ELSEVIER

Scaling of bite force in the blacktip shark *Carcharhinus limbatus*

Daniel R. Huber*, Christina L. Weggelaar, Philip J. Motta

Department of Biology, University of South Florida, 4202 E. Fowler Ave., SCA 110, Tampa, FL 33620, USA

Abstract

Although bite force is a frequently studied performance measure of feeding ecology, changes in bite force over ontogeny have rarely been investigated. Biting by the blacktip shark *Carcharhinus limbatus* was theoretically modeled over ontogeny to investigate the scaling of bite force, the morphological basis of the observed scaling relationship, the ecological consequences of ontogenetic changes in performance, and whether cranial morphometrics can be used as an accurate proxy for bite force. Theoretical bite force, which was positively allometric with respect to total length (TL), ranged from 32 N (61 cm TL) to 423 N (152 cm TL) at the anterior tips of the jaws and from 107 (61 cm TL) to 1083 N (152 cm TL) at the posterior teeth. This observation is attributed to positive allometry in the mechanical advantage of the jaw-adducting mechanism and the cross-sectional area of all four jaw-adducting muscles. Theoretical bite force was accurately predicted by cranial morphometrics including prebranchial length and head width as well. Although positive allometry of bite force in *C. limbatus* would seem to indicate an ecological necessity for this phenomenon, dietary analyses do not necessarily indicate any ontogenetic shift in prey types requiring larger bite forces. The positively allometric increase in theoretical bite force may be associated with numerous other selective pressures including maintenance of an apical position within the ecosystem.
© 2006 Elsevier GmbH. All rights reserved.

Keywords: Elasmobranch; Cranial morphometrics; Performance studies; Feeding ecology

Introduction

Many organisms undergo dramatic morphological changes throughout ontogeny. Studying an organism's morphology at a specific point in its ontogenetic trajectory can help elucidate numerous aspects of its ecology. However, a thorough understanding of organismal ecology requires knowledge of how the functional integrity of morphological systems is maintained and/or enhanced during growth (Schmidt-Nielson,

1984). Functional integrity can be maintained and/or enhanced in a number of ways including changes in the size, architecture, and material properties of anatomical structures. While the morphological changes responsible for maintaining or enhancing function can often be readily identified, determining the ecological consequences of these changes is problematic (Arnold, 1983; McBrayer, 2004; Pike and Maitland, 2004). Performance studies can identify the morphological basis of differential ecological success by quantifying the level at which morphological attributes are utilized for ecological tasks (Domenici and Blake, 2000). Performance levels are directly attributable to morphology, and can

---

*Corresponding author.

E-mail address: drhuber@mail.usf.edu (D.R. Huber).

therefore vary concomitantly with morphology over ontogeny.

Bite force is an informative measure of organismal performance because survival is contingent upon food acquisition. Bite force has been shown to affect resource partitioning (Kiltie, 1982; Herrel et al., 2001b), dietary diversity (Wainwright, 1988; Clifton and Motta, 1998), and ontogenetic shifts in prey exploitation (Hernandez and Motta, 1997). Magnitudes and patterns of force generated by the cranial musculature and the resultant bite forces have been related to the geometry of cranial structures (Herrel et al., 2001a; Preuschoft and Witzel, 2004; Summers et al., 2004), as well as the type of dentition (Maschner, 2000; Spencer, 2003; Macho, 2004) in a wide variety of vertebrate taxa. Given the apparent relevance of bite force as a mediator between cranial morphology and resource exploitation, it is surprising that so few studies have investigated bite force over ontogeny (Hernandez and Motta, 1997; Herrel et al., 1999; Binder and Van Valkenburgh, 2000; Meyers et al., 2002; Erickson et al., 2003; Thompson et al., 2003).

The feeding mechanisms of the elasmobranchs (sharks, skates, and rays) are a model system for investigating the relationship between cranial morphology, bite force, and feeding ecology in fishes because they are composed of few moveable parts and display a high degree of functional diversity (Motta, 2004). Despite limited evolutionary lability due to the low number of kinetic elements, elasmobranch feeding mechanisms have diversified to exploit prey resources ranging from zooplankton to marine mammals (Schaefer and Lauder, 1996; Sims, 1999; Klimley et al., 2001). Although recent studies have begun to elucidate the relationship between morphology, performance, and ecology within these systems (Motta et al., 1997, 2002; Ferry-Graham, 1998a, b; Wilga and Motta, 1998, 2000; Dean and Motta, 2004a, b; Huber et al., 2005), functional changes in elasmobranch feeding mechanisms have been investigated over ontogeny in only three out of approximately 1000 species (Nelson, 1994; Ferry-Graham, 1998b; Summers, 2000; Summers et al., 2004).

The blacktip shark Carcharhinus limbatus is an ideal elasmobranch in which to study the relationship between morphology, performance, and ecology over ontogeny. C. limbatus is readily abundant in all size classes along the Gulf Coast of Florida. As a ram-feeder which uses jaw prehension to capture elusive prey (Frazzetta and Prange, 1987), its biting capacity dictates its predatory success. Dietary analyses do not indicate any ontogenetic shift in types of prey exploited by C. limbatus, with all size classes consuming teleost fishes primarily (Killiam, 1987; Castro, 1996; Barry, 2002; Heupel and Hueter, 2002; Hoffmayer and Parsons, 2003; Bethea et al., 2004). Additionally, C. limbatus is one of the most commercially important elasmobranchs in the southeastern United States (Cortes et al., 2002).

Information regarding the predatory capacity and feeding ecology of this shark will be useful to population management. The objectives of this study were therefore to (1) determine how theoretical bite force scales over ontogeny in C. limbatus, (2) determine the morphological factors responsible for the observed scaling relationships, (3) discuss the relationship between theoretical bite force and the feeding ecology of C. limbatus, and (4) determine whether external cranial morphometrics can be used as a proxy for estimating theoretical bite force in this species.

Materials and methods

Experimental animals

Fourteen C. limbatus (61–152 cm total length (TL)) were collected from the Gulf Coast of Florida during routine elasmobranch population assessments, and remained frozen until morphological analysis. Specimens were split into age classifications based on TL: neonate 27–72 cm, juvenile 73–119 cm, adult >120 cm (Compagno, 1984). All analyses were performed in accordance with the policies of the Institutional Animal Care and Use Committee of the University of South Florida (protocol # 2423).

