Feeding biomechanics and theoretical calculations of bite force in bull sharks (*Carcharhinus leucas*) during ontogeny

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ABSTRACT

Evaluations of bite force, either measured directly or calculated theoretically, have been used to investigate the maximum feeding performance of a wide variety of vertebrates. However, bite force studies of fishes have focused primarily on small species due to the intractable nature of large apex predators. More massive muscles can generate higher forces and many of these fishes attain immense sizes; it is unclear how much of their biting performance is driven purely by dramatic ontogenetic increases in body size versus size-specific selection for enhanced feeding performance. In this study, we investigated biting performance and feeding biomechanics of immature and mature individuals from an ontogenetic series of an apex predator, the bull shark, *Carcharhinus leucas* (73–285 cm total length). Theoretical bite force ranged from 36 to 2128 N at the most anterior bite point, and 170 to 5914 N at the most posterior bite point over the ontogenetic series. Scaling patterns differed among the two age groups investigated; immature bull shark bite force scaled with positive allometry, whereas adult bite force scaled isometrically. When the bite force of *C. leucas* was compared to those of 12 other cartilaginous fishes, bull sharks presented the highest mass-specific bite force, greater than that of the white shark or the great hammerhead shark. A phylogenetic independent contrast analysis of anatomical and dietary variables as determinants of bite force in these 13 species indicated that the evolution of large adult bite forces in cartilaginous fishes is linked predominantly to the evolution of large body size. Multiple regressions based on mass-specific standardized contrasts suggest that the evolution of high bite forces in Chondrichthyes is further correlated with hypertrophication of the jaw adductors, increased leverage for anterior biting, and widening of the head. Lastly, we discuss the ecological significance of positive allometry in bite force as a possible "performance gain" early in the life history of *C. leucas*.

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1. Introduction

Bite force, a measure of feeding performance, can have a profound effect on trophic ecology and consequently survival and fitness (Herrel and O'Reilly, 2006; Huber et al., 2006; Kolmann and Huber, 2009). Barring restrictions from gape size or prey capture performance limitation, larger absolute bite force allows a predator to ingest a wider range of foods and therefore can be considered to confer a selective advantage. It is therefore pertinent to ask how such high performance develops, both during ontogeny and on an evolutionary scale.

A straightforward way to increase bite force during development is to simply increase the overall size of the animal, as this will also increase the cross-sectional area of feeding muscles, and therefore the maximum force produced. If changes in bite force and size during ontogeny are proportional (isometry), the increase in performance can be attributed to the animal simply getting bigger. However, bite force may also scale faster (positive allometry) or slower (negative allometry) than overall growth of the body, through size-independent modifications to the anatomy and/or physiology of the feeding mechanism such as changes in jaw leverage. Determining whether performance changes are rooted simply in growth or in restructuring of the feeding mechanism during growth can help us to understand the mechanistic bases for changes in trophic structure on multiple time scales.

Unfortunately, the ecological consequences of isometric vs. allometric growth trajectories are difficult to demonstrate. Positive allometry of vertebrate bite forces has been commonly reported (Erickson et al., 2003; Herrel and Gibb, 2006; Huber et al., 2006), often in association with ontogenetic changes in diet (Wainwright, 1988; Hernandez and Motta, 1997; Erickson et al., 2003; Herrel

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et al., 2005a; Herrel and O'Reilly, 2006; Huber et al., 2008). It has been argued that such allometric trajectories may be beneficial by making functionally difficult prey obtainable earlier in life and allowing access to food sources inaccessible to sympatric individuals of similar size but lower performance and/or with isometric performance trajectories (Kolmann and Huber, 2009). Although positive allometry of bite force during ontogeny has been demonstrated in all intraspecific studies of cartilaginous fishes (sharks and relatives; Huber et al., 2006, 2008; Kolmann and Huber, 2009), an interspecific examination of maximum performance among adults of 10 species demonstrated an isometric increase in bite force with species size (Huber et al., 2009). In other words, large adult sharks appear to have high bite forces simply by virtue of their large size and not owing to size-independent modifications of the feeding mechanism on a phylogenetic scale.

The observed size variation in sharks may therefore reflect a critical determinant of their predatory performance. Interspecific and ontogenetic intraspecific variation in shark body size can be huge and, as they are aquatic poikilotherms with indeterminate growth, some species can become extremely large. Although the ontogenetic development of bite force has been examined in several small to medium-sized species, the degree to which the largest sharks "rely" on increasing body size versus size-independent modifications for bite force development is unknown, particularly since these species are difficult or impossible to study in captivity, in the wild or across ontogeny.

In the present study we investigated the theoretical bite force and feeding biomechanics over ontogeny of a large apex predator, the bull shark Carcharhinus leucas. We relate ontogenetic changes in bite performance to the diet of this species and propose possible benefits of positive allometry of bite force early in life. Finally, we incorporate our data into a phylogenetic investigation of bite force performance, cranial morphometrics and dietary variables across 13 species of cartilaginous fishes.

The bull shark, C. leucas, is a coastal species with a robust body, broad head, and maximum size of up to at least 340 cm total length (TL) and 230 kg in weight, with males reaching maturity at 157–226 cm TL and females at 180–230 cm TL (Compagno, 1984). This species exhibits a pronounced dietary shift toward much larger and more functionally difficult prey, with bull sharks smaller than 140 cm TL preying mostly on bony fishes, and those larger than 140 cm TL preying on large sharks, marine mammals and occasionally turtles (Compagno, 1984; Cockcroft et al., 1989; Cliff and Dudley, 1991; Last and Stevens, 1994; Heithaus, 2001). However, marine mammals are most common in the diet of individuals larger than 180 cm TL (Cliff and Dudley, 1991). Although the material properties of many of these prey items are unknown, large specimens of turtles, mammals and elasmobranchs are surely more functionally difficult prey to process, given the larger skeletal elements, and higher stiffness and puncture resistance of mammalian bone and shark skin relative to teleost skin and bone (Currey, 1987; Erickson et al., 2002; Horton and Summers, 2009; Whitenack and Motta, 2010).

Being large apex predators that undergo ontogenetic dietary change, bull sharks offer an interesting group in which to study bite performance during ontogeny, providing an opportunity for examination of the relationship between size-dependent and size-independent determinants of bite force, and their links to ecology. The ontogenetic diet switch of bull sharks and data for other shark species suggest positively allometric bite force development. However, the large body size of bull sharks implies that size-independent modifications of the feeding mechanism (e.g., changes in cranial proportions) may be "unnecessary" and an isometric growth curve could be more likely, especially at later ages. To clarify the relative importance of these mechanisms, we examine bite force development over a ~3.5-fold increase in animal length and

~57-fold increase in animal mass. This study represents the first examination of bite force ontogeny in a very large shark species (>200 cm TL).

2. Materials and methods

2.1. Theoretical calculations of bite force

Fifteen C. leucas (2470–140,341 g, 73–258 cm TL) were obtained from commercial and recreational fishers off the Gulf coast of Florida, except for the largest individual of this study (192,976 g, 285 cm TL), which was obtained from Cronulla, NSW, Australia. Animals were kept frozen until dissection. Unilateral dissections of the adductor mandibulae complex were performed following Motta and Wilga (1995).

