

Bite Force and Performance in the Durophagous Bonnethead Shark, *Sphyrna tiburo*

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ABSTRACT Bite force, a measure of performance, can be used to link anatomical form and function. Earlier studies have shown bite force to have a significant influence on dietary constraints and ontogenetic shifts in resource utilization. The bonnethead shark, *Sphyrna tiburo*, is a durophagous member of the family Sphyrnidae. Its diet in South Florida waters consists almost entirely of blue crabs, which are crushed or ingested whole. This abundant coastal predator's feeding mechanism is specialized for the consumption of hard prey, including a modified biting pattern and molariform teeth. The goals of this research were to (1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and in vivo bite force measurements; (2) compare the bite force of *S. tiburo* with those of other fishes; and (3) identify functional constraints on prey capture by comparing the bite force of *S. tiburo* with the fracture properties of its primary prey item, blue crabs. Maximum theoretical bite force ranged from 25.7 N anteriorly to 107.9 N posteriorly. *S. tiburo* has the second lowest mass specific bite force for any fish studied to date, and its posterior mechanical advantage of 0.88 is lower than other durophagous chondrichthyans, indicating that this independent evolutionary acquisition of durophagy was not accompanied by the associated morphological changes found in other durophagous cartilaginous fishes. Blue crab fracture forces (30.0–490.0 N) range well above the maximum bite force of *S. tiburo*, suggesting that prey material properties functionally constrain dietary ecology to some degree. *J. Exp. Zool.* 311A, 2009. © 2009 Wiley-Liss, Inc.

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Although the relationship between form and function is often times apparent, a key component to understanding the relationship between these parameters and ecology is performance, the ability of an organism to accomplish ecologically relevant tasks (Arnold, '83; Irschick, 2002). More so, to draw substantive conclusions regarding such relationships both within and among species, these data must be investigated in light of the functional constraints imposed by ecological tasks. Doing so has elucidated numerous correlations between morphology and variables such as prey type, habitat, and community structure (Herrel et al., '96; Irschick and Losos, '99; Korff and Wainwright, 2004; Toro et al., 2004). Bite force influences the ability to acquire food resources, and has thus been an extensively studied performance measure in vertebrates (fish (Wainwright, '88; Herrel et al., 2002a; Korff and Wainwright, 2004; Grubich, 2005; Huber et al., 2005, 2009;

Kolmann and Huber, 2009), lizards (Herrel et al., 2001a; Lailvaux and Irschick, 2007), crocodylians (Erickson et al., 2003), birds (van der Meij and Bout, 2000; Herrel et al., 2005a,b; van der Meij and Bout, 2006), and mammals (Kiltie, '82; Aguirre et al., 2003; Herrel et al., 2008).

Although bite forces are informative regarding the relative and absolute abilities of animals to capture and process prey, ecological conclusions drawn from these data are suspect without specific attention paid to the functional constraints imposed by these prey items. For durophagous

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species (consumers of hard prey), bite force is particularly influential in shaping diet because the exoskeletal armaments of their prey are among the most durable biological materials found in the aquatic environment (Wainwright et al., '76; Summers and Long Jr., 2006). Despite the diversity of bite force studies, few have related bite force to prey characteristics in fish (Wainwright, '88; Hernandez and Motta, '97; Korff and Wainwright, 2004; Grubich, 2005; Huber et al., 2009), with only a single study investigating this in cartilaginous fishes (Kolmann and Huber, 2009).

The feeding mechanisms of chondrichthyans are remarkably different from those of bony fishes. They lack pharyngeal jaws to further process prey and have skeletons composed of prismatically calcified cartilage. Despite having jaws primarily composed of a pliant skeletal material, durophagy has convergently evolved at least eight times in groups such as the heterodontids, orectolobids, triakids, sphyrnids, and chimaeroids (Compagno et al., 2005; Huber et al., 2005; Ramsay and Wilga, 2007; Huber et al., 2008). Durophagy in chondrichthyan fishes is often associated with hypertrophy of their jaws and adductor muscles, molariform teeth, high bite force, and fused jaw symphyses in some cases (Summers, 2000; Summers et al., 2004; Huber et al., 2005). Behavioral and functional modifications associated with hard prey consumption also include unilateral biting and asynchronous muscle activity (Summers, 2000), tooth reorientation during biting (Ramsay and Wilga, 2007), and specialized motor patterns (Summers, 2000; Wilga and Motta, 2000). Collectively these characteristics are often related to dietary specialization (*S. tiburo*, Cortés et al., '96; *Heterodontus francisci*, Huber et al., 2005; *Rhinoptera bonasus*, Summers, 2000; Sasko et al., 2006).