Morphological analysis

Pre-branchial length (distance from snout to 1st gill slit), head height (distance from ventral to dorsal surfaces at the 1st gill slit), and head width (distance across the head between the 1st gill slits) were measured on all C. limbatus specimens. Using the tip of the snout as the center of a three-dimensional coordinate system, the origins and insertions of the four muscles involved in adducting the lower jaw of C. limbatus (preorbitalis dorsal, preorbitalis ventral, quadratomandibularis dorsal, quadratomandibularis ventral (Fig. 1)) were determined by measuring the distance of these points from the respective X (frontal), Y (sagittal), and Z (transverse) planes intersecting the tip of the snout. The positions of the center of rotation of the jaw joints (dual lateral and medial quadratomandibular articulation) and bite points at the anterior tip and posterior margin of the functional tooth row of the lower jaw were determined in this manner as well. Each muscle was then unilaterally excised, bisected through its center of mass perpendicular to the principal fiber direction, and digital images of the cross-sections were taken. Center of mass was estimated by suspending a muscle from a pin attached to a weighted line, and tracing that line onto the muscle. After repeating this from a second point, the intersection of the two tracings indicated the center of
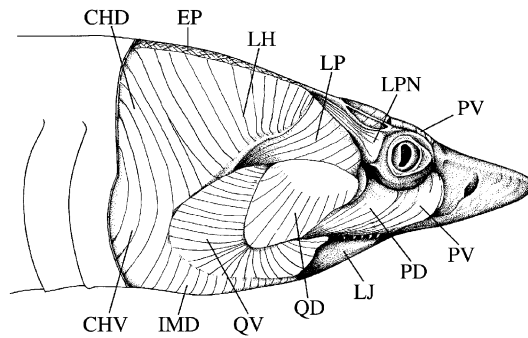
Fig. 1. Right lateral view of the cranial musculature of *Carcharhinus limbatus*. CHD, constrictor hyoideus dorsalis; CHV, constrictor hyoideus ventralis; EP, epaxialis; IMD, intermandibularis; LH, levator hyoideus; LJ, lower jaw; LP, levator palatoquadrati; LPN, levator palpebrae nictitantis; PD, dorsal preorbitalis; PV, ventral preorbitalis; QD, dorsal quadratomandibularis; QV, ventral quadratomandibularis.

mass. The quadratomandibularis muscle attaches broadly to the lateral surface of the jaws, making specific origins and insertions of the dorsal and ventral divisions difficult to determine. These points were therefore defined as the end points of the line of action passing through the center of mass of each muscle, as determined from their superficial fiber architecture. Anatomical cross-sectional area (ACSA) was determined from the digital images using SigmaScan Pro 4 image analysis software (SPSS, Inc.).

Theoretical maximum tetanic tension (P_O), or theoretical maximum force, for each muscle was calculated by multiplying its cross-sectional area (CSA) by the specific tension of elasmobranch white muscle ($28.9\,N/cm^2$) (Lou et al., 2002):

$$P_O = CSA \times \text{specific tension.}$$

Two (A1, A2) of the four divisions (A1–A4) of the dorsal quadratomandibularis undergo a transition from parallel to pinnate fiber architecture over ontogeny. Scanning electron microscopy revealed that this transition occurs at approximately 87 cm TL (see below). The force generated by the dorsal quadratomandibularis was calculated based on the summed ACSAs of the individual divisions for *C. limbatus* smaller than 87 cm. For specimens 87 cm and longer, the physiological cross-sectional areas (PCSA) of the A1 and A2 divisions of the quadratomandibularis muscle were determined using the equation of Powell et al. (1984):

$$PCSA = (\text{muscle mass} \times \cos\Theta)/(FL \times \text{muscle density}),$$

where Θ is the average angle of pinnation from the central tendon of the muscle, FL is the fiber length of the muscle divisions, and the density of fish muscle is 1.05 g/cm³ (Wainwright, 1988). Pinnation angles and fiber lengths of the A1 and A2 divisions of the quadrato-

mandibularis were measured from digital images using SigmaScan Pro 4 (SPSS, Inc., 1997). Each muscle was bisected perpendicular to its central tendon in line with the superficial fiber architecture to reveal its bipinnate architecture. Five measurements of pinnation angle and fiber length (distance from the central tendon to the perimeter of the muscle along a given fiber bundle (Huber and Motta, 2004)) were collected. The means of these measurements were used in the calculation of PCSA. The force generated by the dorsal quadratomandibularis in individuals larger than 87 cm TL was based on the summed anatomical and physiological CSAs of the respective divisions. Three-dimensional force vectors for each muscle were then created using their respective P_O values and coordinates of origin and insertion.

In-lever measurements for each muscle were determined from the three-dimensional coordinates of the jaw joint and the origin of each muscle along the lower jaw. A weighted average of these in-levers based on their P_O values was then used to estimate a resolved in-lever. Out-levers for biting at the front and back of the jaws were determined from the three-dimensional coordinates of the jaw joint and the bite points at the anterior and posterior margins of the functional tooth row on the lower jaw. Jaw-adducting mechanical advantages for biting at the anterior and posterior bite points were then estimated by taking the ratio of the resolved in-lever to the respective out-levers for each individual (Fig. 2a).

Following Huber et al. (2005), theoretical maximum bite forces at the anterior and posterior bite points of the lower jaw were determined using Mathcad 11.1 (Mathsoft, Inc.) by summing the moments generated by the adductive musculature about the jaw joints. The static equilibrium condition for the forces acting on the lower jaw (F_{LJ}) was

$$\sum F_{LJ} = F_{QD} + F_{QV} + F_{PD} + F_{PV} + F_{JR} + F_B = 0,$$

where F_B is the bite reaction force from a prey item, F_{JR} is the jaw joint reaction force, F_{PD} is the force generated by the dorsal preorbitalis, F_{PV} is the force generated by the ventral preorbitalis, F_{QD} is the force generated by the dorsal quadratomandibularis, and F_{QV} is the force generated by the ventral quadratomandibularis (Fig. 2b). Joint reaction forces maintain the static equilibrium of feeding mechanisms by balancing the moments acting upon the jaws via their associated musculature and contact with prey items. These values are not reported. Previous studies have demonstrated that theoretical estimates of maximum bite force from static modeling are statistically equivalent to bite forces measured during tetanic stimulation of the jaw-adducting muscles in the spiny dogfish *Squalus acanthias* and horn shark *Heterodontus francisci* (Huber and Motta, 2004; Huber et al., 2005).
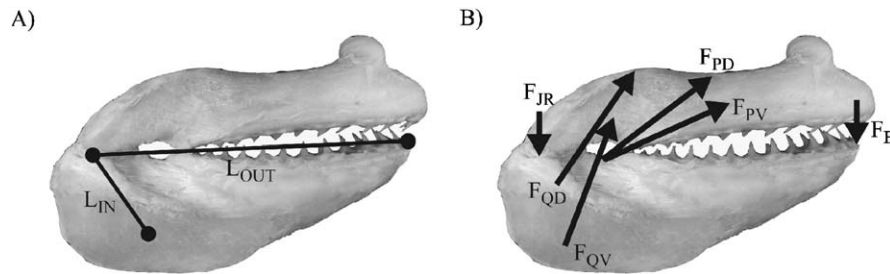
Fig. 2. Right lateral view of the jaws of *Carcharhinus limbatus* indicating (A) lever measurements for determining mechanical advantage and (B) static equilibrium conditions for estimating theoretical maximum bite force. L_{IN}, in-lever; L_{OUT}, out-lever; F_B, bite reaction force; F_{JR}, joint reaction force; F_{PD}, force generated by the dorsal preorbitalis; F_{PV}, force generated by the ventral preorbitalis; F_{QD}, force generated by the dorsal quadratomandibularis; F_{QV}, force generated by the ventral quadratomandibularis. Size of force vectors does not indicate magnitude of force.