The muscles involved in jaw adduction are: preorbitalis dorsalis (POD), preorbitalis ventralis (POV), quadratomandibularis dorsal division 1 and 2 (QD 1 + 2), quadratomandibularis dorsal division 3 (QD 3), quadratomandibularis dorsal division 4 (QD 4) and quadratomandibularis ventral (QV). All the subdivisions of the adductor mandibulae complex were removed and sectioned through the center of mass perpendicular to the principal fiber direction. The center of mass was found by suspending each muscle at different points with a weighted line and locating their point of intersection. The anatomical cross-sectional area (a-CSA) was traced from digital pictures (Canon PowerShot A710 IS; Canon Inc., Tokyo, Japan) using Sigma Scan Pro version 4 (Systat Software Inc., Point Richmond, CA, USA) in all the parallel-fibered subdivisions of the adductor mandibulae complex. Since only QD 1 + 2 showed a pinnate architecture, physiological cross-sectional area (pCSA) was calculated according to Powell et al. (1984):

$$\text{pCSA} = \frac{\text{muscle mass}}{\text{muscle density}} \times \cos \Theta \times \frac{1}{\text{fiber length}},$$

where the density of fish muscle is 1.05 g/cm^3 (Powell et al., 1984; Wainwright, 1988), Θ is the angle of fiber pinnation obtained from the average angle of 5 pinnate fibers evenly distributed across the muscle, and fiber length is the distance from the central tendon to the perimeter of the muscle along a fiber bundle. To visualize a fiber bundle, it was necessary to bisect the muscle through its center of mass and parallel to the main fiber angle to expose the central tendon. Fiber length and angle were estimated from digital pictures (Canon PowerShot A710 IS) using Sigma Scan Pro 4. We calculated the a-CSA of the QD 1 + 2 (rather than the p-CSA) for the smallest and the largest individuals in this study due to logistic reasons[1] (73 and 285 cm TL). Theoretical maximum tetanic force (Po) was then calculated for each subdivision following Powell et al. (1984):

$$P_{\text{O}} = \text{CSA} \times \text{TS},$$

where CSA was either the anatomical or physiological cross-sectional area of each muscle and TS is the specific tension of elasmobranch white muscle (28.9 N/cm^2, Lou et al., 2002).

Three-dimensional coordinates of origin and insertion of each adductor subdivision, jaw joint, and two bite points along the lower jaw (most proximal and most distal bite points) were obtained for each individual using a three-dimensional digitizer (Patriot Digitizer; Polhemus, Colchester, VT, USA). These coordinates were localized with the jaws completely adducted, which may slightly underestimate the output bite force (Ferrara et al., 2011). In-lever (IL), the distance from jaw joint to the insertion of each adductor muscle subdivision (jaws closed) and out-lever (anterior out-lever,

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[1] This division on the smallest animal was difficult to observe; the largest animal was dissected in a different facility.
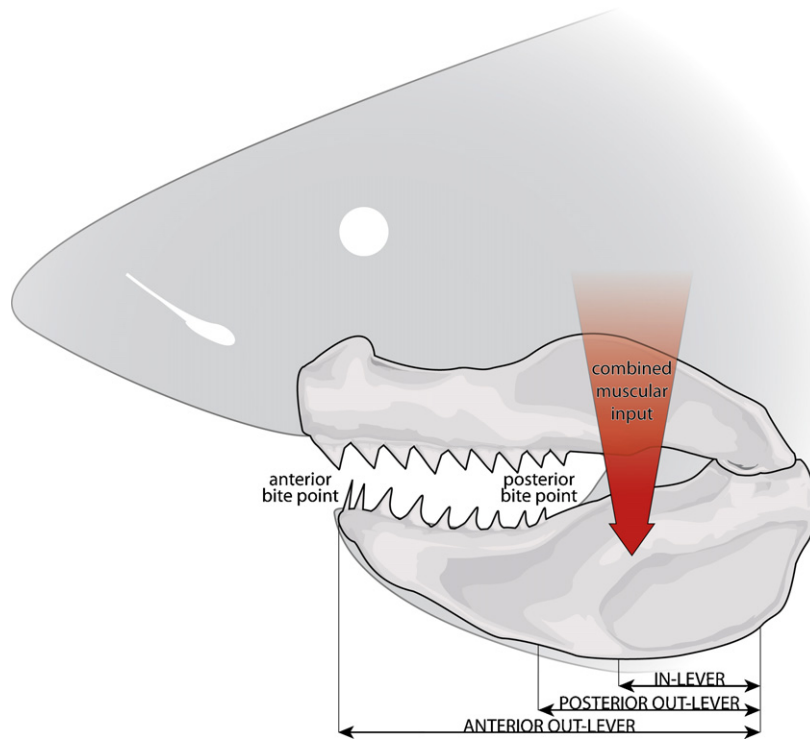
Fig. 1. Schematic of weighted in-lever/out-lever and bite point locations in the jaws of the bull shark, *Carcharhinus leucas* (jaws closed). The combined muscular input represents the resolved input vector from all jaw adductor muscles.

AOL, and posterior out-lever, POL), the distance from the jaw articulation to the anterior and posterior bite points (jaws closed) were calculated from these points (Fig. 1). Mechanical advantage (anterior mechanical advantage, AMA, and posterior mechanical advantage, PMA) was then calculated for each bite point as the ratio of the weighted in-lever (based on the proportional contribution of force of each muscle) and out-lever lengths, relative to the jaw joint. Three-dimensional (3D) force vectors were calculated for each subdivision of the adductor mandibulae complex that inserts on the lower jaw using P_O and the 3D position for each muscle. Theoretical maximum bite force produced along the lower jaw was calculated in Mathcad 13 (Mathsoft Inc., Cambridge, MA, USA) via summation of bending moments about the jaw joint in a 3D static equilibrium model, following Huber et al. (2005):

$$\sum F_{LJ} = F_{JR} + F_{POD} + F_{POV} + F_{QD12} + F_{QD3} + F_{QD4} + F_{QV} + F_B = 0,$$

where F_{LJ} are the forces acting on the lower jaw, F_{JR} is the jaw joint reaction, F_{POD}, F_{POV}, F_{QD12}, F_{QD3}, F_{QD4}, F_{QV} are the forces generated by each division of the adductor mandibulae complex and F_B is the bite reaction force from the prey item (Huber et al., 2005).

Since ontogenetic changes in performance may be crucial in early life stages, scaling relationships of bite force and all biomechanical variables were first investigated separately in immature (73–117 cm TL; 2470–11,174 g; $n = 11$), then mature individuals (187–285 cm TL; 50,106–192,976 g; $n = 5$). For comparative purposes, similar scaling analyses were performed on the complete ontogenetic series ($n = 16$).

Due to the possible correlation of the variables, principal component analysis (PCA, correlation matrix) was first utilized to reduce the dimensionality of the dataset and consequently to decrease error in the scaling analysis. All variables (except bite force and mass) were regressed against mass and the residuals obtained were utilized in the PCA. Principal component analysis was performed for the three datasets (immature, mature and complete). The axes that contributed to most of the variation were taken into consideration

(axis 1–5). Variables that did not load heavily on any of these axes (loadings < 0.5) and, hence, did not contribute much to the variation of the dataset were excluded from further analysis (immature dataset: AOL, POL; mature dataset: CSA of PV and PD, AMA, IL; entire dataset: CSA of PV, AMA and POL).

All variables kept in the analysis (immature dataset: CSA of all the muscles, AMA and PMA and IL; mature dataset: CSA of QD and QV, PMA and AOL, and POL; entire dataset: CSA of PD, QD and QV, PMA, IL and POL) were log-transformed and regressed using major axis (MA) regression against mass.