The bonnethead shark, *S. tiburo*, (Elasmobranchii, Sphyrnidae) is purportedly the most derived hammerhead species (Martin, '93; Martin and Palumbi, '93), specializing almost exclusively on crustacean prey, particularly swimming crabs (*Callinectes* sp.) in South Florida (Compagno, '84; Cortés et al., '96; Lessa and Almeida, '98). Compared with other sharks, the bonnethead shark exhibits less upper jaw protrusion, prolonged jaw adductor activity patterns, enlarged maximum gape, and is the only hammerhead shark with posterior molariform teeth (Wilga and Motta, 2000; Motta and Wilga, 2001). However, durophagy in *S. tiburo* is enigmatic in that it is accomplished with some, but not all, of the characteristics associated with durophagy in other

chondrichthyans. In particular, they lack robust jaws, hypertrophied feeding muscles, and fused jaw symphyses (Wilga and Motta, 2000). However, relatively little is known about how feeding morphology contributes to force generation and shapes not only diet but also feeding ecology in *S. tiburo*. The goals of this study were therefore to (1) characterize the mechanical function of the feeding mechanism of *S. tiburo* through biomechanical modeling of biting and bite force measurements obtained via tetanic stimulation of jaw muscles and restraint of live animals; (2) compare the bite force of *S. tiburo* with that of other fishes; and (3) identify functional constraints on prey capture and diet by comparing the bite force of *S. tiburo* to the fracture properties of its primary prey item, blue crabs.

MATERIALS AND METHODS

Experimental animals

Ten *S. tiburo* (55.2–68.7 cm precaudal length (PCL), 73.0–91.5 cm total length (TL), 1,644–3,420 g) were collected from the Gulf of Mexico off Sarasota, Florida using a combination of long-line and gill net fishing. Sharks were chosen within a narrow size range to remove the effect of ontogeny. For ease of comparison to dietary data (Cortés et al., '96), shark PCL is used throughout. Individuals were housed in a $9.1 \times 16.8 \times 1.8 \text{ m}^3$, 22.7 kL oval tank located at Mote Marine Laboratory in Sarasota, Florida. Animals were fed bi-weekly with a diet of threadfin herring (*Opisthonema oglinum*) and white shrimp (*Penaeus setiferus*) as attempts to feed *S. tiburo* blue crabs in captivity were unsuccessful. However, cranial muscle plasticity data for elasmobranchs is lacking, therefore the potential effects of diet on muscle atrophy are unknown. In South Florida, the index of relative importance (IRI) (Pinkas et al., '71) indicates that the diet of *S. tiburo* is dominated by blue crab, *Callinectes sapidus* (85%). Within the size range of shark studied here, the occurrence of *C. sapidus* in the diet increases to 90% with the remaining diet being seagrass, most likely incidentally ingested (Cortés et al., '96). Upon completion of in vivo force measurements all animals were euthanized with an overdose of tricaine methanesulphonate (MS-222 0.1 g/L). All experimental procedures followed the Institutional Animal Care and Use Committee guidelines of Mote Marine Laboratory

(08-10-RH1, 07-10-PM1) and the University of South Florida (T3198, R3205, W3514).