Scanning electron microscopy

Scanning electron microscopy was used to determine the TL at which the A1 and A2 divisions of the dorsal quadratomandibularis changed from parallel to pinnate fiber architecture. These divisions were removed as a unit from four individuals (61–87 cm TL) and bisected perpendicular to the central tendon in line with the superficial fiber architecture to reveal potential fiber pinnation (Motta and Wilga, 1995). The specimens were then treated with Trump's Fixative (4% formaldehyde, 1% gluteraldehyde) for 24 h and rinsed in a 0.2 M solution of sodium cacodylate buffer with glucose. The specimens were then post-fixed in 2% osmium tetraoxide, rinsed again in sodium cacodylate buffer with glucose, and sequentially dehydrated to 100% ethanol. Samples were then dried with a Ladd Research Industries critical point dryer (Williston, VT), mounted, and sputter coated with a Pelco International Model 3 sputter coater (Redding, CA). Prepared specimens were viewed and photographed with a JEOL JSM-35 scanning microscope (Peabody, MA) at a working distance of 39 mm and an accelerating voltage of 15 kV.

Statistical analysis

To identify scaling relationships in the 11 biomechanical variables investigated, muscle CSAs, in-lever and out-lever measurements, mechanical advantages, and theoretical anterior and posterior bite force were Log_{10} transformed and linearly regressed against Log_{10} transformed TL. The scaling coefficients from these regressions were used to create residuals for each variable relative to the appropriate isometric slope (0 for mechanical advantages, 1 for lever arms, 2 for areas and forces). These residuals were then linearly regressed against Log_{10} transformed TL and ANOVA was used to determine whether the slopes of the normalized data significantly deviated from isometry.

Linear regressions were performed between each external cranial morphometric (pre-branchial length, head height, head width) and theoretical anterior bite force to determine if any of these variables could be used as predictors of bite force in *C. limbatus*. Subsequent multiple linear regressions between all combinations of external cranial morphometrics and theoretical anterior bite force were used to determine whether a combination of morphometric variables could better predict theoretical anterior bite force. Additionally, a Pearson Product Moment correlation was performed to identify relationships among the morphometric variables. All statistical analyses were performed in SigmaStat 2.03 with a *p*-value of 0.05 (SPSS, Inc.).

Results

CSA of all four jaw-adducting muscles scaled with positive allometry relative to TL over the size series of *C. limbatus* investigated (Table 1, Fig. 3a). The ventral quadratomandibularis increased in CSA to a greater extent than the other three muscles over ontogeny (slope = 2.91) and contributed the greatest amount of force to jaw adduction in each of the neonate, juvenile, and adult size classes (Table 1, Fig. 3b). In each size class the dorsal quadratomandibularis, ventral preorbitalis, and dorsal preorbitalis generated smaller forces than the ventral quadratomandibularis, respectively (Fig. 3b).

All lever arms scaled with positive allometry relative to TL (Table 1, Fig. 4a). In-lever distance had a higher scaling coefficient than either the anterior or posterior out-lever distances, indicating an increase in the leverage of the jaw-adducting mechanism of *C. limbatus*. Subsequently, positive allometry was observed in the mechanical advantage ratios measured for biting at both the anterior and posterior margins of the functional tooth row of the lower jaw (Table 1, Fig. 4b). For all

Table 1. Results of scaling analyses on Log_{10} transformed biomechanical variables in the feeding mechanism of *Carcharhinus limbatus*

| Variable	Regression equation	r^2	p-Value
Dorsal preorbitalis CSA (cm^2)	$Log\,Y = 2.58\,Log\,TL - 5.36$	0.920	<0.001
Ventral preorbitalis CSA (cm^2)	$Log\,Y = 2.37\,Log\,TL - 4.55$	0.917	<0.001
Dorsal quadratomandibularis CSA (cm^2)	$Log\,Y = 2.78\,Log\,TL - 5.13$	0.960	<0.001
Ventral quadratomandibularis CSA (cm^2)	$Log\,Y = 2.91\,Log\,TL - 5.17$	0.889	<0.001
In-lever (cm)	$Log\,Y = 1.38\,Log\,TL - 2.21$	0.915	<0.001
Anterior out-lever (cm)	$Log\,Y = 1.12\,Log\,TL - 1.23$	0.962	<0.001
Posterior out-lever (cm)	$Log\,Y = 1.27\,Log\,TL - 2.04$	0.974	<0.001
Anterior mechanical advantage	$Log\,Y = 0.39\,Log\,TL - 1.23$	0.488	<0.001
Posterior mechanical advantage	$Log\,Y = 0.30\,Log\,TL - 0.54$	0.361	<0.001
Anterior bite force (N)	$Log\,Y = 2.61\,Log\,TL - 3.18$	0.961	<0.001
Posterior bite force (N)	$Log\,Y = 2.70\,Log\,TL - 2.81$	0.942	<0.001

individuals, anterior mechanical advantage ratios for jaw adduction ranged from 0.25 to 0.42 (mean = 0.34), while posterior mechanical advantage ranged from 0.79 to 1.36 (mean = 1.09).

Owing to positive allometry in the force produced by the actuators (adducting muscles) and leverage (mechanical advantage) of the feeding mechanism of C. *limbatus*, theoretical estimates of bite force exhibited positive allometry at the anterior and posterior bite points (Table 1, Fig. 5). Across the size range of C. *limbatus* investigated, theoretical anterior and posterior bite forces ranged from 32 to 423 N and 107 to 1083 N, respectively. Theoretical anterior bite force ranged from 32 to 53 N in neonates, 63 to 70 N in juveniles, and 231 to 423 N in adults. Theoretical posterior bite force ranged from 107 to 182 N in neonates, 188 to 252 N in juveniles, and 989 to 1083 N in adults.