In this study, we consistently use mass as a metric for animal size; this is particularly important for the interspecific studies we performed (see Section 2.2) because chondrichthyan fishes show great variation in relative snout and tail length, making standard length and especially total length (TL) measurements misleading descriptors. To avoid variability from dissections among individuals, the CSA of all the subdivisions of the QD muscle were summed and the scaling pattern was analyzed for the muscle complex as a whole. Scaling relationships were verified by using 95% confidence intervals to compare the slopes obtained from MA regressions to the slopes expected from geometric similarity (isometry: bite force = 0.67, cross-sectional area = 0.67, mechanical advantage = 0.00, lever arms = 0.33) (Zar, 1998). Variables were considered to grow allometrically when their predicted slopes fell outside of the confidence limits for isometry. All statistical analyses were performed in PAST (Hammer et al., 2001).

2.2. Comparison of bite force among cartilaginous fishes

The highest mass-specific value of anterior bite force (ABF) for *C. leucas* (192,976 g; 285 cm TL) was compared to the highest mass-specific values of ABF from studies of 12 other species of cartilaginous fishes (Huber and Motta, 2004; Huber, 2006; Huber et al., 2005, 2006, 2008, 2009; Wroe et al., 2008; Mara et al., 2009; Mara, 2010; J. Claes, pers. comm.). To accomplish this, bite forces for all

individuals of a given species (including *C. leucas*), were separately regressed against mass and the individual with the highest residual bite force for that species was retained for interspecific analyses. The absolute bite forces of these individuals were then regressed against mass and residuals were used to rank all 13 species by mass-specific bite force. Regressions were performed in Sigmastat 2.03 (Systat Software Inc., San Jose, CA, USA).

2.3. Phylogenetic analyses

We explored interspecific scaling relationships using phylogenetically informed methods to account for the relatedness of species (Felsenstein, 1985; Garland et al., 2005). First, a tree of the 13 included species was constructed (Fig. 2), using a distillation of both molecular and morphological literature sources (Shirai, 1996; Winchell et al., 2004; Compagno, 2005; Iglesias et al., 2005; Huber et al., 2009). We set all branch lengths to 1.0, because accepted

divergence time data are not yet available for this clade (Garland et al., 1999). As in the previous interspecific analysis above (Section 2.2), we used data from those adults of each species that exhibited the highest mass-specific bite force; we also included data describing external morphometrics (total length, TL; pre-branchial length, PL; head width, HW; head height, HH), internal morphometrics (jaw length, JL; adductor musculature cross-sectional area, adductor CSA; mechanical advantages, AMA and PMA) and performance (ABF and PBF). We introduced quantitative dietary information for the studied species (percent fish, cephalopod, decapod crustacean and mollusk in the diet, and overall trophic level; MacPherson, 1980; Mauchline and Gordon, 1983; Cortés, 1999; Dunn et al., 2010) in order to investigate the relationships of cranial morphometrics and performance with diet, and the feasibility of using quantitative ecological data in studies of chondrichthyan bite performance. For those species lacking data, we used dietary information from closely related species. As such and because diets for some species
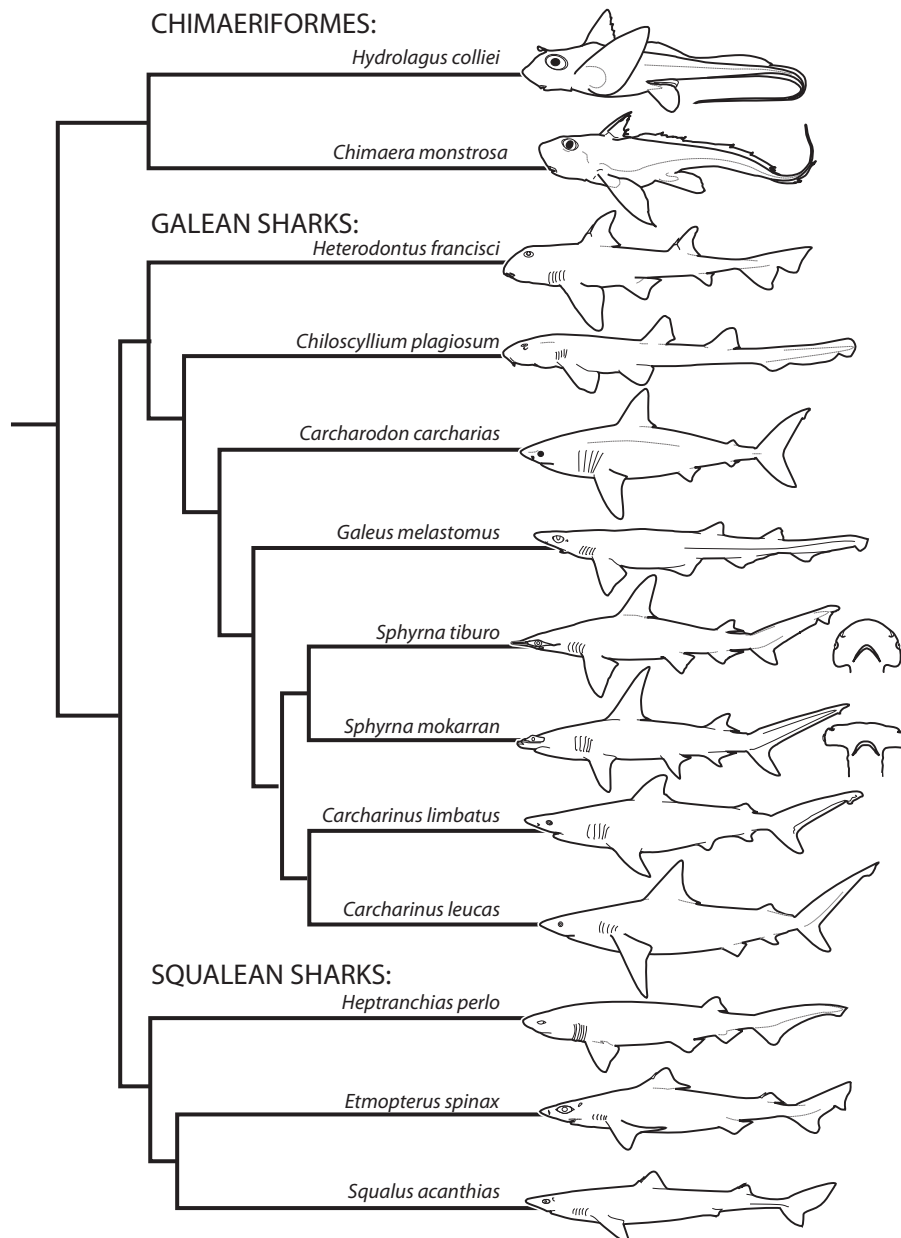

Fig. 2. Phylogeny of 13 chondrichthyan species used in the interspecific analysis of bite force allometry. Species span five orders of magnitude in size and so are not drawn to scale. Individual species data were gathered from other works and tree topology is based on a consensus from several literature sources (see text).

surely differ by geographic location, we interpreted these data cautiously and used them more as a suggestion for their utility in future chondrichthyan studies combining ecological and biomechanical works.