Theoretical bite force

The three-dimensional coordinates of the origins and insertions for the four principle muscles involved in jaw adduction (preorbitalis dorsal (POD), preorbitalis ventral (POV), quadratomandibularis dorsal (QMD), and quadratomandibularis ventral (QMV)) (Wilga and Motta, 2000) (Fig. 1), the jaw joint, and anterior and posterior bite points along the lower jaw were obtained using a three-dimensional Patriot digitizer (Polhemus, Colchester, VT) with the tip of the rostrum as the center of a three-dimensional coordinate system. Following Huber et al. (2005), each muscle was unilaterally excised and the center of mass was determined. Center of mass and the superficial muscle fiber architecture were then used to estimate the line of action of each muscle, from which muscle origins and insertions were determined. The in-lever for each muscle was calculated based on the coordinates of its insertion on the lower jaw and the jaw joint. A resolved in-lever for jaw adduction was then determined from a weighted average of these individual in-levers based on the proportion of force that each muscle contributed to overall force production. Out-lever distances to the anterior and posterior bite points were determined from the coordinates of the anterior and posterior margins of the functional tooth row and the jaw joint. Gear ratio for jaw adduction at the anterior and posterior bite points was then calculated by dividing the weighted in-lever by the respective out-lever (Huber et al., 2006, 2008). It is assumed that all skeletal elements act as rigid beams and gear ratio is equivalent to mechanical advantage in this system. The mechanical advantage of a jaw adducting

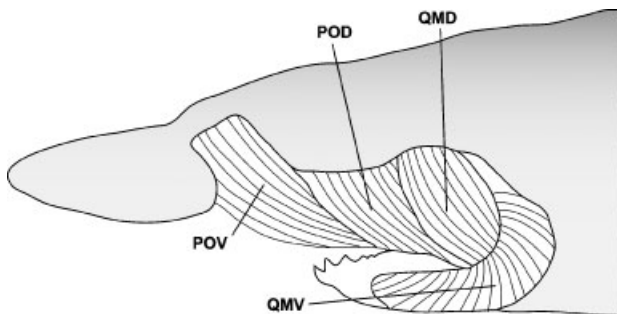


Fig. 1. Feeding musculature of *S. tiburo*. QMV, quadratomandibularis ventral; QMD, quadratomandibularis dorsal; POV, preorbitalis ventral; POD, preorbitalis dorsal. Redrawn and modified from Wilga and Motta (2000).

system indicates the ability of the system to transfer muscle forces to prey either rapidly (low mechanical advantage) or forcefully (high mechanical advantage) (Westneat, 2003).

Following excision, each muscle was bisected perpendicular to the principle fiber direction through the center of mass and the cross sectional area was digitized with Sigma Scan Pro 4 (SYSTAT Software Inc., Point Richmond, CA) (Huber et al., 2005). Maximum tetanic tension for each muscle was calculated by multiplying the cross-sectional area by the specific tension of elasmobranch white muscle (28.9 N/cm^2 , Lou et al., 2002). Forces and positions were then used to create three-dimensional force vectors for each muscle.

Bilateral theoretical maximum bite force at anterior and posterior bite points was modeled in 3D with Mathcad 13 (Mathsoft, Inc., Cambridge, MA) by summation of the moments generated about the jaw joints by each muscle (Huber et al., 2005). The static equilibrium model for lower jaw adduction is

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

where F_{PD} is the force contributed by the POD, F_{PV} is the force contributed by the POV, F_{QD} is the force contributed by the QMD, F_{QV} is the force contributed by the QMV, F_{JR} is the joint reaction force, and F_B is the reaction force from the prey.

Restrained bite force

Previous studies have demonstrated that theoretical modeling of bite force in chondrichthyans is a good proxy for in vivo maximum biting performance (Huber et al., 2005). However, no study has investigated the predictive power of theoretical bite force calculations in a species with morphological divergence in head shape. The collection of in vivo data allows for verification of the theoretical model. All in vivo bite force measurements were collected with a modified single-point load cell (AmCells Corp., Vista, CA) that was calibrated using a digital scale (Siltec Scales, Santa Clara, CA). The transducer was connected to a P-3500 strain indicator (Vishay Measurements Group, Raleigh, NC). Data were sent to a 6020E data acquisition board and imported into LabVIEW 6.0 software (National Instruments Corp., Austin, TX). Individual animals were removed from the holding tank and restrained on a foam padded platform such that their head hung over the edge of the platform. The tip of the rostrum was elevated and the metal arms

of the transducer were placed between the anterior tips of the jaws eliciting a bite. The anterior placement of the force transducer was chosen because it cannot be placed farther back due to gape constraints. This procedure was repeated 3–5 times for each individual and the largest of the 3–5 values was recorded as the maximum bite force for that individual. The procedure took no longer than 5 min per individual.