Strong positive relationships were found between both prebranchial length and head width with theoretical anterior bite force (width $r^2 = 0.927$, length $r^2 = 0.926$), although head height was of less predictive value ($r^2 = 0.772$) (Table 2). Multiple linear regressions marginally improved the accuracy with which cranial morphometrics could predict theoretical anterior bite force. The combined predictive power of prebranchial length and head width had a stronger linear relationship with theoretical anterior bite force ($r^2 = 0.929$) than any other multivariate combination or univariate analysis (Table 2). Multiple regression models did not substantially improve upon the predictive ability of individual cranial morphometrics due to considerable collinearity among morphometric variables, which had correlation coefficients ranging from 0.92 to 0.98.
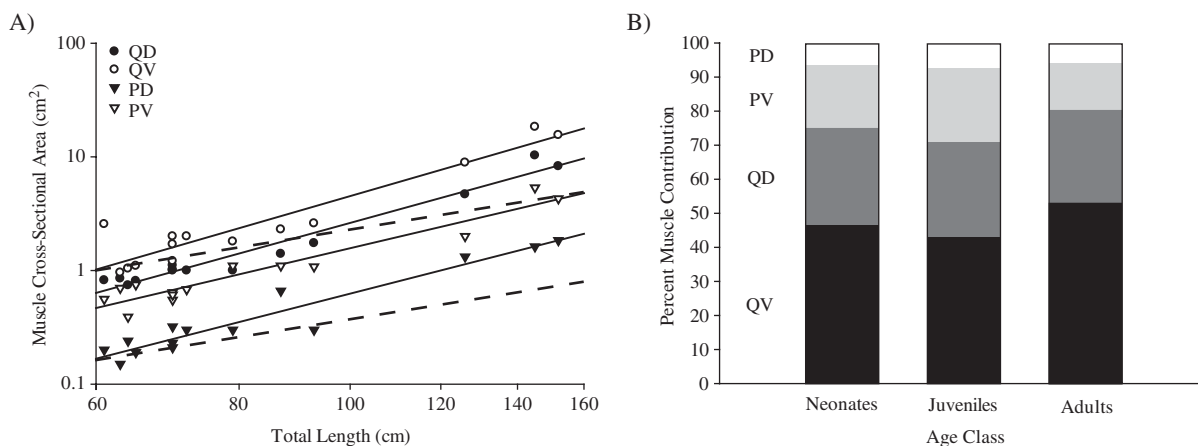
Fig. 3. (A) Cross-sectional area (cm^2) of the four jaw-adducting muscles of *Carcharhinus limbatus* plotted versus total length (cm) on logarithmic axes. The dashed lines indicate an isometric slope of 2. (B) Percent contributions of each jaw-adducting muscle to the total adductive force produced by *Carcharhinus limbatus* in the neonate, juvenile, and adult age classes. PD, dorsal preorbitalis; PV, ventral preorbitalis; QD, dorsal quadratomandibularis; QV, ventral quadratomandibularis.
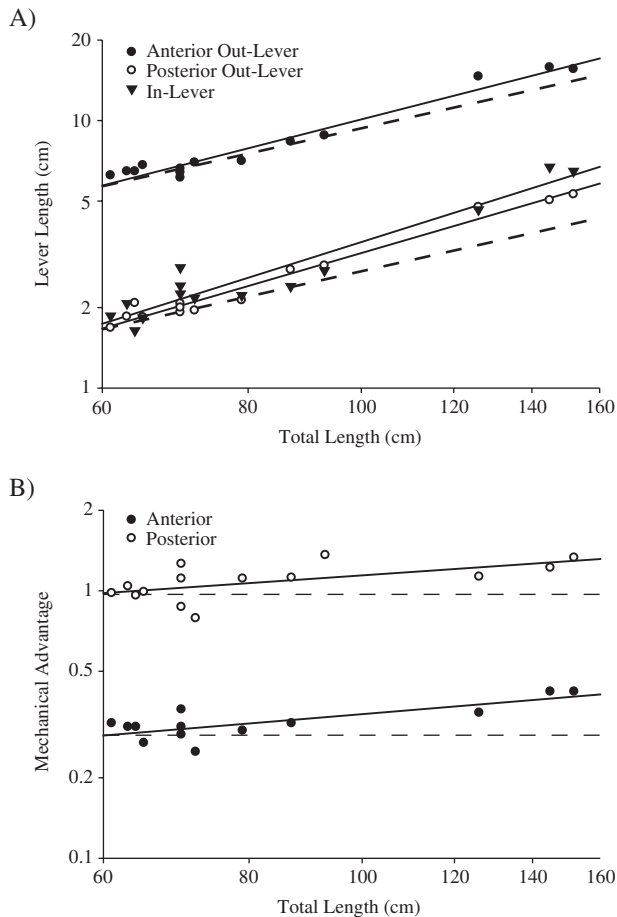
Fig. 4. (A) Jaw-adducting lever arms (cm) and (B) mechanical advantage of *Carcharhinus limbatus* for anterior and posterior biting plotted versus total length (cm) on logarithmic axes. The dashed lines indicate isometric slopes of 1 for lever arms and 0 for mechanical advantages.
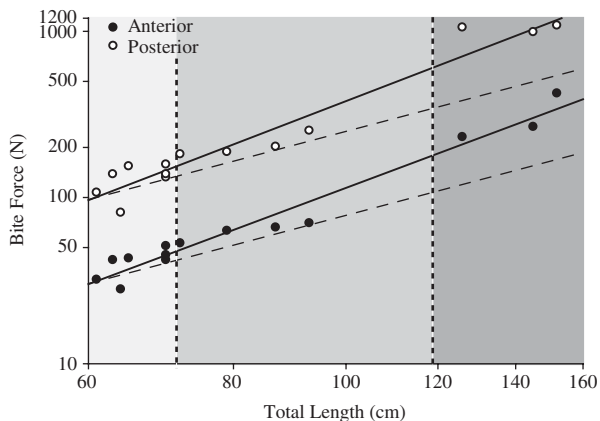
Fig. 5. Anterior and posterior bite force (N) of *Carcharhinus limbatus* plotted versus total length (cm) on logarithmic axes. The dashed lines indicate an isometric slope of 2. Shading between vertical demarcations indicates age class; light shading = neonate; medium shading = juvenile; dark shading = adult.

Discussion

Adult *C. limbatus* are theoretically capable of generating the highest bite forces ever estimated or recorded in a fish (anterior = 423 N, posterior = 1083 N). Although a possibly higher bite force estimate has been published for the silky shark *Carcharhinus falciformis* (889 N, ~200 cm TL), the methodology used in this investigation was subject to significant measurement error and the position in the mouth at which the bite occurred was not reported (Snodgrass and Gilbert, 1967; Evans and Gilbert, 1971). The large theoretical bite forces of the adult size class of *C. limbatus* are the product of positive allometry of bite force with respect to TL. This finding was due to positive allometry in the CSAs of all four jaw-adducting muscles and the mechanical advantage of the jaw-adducting mechanism. The force generated by a contracting muscle is a function of its magnitude of motor unit recruitment, the maximum of which is approximated by its CSA. Therefore, relative increases in muscle CSA indicate relative increases in maximum potential force production. Mechanical advantage is a measurement of the tradeoff between force and velocity in mechanical lever systems, with values closer to 1.0 indicating high force transmission and values closer to 0.0 indicating high velocity transmission. Thus, relative increases in mechanical advantage indicate relative increases in force transmission.

