



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):

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

where the density of fish muscle is 1.05 g/cm³ (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 reasons¹ (73 and 285 cm TL). Theoretical maximum tetanic force (P_0) was then calculated for each subdivision following Powell et al. (1984):

$$P_0 = CSA \times TS,$$

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/cm², 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,

¹ This division on the smallest animal was difficult to observe; the largest animal was dissected in a different facility.

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