Tetanic bite force

Following restrained bite force measurements, the sharks were anesthetized with a re-circulating, aerated solution of MS-222 (0.133 g/L) and seawater. Once fully anesthetized, the sharks were placed ventral side up in a holding apparatus and the POV, QMD, and QMV muscles were implanted with bipolar electrodes connected to a SD9 stimulator (Grass Instruments, Quincy, MA). The POD was not stimulated because its small size and location made it difficult to implant. The jaw muscles were tetanically stimulated with the bite force transducer placed between the anterior tips of the jaws (20 V, 100 Hz, 0.02 msec delay, 3 msec pulse duration). Each individual was stimulated 3–4 times with a minimum of 1–2 min between successive stimulation events, during which their gills were perfused with the aerated anesthetic solution. The maximum force value for each individual was recorded. Posterior forces for all in vivo tests were calculated by multiplying the anterior force by the ratio of anterior to posterior out-levers.

Performance testing of prey

Eighteen live intermolt *C. sapidus* (23.3–68.4 mm carapace length (CL)) representing the crabs greater than or equal to the size range consumed by our sample of sharks (Cortés et al., '96) were purchased from local bait shops or collected by beach seine. The carapace width (spine to spine), length, depth, and mass were recorded for all *C. sapidus* before material testing.

Upper and lower jaws were removed from an adult 78.4 cm PCL *S. tiburo* and dried in 95% ethanol for 12 hr in order to bond them to steel plates such that the occlusal surfaces of the teeth were aligned. The jaws of this individual are comparable to those of sharks from our sample size both in size and shape. The plates were mounted in a Mini Bionix II Material Testing System (MTS, Eden Prairie, MN) with an in-line 5 kN load cell. Live crabs were immobilized with a

combination of MS-222, ~0.1 g/L, and tonic immobility (Fedotov et al., 2006), and placed between the mounted jaws. Live crabs are required for this type of experiment because the mechanical properties of biomaterials can change postmortem (LaBarbera and Merz, '92). Crabs were crushed at a displacement rate of ~370 mm/sec, which is the average velocity of lower jaw elevation in *S. tiburo* (Mara and Motta, unpublished data). In order to ensure mechanical failure of the carapace, the displacement distance was adjusted to 33% carapace depth for each crab. A successful crushing event was defined as a large crack produced in the carapace, with peak force occurring immediately before carapace failure.

Statistical analyses

All bite force variables, muscle masses, muscle forces, and mechanical advantages were \log_{10} transformed and linearly regressed against shark total length to examine the effect of size on bite force. Given the small size range of *S. tiburo* in this study, regressions showed no size effects, therefore, \log_{10} transformed (nonresidual) values were used for the remaining statistical tests. Paired *t*-tests were used to identify differences among bite forces measured from theoretical, in vivo restrained, and in vivo stimulated treatments. A forward stepwise multiple linear regression was also performed to examine which morphological traits best explained variation in anterior theoretical bite force.

To gain an understanding of how the bite force of *S. tiburo* compares to that of other fishes, particularly durophagous ones, maximum bite forces and body masses were compiled from the literature for 18 species (Hernandez and Motta, '97; Clifton and Motta, '98; Huber and Motta, 2004; Korff and Wainwright, 2004; Huber et al., 2005, 2006, 2008, 2009; Huber and Mara, unpublished). Bite forces and body masses for all species were \log_{10} transformed and linearly regressed to determine mass-specific bite force, which was compared among species.

Failure forces obtained during performance testing of prey were \log_{10} transformed and linearly regressed against crab carapace width, length, depth, and mass to examine the scaling of prey properties. The slopes of the scaling relationships were compared with an isometric slope of 2 with respect to crab width, length, and depth, and 0.67 with respect to mass using a two-tailed *t*-test. All regressions and paired *t*-tests were performed in

SigmaStat 3.1 (SYSTAT Software Inc., Point Richmond, CA) and *t*-tests of scaling relationships were performed manually.