The CSAs of the ventral and dorsal preorbitalis muscles had the lowest scaling coefficients of the four muscles, respectively, suggesting that bite force generation may be their subordinate role (Table 1, Fig. 3). Their primary role is likely to rotate the upper jaw antero-ventrally away from the skull during jaw protrusion. This assumption is corroborated by their acute insertion angles relative to the lower jaw (Fig. 1), giving them high leverage over anterior motion of the jaws. These findings support electromyographic data and a model of jaw protrusion developed for the closely related lemon shark *Negaprion brevirostris* (Motta et al., 1997). Upper jaw protrusion in elasmobranchs has been hypothesized, in part, to augment prey capture efficiency by minimizing time to prey capture, allowing for more precise manipulation of prey, and facilitating the cutting of prey by the teeth (Wilga et al., 2001; Dean and Motta, 2004a; Motta, 2004).

Although the feeding mechanism of *C. limbatus* is suited for extensive protrusion of the upper jaw, the theoretical static model of bite force used in this study did not account for the antero-ventral rotation of the upper jaw away from the chondrocranium that occurs during protrusion. Upper jaw kinesis will modify the relative three-dimensional orientation of components in the feeding mechanism, which can affect the estimated maximum theoretical bite force (Herrel et al., 2000).

Table 2. Results of regression analyses to determine which cranial morphometrics were most predictive of anterior bite force (ABF) in *Carcharhinus limbatus*

Variable	Regression equation	r^2
Prebranchial length	ABF = 15.74PBL–176.06	0.927
Head width	ABF = 17.69HW–114.00	0.926
Head height	ABF = 21.33HH–56.01	0.772
Prebranchial length + head width	ABF = 8.19PBL + 8.63HW–147.98	0.929
Prebranchial length + head height	ABF = 18.62PBL—4.96HH–184.34	0.925
Head width + head height	ABF = 17.35HW + 0.52HH–114.23	0.920
Prebranchial length + head width + head height	ABF = 11.59PBL + 7.38HW–4.02HH–157.91	0.925

Modeling bite force based on muscle architecture may underestimate maximum bite performance as well. Active lengthening of the jaw adductors during depression of the lower jaw (eccentric contraction) can increase the force generated by these muscles due to the storage of elastic strain energy in the series elastic components of muscle fibers (Linstedt et al., 2002). Despite these dynamic effects, static estimates of maximum bite forces have been statistically equivalent to bite forces measured during tetanic stimulation of the adductor musculature in the sharks *S. acanthias* and *H. francisci* (Huber and Motta, 2004; Huber et al., 2005).

Comparative feeding mechanics

The theoretical anterior bite force of the smallest *C. limbatus* in this study (32 N, 61 cm; Fig. 5) was comparable to the maximum bite force measured from the suction feeding *S. acanthias* of approximately the same length (20 N, 53 cm) (Huber and Motta, 2004). However, the bite forces of both these sharks are substantially lower than that of similarly sized *H. francisci* (128 N, 61 cm; Huber et al., 2005). The dramatic difference between the bite forces of these sharks can be illustrated by the mechanical advantages of their feeding mechanisms and the force producing capacity of their adductor musculature. *H. francisci* has a jaw-adducting mechanical advantage of 0.51, whereas comparably sized *C. limbatus* and *S. acanthias* have mechanical advantages of 0.29 and 0.28, respectively (Table 1) (Huber and Motta, 2004; Huber et al., 2005). The adductor musculature of *H. francisci* can generate 2.4–3.7 times more force than that of *C. limbatus* and *S. acanthias,* respectively, as well (Huber et al., 2005; D.R. Huber, unpublished) (Table 1).

The differences in anatomy and feeding performance between *C. limbatus*, *S. acanthias*, and *H. francisci* are likely associated with their prey capture behaviors and the hardness of their prey. *C. limbatus* and *S. acanthias* catch mostly elusive, soft-bodied prey using ram and suction feeding, respectively (Frazzetta and Prange, 1987; Castro, 1996; Wilga and Motta, 1998; Alonso et al., 2002; Hoffmayer and Parsons, 2003; Bethea et al.,

2004). Although suction feeders such as *S. acanthias* primarily rely upon the expansion of the feeding mechanism to generate the sub-ambient intraoral pressure required to draw water and prey into the mouth (Muller and Osse, 1984; Svanback et al., 2002), they nonetheless must secure prey within the mouth. Therefore, the rate at which the jaws are adducted may be of equal or greater consequence than the magnitude of bite force generated for predators of elusive prey. Unlike *C. limbatus* and *S. acanthias*, *H. francisci* crushes hard prey including molluscs, crustaceans, and echinoderms (Segura-Zarzosa et al., 1997). Through the coupling of high bite forces, molariform dentition, and robust jaws capable of resisting dorso-ventral flexion, *H. francisci* is behaviorally and morphologically specialized for durophagy (Summers et al., 2004; Huber et al., 2005). The majority of prey consumed by *H. francisci* is non-elusive, emphasizing bite force magnitude over the rate of jaw adduction.

Mechanical advantage for anterior biting by *C. limbatus* ranged from 0.25 to 0.42 over ontogeny. This range of mechanical advantage ratios spans the continuum of ratios for teleost fishes generally segregated between having either ram/suction feeding mechanisms or manipulation-based mechanisms. With respect to the teleosts, mechanical advantages greater than 0.3 are typically considered to be "high", and are found among durophagous fishes (Wainwright and Richard, 1995; Wainwright et al., 2000; Westneat, 2004). While there is limited evidence to suggest that *C. limbatus* undergoes an ontogenetic shift from epibenthic to pelagic teleost prey between the young-of-the-year and juvenile size classes (Bethea et al., 2004), an ontogenetic shift in prey type through adulthood (with associated changes in material properties) does not occur. Therefore, the ecological relevance of a 60% increase in mechanical advantage over ontogeny is unclear.

Feeding ecology

Previous studies of feeding performance have shown bite force to be a strong predictor of trophic ecology.

Teleost fishes with higher bite forces include more hard prey in their diets and have lower dietary diversity (Wainwright, 1988; Hernandez and Motta, 1997; Clifton and Motta, 1998). Huber et al. (2005) have found evidence that not just the magnitude of bite force generated by *H. francisci*, but the dynamic manner in which that force is applied to prey items, may influence feeding efficiency. Increased bite force allows the inclusion of tough plant material in the diets of lizards (Herrel et al., 1998) and greater trophic diversity in rainforest peccaries (Kiltie, 1982). High bite forces can increase prey handling efficiency by minimizing the number of gape cycles required to process prey and/or by minimizing elusive prey's ability to escape (Verwaijen et al., 2002; van der Meij and Bout, 2004).