Data were log-transformed and, using the above-mentioned tree topology, we generated phylogenetically independent contrasts in the PDTREE module of Mesquite OSX (Garland et al., 1999; Midford et al., 2005; Maddison and Maddison, 2006). The standardized contrasts of each variable were then regressed against the standardized contrasts for body mass to determine how changes in body/cranial morphometrics and bite force related to changes in mass as cartilaginous fishes evolved (Garland et al., 1992, 2005; Herrel et al., 2002). We compared these results with similar "non-phylogenetic" regressions run on log-transformed raw data, not contrasts. Major axis (MA) regressions were used in all cases; we consider these regressions more appropriate than ordinary least squares (OLS) regressions as we are most interested in the slopes of the lines (i.e., allometric relationships of variables) (Harvey and Pagel, 1991; Warton et al., 2007). The relationship was considered isometric if the associated theoretical isometric slope fell within the confidence intervals for the calculated slope. All regressions were run using SMATR freeware (Warton et al., 2007); phylogenetic regressions were forced through the origin (Garland et al., 1999).

To examine the relationships between diet, morphometrics and bite force outside of size-related effects, we first removed the effect of size (mass) by regressing the standardized contrasts of all variables against standardized mass contrasts and calculating the residuals. Ordinary least squares regressions (SMATR freeware) were used in this case since major axis and reduced major axis regressions would not completely remove correlations with the x-axis variable (mass) (Warton et al., 2007). We then used a multiple regression analysis (Systat v.10; Systat Software Inc.) of all variables' residual standardized contrasts against the residual standardized contrasts of ABF and PBF to determine which variables, outside of mass, best explain for increases in bite performance. To account for potential masking effects by dominant variables (Zar, 1998) we ran separate regressions for diet variables, internal morphometric variables and external morphometric variables (excluding TL).

3. Results

3.1. Bite force in bull sharks

Bite force values for *C. leucas* ranged from 36 to 2128 N at the most anterior bite point and 170 to 5914 N at the most posterior bite point (mass = 2470–192,976 g, respectively). Mechanical advantage varied from 0.24 to 0.37 (mean = 0.31) at the most anterior bite point (AMA) and from 0.87 to 1.6 (mean = 1.1) at the most posterior bite point (PMA).

Principal component analysis showed different results for each dataset. For the immature dataset axes 1–5 accounted for most of the variation (96.8%) and the variables that loaded heavily on those axes were CSA of all the muscles, PMA and AMA, and IL. For the mature dataset axes 1–3 accounted for most of the variation (97.5%). The variables that loaded heavily on those axes were CSA of QD and QV, PMA, POL and AOL. Finally, for the entire dataset axes 1–5 accounted for most of the variation (96.9%) and variables that loaded heavily on those axes were CSA of PD, QD and QV, PMA, IL and AOL (Table 1).

Bite force values from immature ($n = 11$; 2469.64–11,173.6 g; 73–117 cm TL) and mature ($n = 5$; 50,106.4–192,976 g; 187–285 cm TL) bull sharks showed a significant relationship with mass ($p < 0.0001$ for ABF and PBF in immature sharks; $p = 0.03$ for ABF

Table 1
Results from PCA, loadings and % of variation for (A) immature bull sharks, *Carcharhinus leucas*, (B) mature bull sharks, (C) both datasets. Bold values show variables with loadings ≥0.5 that were included for further analysis. Only axes that contributed to the majority of variation are shown.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
(A)					
PV	0.3	0.3	**−0.5**	0.0	0.2
PD	−0.3	0.4	0.0	0.4	**0.5**
QD total	0.1	0.4	**−0.5**	−0.4	−0.3
QV	0.2	0.3	**0.5**	−0.6	0.5
MA B	−0.2	**0.5**	0.4	0.1	−0.4
MA F	0.4	0.4	0.0	**0.5**	0.0
IL	**0.5**	0.1	0.2	0.2	−0.2
POL	0.4	−0.3	−0.2	0.1	0.3
AOL	0.4	−0.1	0.3	0.0	−0.2
% Variation	46.2	26.9	12.2	7.0	4.5

	Axis 1	Axis 2	Axis 3		
(B)					
PV	0.4	−0.3	0.1		
PD	−0.4	0.3	0.1		
QD total	0.0	−0.4	**0.6**		
QV	−0.4	0.0	**−0.5**		
MA B	−0.1	**0.5**	0.4		
MA F	0.3	0.4	−0.2		
IL	0.4	0.1	−0.2		
POL	0.1	**0.5**	0.2		
AOL	**0.5**	0.1	0.0		
% Variation	51.5	30.5	15.5		

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
(C)					
PV	0.3	0.3	−0.3	0.4	−0.1
PD	−0.2	0.3	**0.5**	0.6	0.5
QD total	−0.1	0.4	**−0.6**	0.3	−0.3
QV	0.2	**0.5**	−0.2	−0.3	0.6
MA B	−0.2	**0.6**	0.3	−0.4	−0.3
MA F	0.4	0.2	0.4	0.1	−0.4
IL	**0.5**	0.1	0.2	−0.1	−0.1
POL	0.4	−0.3	−0.1	0.2	0.1
AOL	**0.5**	0.0	0.0	−0.3	0.1
% Variation	45.8	21.2	17.2	8.1	4.6

and $p = 0.02$ for PBF in mature sharks). Anterior and posterior bite force scaled with positive allometry in immature individuals due to positive allometry of the CSA of one of the divisions of the adductor mandibulae muscle (QD); all other biomechanical variables included in this analysis scaled with isometry (Table 2, Fig. 3). Bite force and all other biomechanical variables scaled with isometry in mature bull sharks (Table 3, Fig. 4).

The scaling pattern was different when the complete dataset was analyzed. Anterior bite force and the CSA's of two divisions of the adductor mandibulae complex (PD and QV) scaled with positive allometry, while PBF and all other variables scaled with isometry when examined across the entire ontogenetic series (2470–192,976 g; 73–285 cm TL; Table 4).

3.2. Comparison of bite force among cartilaginous fishes

There was a significant relationship between the absolute values of bite force and mass among the species compared ($F = 52.8$, df = 12, $p < 0.001$). *C. leucas* had the second highest absolute bite force of the species studied, just below that of the great hammerhead *Sphyrna mokarran*. After removing the effect of mass, the residual bite force of *C. leucas* was the highest of all cartilaginous fishes that have been studied (Table 5).

Table 2
Scaling relationship of immature individuals of *Carcharhinus leucas*. Slopes obtained from the regression equation (in bold) were compared to expected slopes (isometric) by confidence intervals. Significant deviations from geometric similarity were found when expected slopes fell outside confidence limits ($n = 11$).

Variable	Regression equation	R^2	Expected slope	Conf. limits		Scaling pattern
				Lower	Upper	
Anterior bite force (N)	Log ABF = −2.87 + (**1.33** × Log Mass)	0.95	0.67	1.08	1.58	Positive allometry
Posterior bite force (N)	Log PBF = −2.99 + (**1.5** × Log Mass)	0.92	0.67	1.19	1.85	Positive allometry
Cross-sectional area PV	Log PV = −2.75 + (**0.8** × Log Mass)	0.76	0.67	0.46	1.09	Isometry
Cross-sectional area PD	Log PD = −3.2 + (**0.75** × Log Mass)	0.77	0.67	0.45	1.05	Isometry
Cross-sectional area QD	Log QD = −4.19 + (**1.31** × Log Mass)	0.85	0.67	0.91	1.72	Positive allometry
Cross-sectional area QV	Log QV = −2.49 + (**0.84** × Log Mass)	0.91	0.67	0.65	1.03	Isometry
Anterior mechanical advantage	Log AMA = −0.11 − (**0.12** × Log Mass)	0.25	0	−0.27	0.03	Isometry
Posterior mechanical advantage	Log PMA = −0.18 + (**0.06** × Log Mass)	0.01	0	−0.28	0.40	Isometry
In-lever (cm)	Log IL = −0.37 + (**0.19** × Log Mass)	0.20	0.33	−0.08	0.46	Isometry

Table 3
Scaling relationship of mature individuals of *Carcharhinus leucas*. Slopes obtained from the regression equation (in bold) were compared to expected slopes (isometric) by confidence intervals. Significant deviations from geometric similarity were found when expected slopes fell outside confidence limits ($n = 5$).

