hard can a great white bite? *J. Zool.* **276**, 336–342.
- Zar, J.H. (2010). *Biostatistical analysis*. Englewood Cliffs, NJ: Prentice Hall.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Material S1.** Theoretical calculations of bite force based on a 3D static equilibrium model (Huber *et al.*, 2005).

**Figure S1.** Phylogenetic relationships among five billfishes species (blue marlin *Makaira nigricans*, shorbill spearfish *Tetrapturus angustirostris*, swordfish *Xiphias gladius*, sailfish *Istiophorus albicans*, white marlin *Tetrapturus albidus* and a non-billfish species used as the out-group (wahoo; *Acanthocybium solandri*). Tree topology was based on Santini & Sorenson (2013), and internode branch-lengths were based on known divergence times reported by Hedges *et al.* (2006).