Several other studies have identified positively allometric increases in bite force over ontogeny, although not all of these have explored the link between these changes and the organisms' trophic ecology (Hernandez and Motta, 1997; Herrel et al., 1999; Meyers et al., 2002; Erickson et al., 2003). Hernandez and Motta (1997) and Erickson et al. (2003) correlated relative increases in the bite force of the sheepshead *Archosargus probatocephalus* and the American alligator *Alligator mississippiensis* with ontogenetic dietary shifts to harder and/or larger prey. Herrel et al. (1999) found that relative increases in bite force allow adult Canary Island lizards *Gallotia galloti* to consume a greater variety of invertebrate prey and plant matter than juveniles.

There is no evidence for a change in dietary diversity or prey type over ontogeny in *C. limbatus* (Killiam, 1987; Castro, 1996; Barry, 2002; Heupel and Hueter, 2002; Hoffmayer and Parsons, 2003; Bethea et al., 2004). All size classes are piscivorous and consume a variety of teleost prey, although 3–4% of larger individuals consume some elasmobranchs (Castro, 1996; Hoffmayer and Parsons, 2003). *C. limbatus* does, however, routinely consume large prey (>20% of body length), with an ontogenetic increase in the size of prey consumed (Bethea et al., 2004). Volume increases at a faster rate than length. Therefore, larger prey have relatively thicker bodies than smaller prey, perhaps necessitating relatively higher bite forces to overcome the increased frictional resistance associated with penetrating the body deep enough to inflict a fatal wound (Meers, 2002).

Several additional hypotheses may explain positive allometry of theoretical bite force over ontogeny. *C. limbatus* has positively allometric growth of body mass relative to TL (Castro, 1996). Body size is a critical determinant of community structure and is known to impact species interactions with respect to nutrient acquisition, habitat selection, and reproduction (Werner and Gilliam, 1984; Warner, 1988; Almada et al., 1994). Positive allometry of theoretical bite force may be a by-product of allometrically increasing body mass, a means by which *C. limbatus* maintains an apical position within the ecosystem. Allometric increase in theoretical bite force may also be related to differences in prey abundance between the highly productive inshore nursery grounds *C. limbatus* inhabits as a neonate/juvenile and the coastal ecosystem it inhabits later in life (Castro, 1993; Heupel and Hueter, 2002). If prey abundance is lower or patchier in the coastal ecosystem, positive allometry of theoretical bite force may ensure that prey seized between the jaws does not struggle free. Positive allometry of theoretical bite force will help males to restrain females during mating as well. Elasmobranch copulation routinely involves evasion by the female, followed by grasping of the female by the jaws of the male, allowing for proper alignment of the mating pair during clasper insertion (Carrier et al., 2004).

In addition to the application of bite force, upper jaw protrusion and lateral head shaking by *C. limbatus* augment its ability to capture and process prey. Protrusion exposes the blade-like teeth of the upper jaw, reducing the time to jaw closure and facilitating penetration of the teeth into prey. Once the teeth have penetrated, lateral head shaking induces tissue rupture via unidirectional draw of the teeth through their substrate (Frazzetta, 1988; Wilga et al., 2001; Motta, 2004). This mechanism is only effective for teeth with blade-like lateral surfaces, such as those found in carcharhinid sharks (Frazzetta, 1988; Abler, 1992). This may explain why carcharhinid sharks frequently employ lateral head shaking when manipulating larger prey (Moss, 1972; Frazzetta and Prange, 1987; Motta et al., 1997), whereas suction feeding orectolobid and heterodontid sharks utilize a spit-suck manipulation behavior to reduce prey in size (Edmonds et al., 2001; Motta et al., 2002; Matott et al., 2005).

Cranial morphometrics

Although maximum bite force does not appear to be predictive of diet in *C. limbatus*, it is related to cranial morphometrics. Approximately 93% of the variability in anterior bite force was explained via the combinatorial power of head width and prebranchial length. This combination of variables can provide an accurate approximation of anterior bite force in *C. limbatus* from 61 to 152 cm TL, in lieu of conducting additional biomechanical analyses. Either head width or prebranchial length, both of which individually explained nearly as much variability in anterior bite force as they did in combination, can also be used to predict the theoretical bite force of *C. limbatus*.

Numerous studies have investigated the link between variability in cranial morphometrics and bite performance (Raadsheer et al., 1999; Binder and Van Valkenburgh, 2000; Herrel et al., 2001a, 2005; Verwaijen

et al., 2002; McBrayer, 2004). However, none of these studies have examined the use of cranial morphometrics in predicting bite force. Because sharks have been implicated in human fatalities and destruction of marine technologies (Hurley et al., 1987; Marra, 1989; Burgess and Callahan, 1996), understanding bite force in large sharks such as *C. limbatus* will aid in diagnosing trauma associated with shark-inflicted injuries on humans, as well as in the development of shark-resistant marine technologies. The simple morphometric proxy for bite force in *C. limbatus* determined in this study will allow for rapid estimations of its bite force.

Anatomical evidence suggests that *C. limbatus* is under strong selection for positively allometric bite force due to relative increases in the leverage of and adductive force produced by its feeding mechanism. Although this study has quantified the connection between morphological variability and the bite performance capacity of *C. limbatus*, the more global and informative link between this shark's morphology, performance, *and* ecology remains ambiguous. A comprehensive knowledge of all the selective pressures acting on the feeding mechanism of *C. limbatus* is required to answer these questions. Investigation of the relationship between biting performance and tooth cutting dynamics will help clarify the relationship between morphology, performance, and ecology in elasmobranch feeding mechanisms.

Acknowledgments

References

Abler, W.L., 1992. The serrated teeth of tyrannosaurid dinosaurs, and biting structures in other animals. Paleobiology 18, 161–183.

Almada, V.C., Goncalves, E.J., Santos, A.J., Baptista, C., 1994. Breeding ecology of nest aggregations in a population of *Salaria pavo* (Pisces: Blenniidae) in an area where nest sites are very scarce. J. Fish Biol. 45, 819–830.

Alonso, M.K., Crespo, E.A., Garcia, N.A., Pedraza, S.N., Mariotti, P.A., Mora, N.J., 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus*

acanthias, in Patagonian waters, Argentina. Environ. Biol. Fishes 63, 193–202.

Arnold, S.J., 1983. Morphology, performance, and fitness. Am. Zool. 23, 347–361.

Barry, K.P., 2002. Feeding habits of blacktip sharks, *Carcharhinus limbatus*, and Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, in Louisiana coastal waters. MS Thesis, Louisiana State University.