Variable	Regression equation	R^2	Expected slope	Conf. limits		Scaling pattern
				Lower	Upper	
Anterior bite force (N)	Log ABF = −0.97 + (**0.80** × Log Mass)	0.84	0.67	0.18	1.42	Isometry
Posterior bite force (N)	Log PBF = −1.9 + (**1.07** × Log Mass)	0.88	0.67	0.37	1.78	Isometry
Cross-sectional area QD	Log QD = −1.92 + (**0.68** × Log Mass)	0.37	0.67	−0.71	2.07	Isometry
Cross-sectional area QV	Log QV = −1.5 + (**0.62** × Log Mass)	0.83	0.67	0.11	1.12	Isometry
Posterior mechanical advantage	Log PMA = −0.02 + (**0.01** × Log Mass)	0.00	0	−0.40	0.42	Isometry
Anterior out-lever (cm)	Log AOL = −0.11 + (**0.29** × Log Mass)	0.75	0.33	−0.01	0.60	Isometry
Posterior out-lever (cm)	Log POL = −0.87 + (**0.34** × Log Mass)	0.28	0.33	−0.56	1.24	Isometry

Table 4
Scaling relationship of immature and mature *Carcharhinus leucas* during ontogeny. Slopes obtained from the regression equation (in bold) were compared to expected slopes (isometric) by confidence intervals. Significant deviations from geometric similarity were found when expected slopes fell outside confidence limits ($n = 16$).

Variable	Regression equation	R^2	Expected slope	Conf. limits		Scaling pattern
				Lower	Upper	
Anterior bite force (N)	Log ABF = −1.1 + (**0.84** × Log Mass)	0.96	0.67	0.74	0.93	Positive allometry
Posterior bite force (N)	Log PBF = −0.33 + (**0.77** × Log Mass)	0.91	0.67	0.64	0.91	Isometry
Cross-sectional area PD	Log PD = −3.6 + (**0.85** × Log Mass)	0.98	0.67	0.78	0.93	Positive allometry
Cross-sectional area QD	Log QD = −2.1 + (**0.73** × Log Mass)	0.91	0.67	0.60	0.86	Isometry
Cross-sectional area QV	Log QV = −2.21 + (**0.76** × Log Mass)	0.99	0.67	0.71	0.81	Positive allometry
Posterior mechanical advantage	Log PMA = −0.03 + (**0.00** × Log Mass)	0.00	0	−0.07	0.07	Isometry
In-lever (cm)	Log IL = −1.03 + (**0.38** × Log Mass)	0.90	0.33	0.31	0.45	Isometry
Anterior out-lever (cm)	Log AOL = −0.4 + (**0.35** × Log Mass)	0.81	0.33	0.28	0.49	Isometry

Table 5
Maximal bite force among cartilaginous fishes.

Species name	Common name	Mass (g)	ABF (N)	Residuals
Carcharhinus leucas	Bull shark	192,976.11	2128.00	2.901
Carcharodon carcharias[a]	White shark	240,000.00	1602.00	0.839
Carcharhinus limbatus[b]	Blacktip shark	9833.00	423.00	0.531
Heptranchias perlo[c]	Sharpnose sevengill shark	1614.00	245.00	0.147
Heterodontus francisci[d]	Horn shark	1616.00	117.20	−0.205
Chiloscyllium plagiosum[c]	Whitespotted bamboo shark	1219.00	93.10	−0.267
Hydrolagus colliei[e]	Spotted chimaera	515.00	89.00	−0.269
Chimaera monstrosa[f]	Giant chimaera	98.87	30.42	−0.425
Etmopterus spinax[f]	Velvet belly lanternshark	190.84	21.09	−0.452
Sphyrna tiburo[g]	Bonnethead shark	2920.00	25.62	−0.474
Galeus melastomus[f]	Blackmouth catshark	742.13	11.83	−0.485
Squalus acanthias[h]	Spiny dogfish	386.00	8.14	−0.49
Sphyrna mokarran[i,j]	Great hammerhead shark	580,598.00	2432.00	−2.717

[a] Wroe et al. (2008).
[b] Huber et al. (2006).
[c] Huber (2006).
[d] Huber et al. (2005).
[e] Huber et al. (2008).
[f] J. Claes (pers. comm.)
[g] Mara et al. (2009).
[h] Huber and Motta (2004).
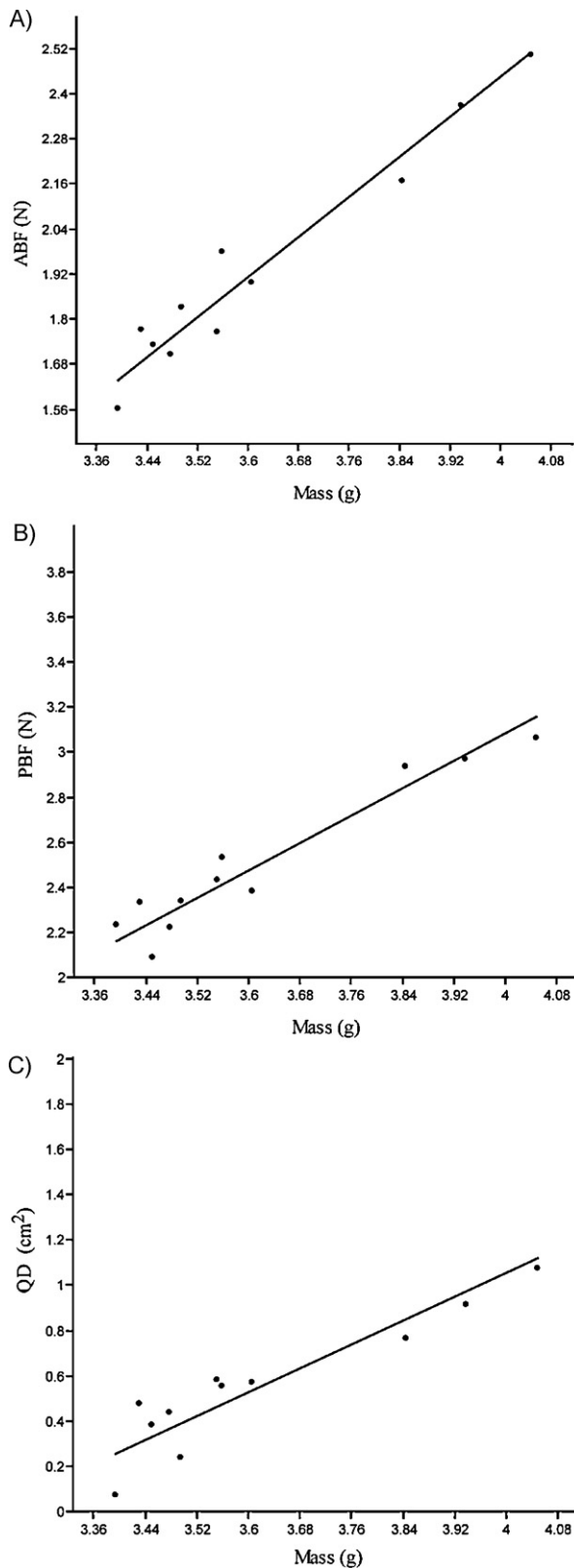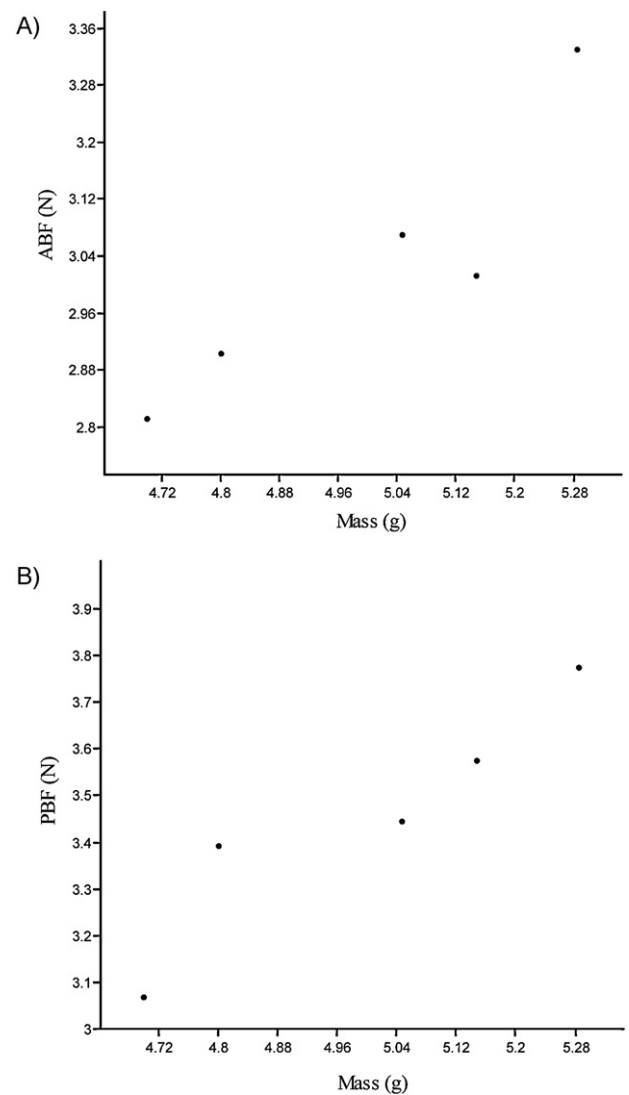[i] Huber et al. (2009).
[j] Mara (2010).