Bethea, D.M., Buckel, J.A., Carlson, J.K., 2004. Foraging ecology of the early life stages of four sympatric shark species. Mar. Ecol. Prog. Ser. 268, 245–264.

Binder, W.J., Van Valkenburgh, B.V., 2000. Development of bite strength and feeding behavior in juvenile spotted hyenas (*Crocuta crocuta*). J. Zool. (London) 252, 273–283.

Burgess, G.H., Callahan, M., 1996. Worldwide patterns of white shark attacks on humans. In: Klimley, P., Ainley, D. (Eds.), Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press, San Diego, pp. 457–470.

Carrier, J.C., Pratt Jr., H.L., Castro, J.I., 2004. Reproductive biology of elasmobranchs. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Biology of Sharks and Their Relatives. CRC Press, Boca Raton, FL, pp. 269–286.

Castro, J.I., 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ. Biol. Fishes 38, 37–48.

Castro, J.I., 1996. Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. Bull. Mar. Sci. 59, 508–522.

Clifton, K.B., Motta, P.J., 1998. Feeding morphology, diet, and ecomorphological relationships among five Caribbean labrids (Teleostei, Labridae). Copeia, 953–966.

Compagno, L.J.V., 1984. FAO Species Catalogue. Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date. Part 2: Carcharhiniformes. Food and Agriculture Organization of the United Nations, Rome, p. 655.

Cortes, E., Brooks, L., Scott, G., 2002. Stock assessment of large coastal sharks in the U.S. Atlantic and Gulf of Mexico. National Marine Fisheries Service, p. 63.

Dean, M., Motta, P.J., 2004a. Anatomy and functional morphology of the feeding apparatus of the lesser electric ray, *Narcine basiliensis* (Elasmobranchii: Batoidea). J. Morphol. 262, 462–483.

Dean, M., Motta, P.J., 2004b. Feeding behavior and kinematics of the lesser electric ray, *Narcine brasiliensis* (Elasmobranchii: Batoidea). Zoology 107, 171–189.

Domenici, P., Blake, R.W., 2000. Biomechanics in behavior. In: Domenici, P., Blake, R.W. (Eds.), Biomechanics in Animal Behavior. BIOS Scientific Publishers Ltd., Oxford, pp. 1–17.

Edmonds, M.A., Motta, P.J., Hueter, R.E., 2001. Food capture kinematics of the suction feeding horn shark *Heterodontus francisci*. Environ. Biol. Fishes 62, 415–427.

Erickson, G.M., Lappin, A.K., Vliet, K.A., 2003. The ontogeny of bite-performance in American alligator (*Alligator mississippiensis*). J. Zool. (London) 260, 317–327.

Evans, W.R., Gilbert, P.W., 1971. The force of bites by the Silky Shark (*Carcharhinus falciformis*) measured under field

conditions. Naval Undersea Research and Development Center, San Diego, pp. 1–12.

Ferry-Graham, L.A., 1998a. Effects of prey size and mobility on prey-capture kinematics in leopard sharks *Triakis semifasciata*. J. Exp. Biol. 201, 2433–2444.

Ferry-Graham, L.A., 1998b. Feeding kinematics of hatchling swellsharks, *Cephaloscyllium ventriosum* (Scyliorhinidae): the importance of predator size. Mar. Biol. 131, 703–718.

Frazzetta, T.H., 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). Zoomorphology 108, 93–107.

Frazzetta, T.H., Prange, C.D., 1987. Movements of cephalic components during feeding in some requiem sharks (Carchariniformes: Carcharhinidae). Copeia, 979–993.

Hernandez, L.P., Motta, P.J., 1997. Trophic consequences of differential performance: ontogeny of oral jaw-crushing performance in the sheepshead, *Archosargus probatocephalus* (Teleostei, Sparidae). J. Zool. (London) 243, 737–756.

Herrel, A., Aerts, P., De Vree, F., 1998. Ecomorphology of the lizard feeding apparatus: a modeling approach. Neth. J. Zool. 48, 1–25.

Herrel, A., Spithoven, L., Van Damme, R., De Vree, F., 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. Funct. Ecol. 13, 289–297.

Herrel, A., Aerts, P., De Vree, F., 2000. Cranial kinesis in geckoes: functional implications. J. Exp. Biol. 203, 1415–1423.

Herrel, A., Grauw, E., Lemos-Espinal, J.A., 2001a. Head shape and bite performance in xenosaurid lizards. J. Exp. Zool. 290, 101–107.

Herrel, A., Van Damme, R., Vanhooydonck, B., De Vree, F., 2001b. The implications of bite force for diet in two species of lacertid lizards. Can. J. Zool. 79, 662–670.

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. J. Evol. Biol. 18, 669–675.

Heupel, M.R., Hueter, R.E., 2002. Importance of prey density in relation to the movement patterns of juvenile blacktip sharks (*Carcharhinus limbatus*) within a coastal nursery area. Mar. Freshwater Res. 53, 543–550.

Hoffmayer, E.R., Parsons, G.R., 2003. Food habits of three shark species from the Mississippi Sound in the northern Gulf of Mexico. Southeast. Nat. 2, 271–280.

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 the bite force and mechanical design of the feeding mechanism of the durophagous horn shark *Heterodontus francisci*. J. Exp. Biol. 208, 3553–3571.

Hurley, G.V., Stone, H.H., Lemon, D., 1987. The dogfish scourge: protecting fishing gear from shark attack. Hurley Fisheries Consulting Ltd., Fisheries Development Branch, Halifax, Nova Scotia, pp. 1–34.

Killiam, K.A., 1987. The reproductive biology, age, and growth of the blacktip shark, *Carcharhinus limbatus* (Valenciennes) near Tampa Bay, Florida. MS Thesis, University of South Florida, p. 109.

Kiltie, R.A., 1982. Bite force as a basis for niche diversification between rain forest peccaries (*Tayassu tajacu* and *T. pecari*). Biotropica 14, 188–195.

Klimley, A.P., Le Boeuf, B.J., Cautara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S., Kelly, J.T., 2001. The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. Mar. Biol. 138, 617–636.

Linstedt, S.L., Reich, T.E., Keim, P., LaStayo, P.C., 2002. Do muscles function as adaptable locomotor springs? J. Exp. Biol. 205, 2211–2216.

Lou, F., Curtin, N.A., Woledge, R.C., 2002. Isometric and isovelocity contractile performance of red muscle fibers from the dogfish *Scyliorhinus canicula*. J. Exp. Biol. 205, 1585–1595.

Macho, G.A., 2004. On the scaling relationship between enamel prism length and enamel thickness in primate molars: a comment. Ann. Anat. 186, 413–416.

Marra, L.J., 1989. Sharkbite on the SL Submarine Lightwave Cable System: history, causes, and resolution. IEEE J. Ocean Eng. 14, 230–237.

Maschner, R.P., 2000. Studies of the tooth strength of the Atlantic cow-nose ray, *Rhinoptera bonasus*. MS Thesis, California State Polytechnic University. p. 54.

Matott, M.P., Motta, P.J., Hueter, R.E., 2005. Modulation in feeding kinematics and motor pattern of the nurse shark *Ginglymostoma cirratum*. Environ. Biol. Fishes 74, 163–174.

McBrayer, L.D., 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. Zool. J. Linn. Soc. 140, 403–416.

Meers, M.B., 2002. Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior. Hist. Biol. 16, 1–12.

Meyers, J.J., Herrel, A., Birch, J., 2002. Scaling of morphology, bite force and feeding kinematics in an iguanian and scleroglossan lizard. In: Aerts, P., D'Aout, K., Herrel, A., Van Damme, R. (Eds.), Topics in Functional and Ecological Vertebrate Morphology. Shaker Publishing, The Netherlands, pp. 47–62.

Moss, S.A., 1972. The feeding mechanism of sharks of the family Carcharhinidae. J. Zool. (London) 167, 423–436.

Motta, P.J., 2004. Prey capture behavior and feeding mechanics of elasmobranchs. In: Carrier, J., Musick, J., Heithaus, M. (Eds.), Biology of Sharks and Their Relatives. CRC Press LLC, Boca Raton, pp. 165–202.

Motta, P.J., Wilga, C.D., 1995. Anatomy of the feeding apparatus of the lemon shark, *Negaprion brevirostris*. J. Morphol. 226, 309–329.

Motta, P.J., Tricas, T.C., Hueter, R.E., Summers, A.P., 1997. Feeding mechanism and functional morphology of the jaws of the lemon shark *Negaprion brevirostris* (Chondrichthyes, Carcharhinidae). J. Exp. Biol. 200, 2765–2780.

Motta, P.J., Hueter, R.E., Tricas, T.C., Summers, A.P., 2002. Kinematic analysis of suction feeding in the nurse shark, *Ginglymostoma cirratum* (Orectolobiformes, Ginglyostomatidae). Copeia, 24–38.

Muller, M., Osse, J.W.M., 1984. Hydrodynamics of suction feeding in fish. Trans. Zool. Soc. London 37, 51–135.

Nelson, J.S., 1994. Fishes of the World, third ed. Wiley, New York.

Pike, A.V.L., Maitland, D.P., 2004. Scaling of bird claws. J. Zool. (London) 262, 73–81.

Powell, P.L., Roy, R.R., Kanim, P., Bello, M.A., Edgerton, V.R., 1984. Predictability of skeletal muscle tension from architectural determinations in guinea pigs. J. Appl. Physiol. 57, 1715–1721.

Preuschoft, H., Witzel, U., 2004. A biomechanical approach to craniofacial shape in primates, using FESA. Ann. Anat. 186, 397–404.

Raadsheer, M.C., van Eijden, T.M.G.J., van Ginkel, F.C., Prahl-Anderson, B., 1999. Contribution of jaw muscle size and craniofacial morphology to human bite force magnitude. J. Dent. Res. 78, 31–42.

Schaefer, S.A., Lauder, G.V., 1996. Testing historical hypotheses of morphological change: biomechanical decoupling in loricaroid catfishes. Evolution 50, 1661–1675.

Schmidt-Nielson, K., 1984. Scaling: Why is Animal Size so Important? Cambridge University Press, Cambridge.

Segura-Zarzosa, J.C., Abitia-Cardenas, L.A., Galvan-Magana, F., 1997. Observations on the feeding habits of the shark *Heterodontus francisci* Girard 1854 (Chondrichthyes: Heterodontidae), in San Ignacio Lagoon, Baja California Sur, Mexico. Cienc. Mar. 23, 111–128.

Sims, D.W., 1999. Threshold foraging behavior of basking sharks on zooplankton: life on an energetic knife-edge? Proc. R. Soc. London B Biol. Sci. 266, 1433–1437.

Snodgrass, J.M., Gilbert, P.W., 1967. A shark-bite meter. In: Gilbert, P.W., Mathewson, R.F., Rall, D.P. (Eds.), Sharks, Skates, and Rays. Johns Hopkins Press, Baltimore, pp. 331–337.

Spencer, M.A., 2003. Tooth-root form and function in platyrrhine sead-eaters. Am. J. Phys. Anthropol. 122, 325–335.

Summers, A.P., 2000. Stiffening the stingray skeleton: an investigation of durophagy in myliobatid stingrays (Chondrichthyes, Batoidea, Myliobatidae). J. Morphol. 243, 113–126.

Summers, A.P., Ketcham, R., Rowe, T., 2004. Structure and function of the horn shark (*Heterodontus francisci*) cranium through ontogeny: the development of a hard prey crusher. J. Morphol. 260, 1–12.

Svanback, R., Wainwright, P.C., Ferry-Graham, L.A., 2002. Linking cranial kinematics, buccal pressure, and suction feeding performance in largemouth bass. Physiol. Biochem. Zool. 75, 532–543.

Thompson, E.N., Biknevicus, A.R., German, R.Z., 2003. Ontogeny of feeding function in the gray short-tailed opossum *Monodelphis domestica*: empirical support for the constrained model of jaw biomechanics. J. Exp. Biol. 206, 923–932.

van der Meij, M.A.A., Bout, R.G., 2004. Scaling of jaw muscle size and maximal bite force in finches. J. Exp. Biol. 207, 2745–2753.

Verwaijen, 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., 1988. Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecology 69, 635–645.

Wainwright, P.C., Richard, B.A., 1995. Predicting patterns of prey use from morphology in fishes. Environ. Biol. Fishes 44, 97–113.

Wainwright, P.C., Westneat, M.W., Bellwood, D.R., 2000. Linking feeding behavior and jaw mechanics in fishes. In: Domenici, P., Blake, R.W. (Eds.), Biomechanics in Animal Behavior. BIOS Scientific Publishers Ltd., Oxford, pp. 207–221.

Warner, R.R., 1988. Sex change in fishes: hypotheses, evidence, and objections. Environ. Biol. Fishes 22, 81–90.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15, 393–425.

Westneat, M.W., 2004. Evolution of levers and linkages in the feeding mechanisms of fishes. Integr. Comp. Biol. 44, 278–289.

Wilga, C.D., Motta, P.J., 1998. Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. J. Exp. Biol. 201, 1345–1358.

Wilga, C.D., Motta, P.J., 2000. Durophagy in sharks: feeding mechanics of the hammerhead *Sphyrna tiburo*. J. Exp. Biol. 203, 2781–2796.

Wilga, C.D., Hueter, R.E., Wainwright, P.C., Motta, P.J., 2001. Evolution of upper jaw protrusion mechanisms in elasmobranchs. Am. Zool. 41, 1248–1257.