Fig. 4. (A) Log-transformed values of anterior bite force (N) for mature *Carcharhinus leucas* (187–285 cm TL) regressed against log-transformed values of mass (g). (B) Log-transformed values of posterior bite force for mature *C. leucas* regressed against log-transformed values of mass.

Fig. 3. (A) Log-transformed values of anterior bite force (N) for immature *Carcharhinus leucas* (73–117 cm TL) regressed against log-transformed values of mass (g). (B) Log-transformed values of posterior bite force for immature *C. leucas* regressed against log-transformed values of mass. (C) Log-transformed values of the cross-sectional area of the adductor muscle QD (cm^2) of immature *C. leucas* regressed against log-transformed values of mass.

3.3. Phylogenetic analyses

Phylogenetic increases in species' adult size (mass) were significantly linked to increases in ABF and PBF, to all morphometric variables except AMA and PMA, to increases in trophic level, and to decreases in the percent of decapod crustaceans in the diet ($p \leq 0.01$; Table 6). Dietary variables included in the analysis suggest that larger chondrichthyans occupy a higher position in the food chain and ingest fewer decapod crustaceans; these dietary variables show significant association with mass, but the relationships only account for a comparatively small percent of the variability in the data (% decapods in the diet $R^2 = 0.51$; tropic level $R^2 = 0.58$). All variables significantly related to changes in mass scale isometrically, except TL and PL, which exhibit negative allometry (Table 6). Therefore, of the species studied, larger (more massive) chondrichthyans have comparatively shorter bodies and heads. "Non-phylogenetic" regressions (run on log-transformed raw data, not contrasts) provided essentially identical results (not shown), except that PL scaled isometrically with mass. In both types of analyses, the isometric relationships between increases in mass and ABF and PBF indicate that the evolution of large (massive) body

Table 6
Phylogenetic allometric regressions of morphometric, diet and performance variables against mass for 13 chondrichthyan species. Gray cells indicate high coefficients of determination ($R^2 > 0.75$), significant relationships with mass ($p < 0.05$) and deviations from isometry. Scaling was determined by comparing experimental confidence intervals (CI) with expected slopes; there were no explicit expectations for dietary allometric slopes.

Variable	R^2	p	Expected slope	Actual slope	CI Low	CI High	Scaling
Total length	0.97	<0.001	0.33	0.26	0.23	0.30	Neg. allometry
Pre-branchial length	0.92	<0.001	0.33	0.27	0.22	0.33	Neg. allometry
Head width	0.89	<0.001	0.33	0.31	0.24	0.39	Isometry
Head height	0.87	0.002	0.33	0.38	0.29	0.48	Isometry
Jaw length	0.78	0.009	0.33	0.39	0.26	0.53	Isometry
Adductor cross-sectional area	0.90	<0.001	0.67	0.76	0.60	0.94	Isometry
Anterior mechanical advantage	0.02	0.809	0.00	0.02	−0.09	0.13	No relationship
Posterior mechanical advantage	0.13	0.480	0.00	0.05	−0.04	0.13	No relationship
Anterior bite force	0.84	0.001	0.67	0.81	0.60	1.08	Isometry
Posterior bite force	0.84	<0.001	0.67	0.81	0.60	1.08	Isometry
% Fish	0.12	0.499	–	0.41	0.40	1.28	–
% Cephalopods	0.00	0.915	–	−0.07	−1.27	−0.37	–
% Molluscs	0.08	0.587	–	−0.23	−1.08	−0.32	–
% Decapods	0.51	0.036	–	−0.42	−0.73	−0.16	–
Trophic level	0.58	0.037	–	0.04	0.02	0.06	–

size in these 13 species is accompanied by proportional (isometric) changes in bite performance (Table 6).

Our investigations with multiple regressions of size-independent predictors of bite performance retained adductor CSA (adj. $R^2 = 0.932$; $p < 0.001$), AMA (adj. $R^2 = 0.932$; $p = 0.007$) and HW (adj. $R^2 = 0.474$; $p = 0.009$) as predictors of ABF, and only adductor CSA (adj. $R^2 = 0.876$; $p < 0.001$) as predictor of PBF. These relationships are outside of the effects of size on bite force and therefore represent morphological predictors of variations around the isometric mass vs. bite force curve (i.e., they explain variation in size-removed data). In other words, chondrichthyans with comparatively high ABF for their body mass also have comparatively wide heads, high mechanical MA and large muscle CSA; whereas comparatively high PBF is linked only to evolutionary increases in mass-specific muscle CSA.

4. Discussion

4.1. Scaling patterns of bite force

Anterior and posterior bite forces develop faster than expected (are positively allometric) in immature bull sharks, but not in mature individuals, which exhibit an isometric increase in bite force. This suggests that a disproportional increase in bite force may be advantageous during early life history as it may allow organisms to exploit resources that are unavailable to others (Kolmann and Huber, 2009). Positive allometry of bite force later in life may not be necessary since these larger individuals are able to produce large absolute bite forces which are likely great enough to overcome any structural constraints imposed by prey (Huber et al., 2009). Similarly, the African catfish, Clarias gariepinus, exhibits positive allometry of bite force in early life stages and grows isometrically at later stages. Interestingly, this species also undergoes an ontogenetic diet shift, switching from harder prey to more evasive prey (Herrel et al., 2005a).

When determining the scaling of bite force for the entire dataset in this study, a different scenario was found. In this case, bull sharks demonstrate an increase in ABF during ontogeny that is disproportionately large compared to their increase in body size, attributable to positive allometry of the CSA of two of the subdivisions of the adductor complex (PD and QV). Positive allometry in bite force has been reported for the horn shark Heterodontus francisci (Kolmann and Huber, 2009), the blacktip shark Carcharhinus limbatus (Huber et al., 2006), the spotted ratfish Hydrolagus colliei (Huber et al., 2008), and several reptile species (lizards – Sceloporus undulates,

Sceloporus magister and Cnemidophorus tigris: Meyers et al., 2002; and the American alligator – Alligator mississippiensis: Erickson et al., 2003). However, the majority of these results were based on analysis of an entire dataset, considering all age groups simultaneously. Results from this current study suggest that performing these analyses on an entire ontogenetic data set may obscure ecologically relevant patterns hidden within size classes. Combining the juvenile and adult data sets can therefore be misleading, as positive allometry in bite force is truly confined, at least in bull sharks, to juvenile stages when disproportionally large bite force (or more rapid development of bite force) may be necessary.

Based on Westneat's (2004) classification, the AMA of bull shark jaws characterizes them as force efficient (i.e., efficient in transferring muscle force to bite force). Mechanical advantage has been found to be a main factor affecting disproportional increases in bite force especially in durophagous species such as in horn sharks and spotted ratfish, in which values of PMA are remarkably high (see Table S1 in Appendix A). We find it particularly noteworthy that, as bull sharks grow, their PMA transitions from 0.87 to 1.6, indicating that the morphology is changing in such a way as to allow an amplification of jaw adductor force at the posterior teeth. Mean values for both AMA and PMA (0.31 and 1.10, respectively) were similar to those of the closely related blacktip shark C. limbatus (0.34 and 1.10, respectively), but lower than those of durophagous species such as the spotted ratfish H. colliei (0.49 and 1.50, respectively) (Huber et al., 2008).

Absolute values of bite force are crucial performance metrics for understanding the maximal capabilities of a predator (Huber et al., 2006). Our calculations suggest that bull sharks can generate extremely high bite forces of 5900 N at the back of the jaw and 2128 N at the most anterior teeth (192,976 g, 285 cm TL). These values are among the highest ever reported for extant vertebrates and are comparable to the bite forces produced by other large sharks such as the great hammerhead S. mokarran (ABF 2432 N, 434 cm TL) (Huber et al., 2009; Mara, 2010) and the white shark, Carcharodon carcharias (ABF 1602 N, 250 cm TL) (Wroe et al., 2008). However, size-specific analyses are valuable for identifying selection for high-performance feeding independent of body size. Comparisons among 13 chondrichthyan species revealed that C. leucas has the highest size-specific bite force, followed by the white shark, C. carcharias and the blacktip shark C. limbatus (Table 5).

Interestingly, the bite forces of bull sharks and other shark species suggest an "over-design" of the feeding mechanism in that these forces appear to be extremely high in comparison to those necessary for shark teeth to penetrate their common prey items

(2–90 N; Whitenack and Motta, 2010), with some species (*C. limbatus*, *S. mokarran*, *C. carcharias* and *C. leucas*) generating bite forces of thousands of Newtons greater than those demanded by their prey's tissues (Huber et al., 2006, 2009; Mara, 2010; Wroe et al., 2008). However, these published performance tests did not include rigid biological materials (e.g., bone) relevant to the later stages of a predation event (i.e., predation mechanics beyond the initial puncture of the prey by the teeth). Similar patterns of "excessive" bite force or other performance measurements have been found in several systems (Gans, 1979), for example in lizards, where prey items showed failure thresholds lower than the forces their predators could exert (Herrel et al., 1999; McBrayer and White, 2002). Additional data on the forces required to severe the integument and skeletal elements of prey such as large teleosts, elasmobranchs, marine mammals, and turtles are needed to determine whether high absolute bite forces are demanded to process this type of prey.

It is possible that the "over-design" of the feeding mechanisms of large sharks is simply a by-product of large body size, although it may also be tied to functions beyond the initial penetration of the prey item. For example, bull sharks generally inhabit murky waters (Compagno et al., 2005) in which the relocation and recapture of wounded prey is likely difficult. Therefore, a "bite and grip" behavior in which prey is held with extremely forceful jaws (high bite force and high MA) could be an effective strategy. This is in contrast to white sharks which may use a "bite, spit and wait" strategy in which wounded prey is left to exsanguinate and is later consumed (Tricas and McCosker, 1984 but see Klimley and Anderson, 1996; Martin et al., 2005). Although bull and white sharks have comparably high bite forces, they appear to be perhaps more excessive in the latter case. A "bite and grip" strategy may also be more important for species that use head-shaking to dismember large prey, where a forceful grasp on the swinging food item is necessary to rip tissue and to avoid considerable damage to the teeth and jaws (Gerry et al., 2010). Combined with the dual articulation between the upper and lower jaws (Motta and Wilga, 1995), powerful adduction of the jaws might prevent damage and dislocation.

4.2. Hypothetical benefits of positive allometry in bite force

C. leucas exhibits a growth curve with a non-hyperallometric portion (i.e., the adult portion of the growth curve) and differences in the rates of bite force development between immature and mature animals. It has been suggested that hyperallometric development of bite force allows a species to access functionally difficult or mechanically challenging prey earlier in life (Kolmann and Huber, 2009). However, this is a difficult argument to test since it demands a comparative foil, an organism or condition over which the advantage was gained. This could be a hypothetical competitor of similar size, but with an isometric growth curve and therefore lower bite force (Kolmann and Huber, 2009).

A more relevant comparison, from the perspective of selection, for the advantage gained by the evolution of positive allometry might be *within* a given species. The bipartite ontogenetic trajectory of bull sharks gives us a unique chance to simulate this "performance gain" hypothesis, since we have determined the slopes of both portions of this species' growth curve. For the purpose of this simulation we calculated "idealized" bite forces based on the curves generated from our data: we first used the generated "immature" growth curve to calculate bite force for the smallest individual in our study (73 cm, 2470 g), then the "mature" curve to calculate bite force for the study's smallest mature individual (187 cm, 50,106 g) (Fig. 5). We then used the "idealized" youngest individual as a vertex from which to extend three lines on a plot of bite force vs. mass (Fig. 5): one simulating observed data and connected directly to the "smallest mature individual" (line A; see explanation of this choice below); one with the isometric slope calculated for adult bull
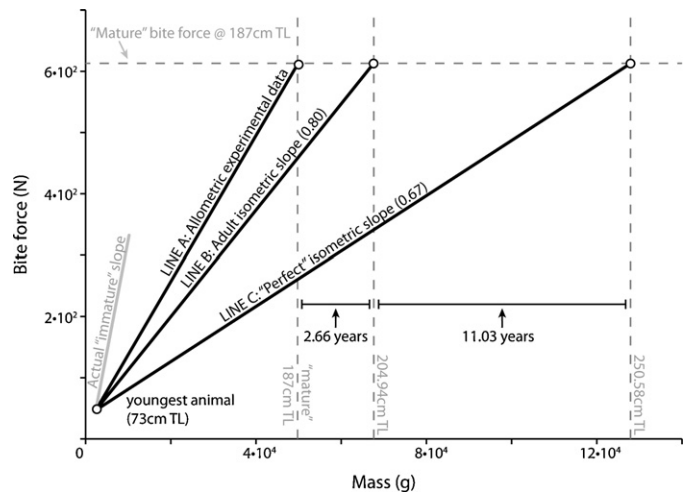

Fig. 5. Simulation illustrating the selective advantage gained due to the period of positive allometry early in the life of the bull shark, *Carcharhinus leucas*. Line A is drawn between this study's smallest animal and the smallest examined "mature" animal (187 cm TL). This is compared to lines B and C – with the experimentally determined adult slope (0.80) and a perfectly isometric slope (0.67), respectively – to determine the masses (vertical dashed lines) at which animals on these curves would reach line A's adult bite force (horizontal dashed line). These masses are converted to units of time based on Branstetter and Stiles' (1987) equations for bull shark growth. The simulation indicates that the early allometric growth rate of bite force allows bull sharks to reach mature bite forces many years before hypothetical isometric members of the same cohort. The actual "immature" slope (short gray line on the far left of the graph) is three times steeper than line A; however, as we have no data for larger immature animals (118–186 cm TL), line A was calculated to connect the study's smallest immature (73 cm TL) and smallest mature (187 cm TL) animals (see text for further reasoning). This results in an underestimated but more conservative slope (see text); thus, the suggested temporal/performance gains from an early hyperallometric slope could in life be even more pronounced.

sharks (line B: 0.8); and a third with a "perfect" isometric slope (line C: 0.67). Using the bite force calculated for the "smallest mature individual", we then calculated the mass at which bull sharks with growth curves characterized by lines B and C would attain this "mature" bite force. These masses were then input into a growth equation for bull sharks from the Gulf of Mexico (similar to our samples; Branstetter and Stiles, 1987) to back-calculate the ages of individuals of these sizes, and therefore identify relationships among mass, bite force, and developmental time.

This simulation indicates that bull sharks, by having a period of positive allometry early in life, receive a large temporal performance gain, reaching mature bite force 2.66 years (line B) and 11.03 years (line C) sooner than simulated isometric individuals from the same litter or cohort (i.e., growing from the same initial size and bite force). This gain can also be examined from a performance perspective: at the time an individual growing on line A reaches "maturity", its bite force is 1.47 and 1.87 times the bite force of animals growing on lines B and C, respectively.

This simulation exercise has clear limitations: we constrained all curves to begin from the youngest individual in our study and used the 187 cm animal as our "smallest adult", when in fact the "inflection point" between immature and adult animals could be anywhere between 73 and 187 cm. But in fact, line A is a conservative reference comparison. Rather than calculating the inflection point by projecting the intersection of the immature and mature curves (which is located in a size range for which we have no specimens), we connected the youngest examined animal directly to the smallest examined mature animal, resulting in a slope shallower than the actual immature slope (Fig. 5). We therefore feel that this analysis, based around experimental data, provides adequate indication of a huge advantage – in the form of time and

performance gained – from this species' period of positive allometric growth early in life. More specifically, as bull sharks present a dietary switch during ontogeny towards larger and more difficult prey (Cliff and Dudley, 1991), consequently this performance gain may facilitate this dietary transition during early ontogeny. This provides support for the notion of positive allometry of bite force providing a large selective advantage over the isometric condition, although evidence of this in chondrichthyan evolution remains to be demonstrated.

4.3. Phylogenetic analysis

Our phylogenetic analysis supports the previous assertion that cartilaginous fishes exhibit an isometric interspecific relationship between bite force and body size (Huber et al., 2009) and also is suggestive of size-independent morphological determinants of bite force differences among species. Mechanical advantage describes the ratio of in- and out-levers involved in generating bite force; therefore, our AMA variable incorporates the resolved position of the attachment of the musculature generating the input force and jaw length (another of our included variables), since the anterior bite point was calculated at the rostral tip of the jaw. Changes in AMA had no relationship to changes in body mass (i.e., showed no relationship in allometric tests), but were significant predictors of changes in size-specific ("size-removed") ABF. As JL showed a significant and isometric relationship with body mass, and no relationship with mass-specific bite force, this suggests that the changes in bite force not explained by changes in size are effected by an evolutionary mobility of the resolved insertion position for the adductor musculature. Since our data indicate that changes to the CSA of the muscles are also involved in size-specific changes in bite force, this suggests that, in addition to increasing absolute bite force through the evolution of large body size, chondrichthyan species attain high mass-specific bite forces through relative adjustments to gross muscular anatomy (i.e., resolved muscular insertion location and muscle size). Adjustments in muscle size are reflected in HW, the single external morphometric that was a significant predictor of size-independent bite force among species. This finding is consistent with studies on other vertebrate groups (Herrel et al., 2005b, 2007). We likely did not observe similar trends for PBF because of its measurement at the caudal-most tooth position, which varies considerably by species and even among individuals of the same species; using this as the POL dilutes the apparent strength of any potential relationships between PMA and bite force.

As in a previous work that employed a phylogenetic analysis including fewer chondrichthyan species (Huber et al., 2009), our analysis shows that as mass increases interspecifically among cartilaginous fish species, bite force increases proportionally. The calculated slope of the relationship between adult size and bite force (0.81; Table 6), although not statistically different from isometry, is greater than 0.67 and therefore indicates the possibility of positive allometry. This could perhaps be resolved with a greater sample size including a broader taxonomic diversity, though based on our results, the null hypothesis of an isometric interspecific pattern is supported. Nonetheless, these results suggest that the large absolute bite forces arising purely from phylogenetic increases in body size in sharks preclude the need for additional size-independent increases in bite force. This is in contrast to findings for other vertebrate clades in which positive allometry of bite force is found in comparing related species of different body sizes (Aguirre et al., 2002; Herrel et al., 2002). Therefore, as a lineage, sharks have achieved high adult bite force performance, not through the evolution of size-independent factors, but through the evolution of large body size. In contrast, selection functions differently within shark species, favoring hyperallometric bite force development

during ontogeny. In bull sharks, however, the strength of selective pressures on bite force apparently differs at different life stages, with increases in bite force early in ontogeny dictated by a disproportionate growth of jaw closing musculature, whereas adult bite force increases are apparently only determined by changes in animal body size.

5. Conclusions

Bite forces from immature bull sharks increase with positive allometry, whereas those of adult bull sharks exhibit geometric similarity with body mass. Positive allometry of bite force appears to be largely associated with the earlier stages of life history for this species, perhaps indicative of a "performance gain" allowing bull sharks to attain higher bite forces and access functionally difficult prey earlier in life. Additionally, posterior bite forces in large *C. leucas* individuals are extremely high, reaching up to ~6000 N (285 cm TL), and the maximum size-specific bite force of *C. leucas* is the highest among all cartilaginous fishes that have been investigated. Phylogenetic analysis of bite force among 13 species of cartilaginous fishes points to phylogenetic increases in mass as the primary determinant of the evolution of high bite force, although our data also suggest that gross muscular anatomy may play a role where bite force exceeds isometric expectation.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.zool.2012.04.007.

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