RESULTS

Feeding biomechanics and bite force

Of the jaw adducting muscles, the largest force was produced by the QMV (33.2 ± 2 SEN), which represented approximately 35% of the adductive force, followed by POV (27.7 ± 1.4 SEN), POD (17.9 ± 1 SEN), and QMD (17.4 ± 0.8 SEN) (Table 1, Fig. 2). Mechanical advantage ranged from 0.24 (± 0.02 SE) to 0.88 (± 0.04 SE) between the anterior and posterior bite points. Based on these adductive forces and leverage of the feeding mechanism, the range of theoretical bite force was (13.4–25.7 N) and (50.3–107.9 N) for anterior and posterior bite points, respectively. Forward step-wise multiple linear regression performed on all biomechanical variables with respect to bite force retained only the force generated by the QMD as a

significant predictor of theoretical bite force ($P = 0.025$). All other variables had no predictive power due to their nonsignificant relationship to theoretical bite force.

Theoretical mean maximum bite force for anterior (20.0 ± 1.4 SEN) and posterior (77.4 ± 5 SEN) biting were greater than restrained anterior (14.2 ± 1.2 SEN, $P = 0.017$) and posterior (53.1 ± 5.2 SEN, $P = 0.014$) bite force. Anterior (17.3 ± 2.1 SEN) and posterior (64.6 ± 8.3 SEN) stimulated bite force were not different from either theoretical or restrained bite forces (Table 2).

Size removed bite force comparison among fishes indicated that *S. tiburo* has the second lowest mass-specific bite force of any fish studied to date irrespective of diet. Only *Etmopterus lucifer* (−1.18) and *Etmopterus spinax* (−2.47) have a lower mass-specific bite force than *S. tiburo* (−1.16). Furthermore, the absolute bite force of *S. tiburo* is among the lowest of any durophagous fish (Table 3).

Performance testing of prey

Carapace fracture trials of *C. sapidus* typically exhibited a steady increase in force until crack propagation began, followed by material failure (Fig. 3). Failure forces ranged from 30.0 to 490.0 N and exhibited linear relationships with all crab morphometrics (carapace length, width, depth, and crab mass) (Fig. 4). Failure force scaled isometrically relative to carapace width and length, and with positive allometry relative to carapace depth and crab mass (Table 4). Deeper heavier crabs require disproportionately more force to fracture than thinner lighter crabs.

For ease of comparison to dietary data, the scaling relationship of CL to failure force will be discussed further. The non-log transformed linear relationship between CL and failure force ($y = 11.08x - 308.08$, $P < 0.001$, $R^2 = 0.95$) was used to estimate the range of *C. sapidus* that sharks in

TABLE 1. Average force and mass \pm standard error of the four principle jaw adducting muscles in *S. tiburo*

Muscle	Force (N)	Mass (g)
Quadratmandibularis ventral	33.2 ± 2	1.37 ± 0.1
Quadratmandibularis dorsal	$17.4 \pm 0.8^*$	0.96 ± 0.1
Preorbitalis ventral	27.7 ± 1.4	2.43 ± 0.1
Preorbitalis dorsal	17.8 ± 1	1.35 ± 0.1

Data represent raw muscle values from ten *S. tiburo* (\bar{x} mass = 2440 g). * $P = 0.025$.

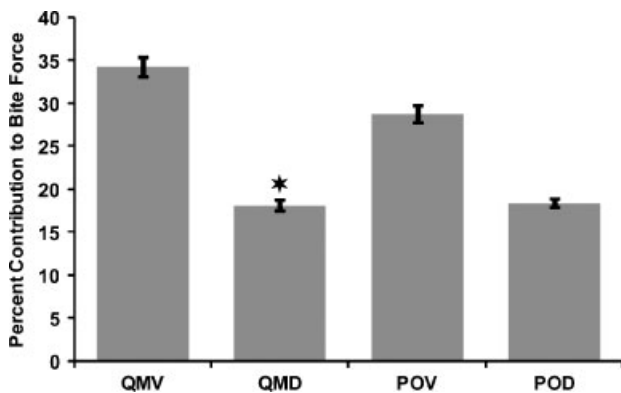


Fig. 2. Percent contribution of each feeding muscle to bite force. Average \pm standard error. Multiple linear regression showed that the only variable that predicted theoretical bite force was QMD ($P = 0.025$). All other muscles had no predictive power due to their nonlinear relationship to theoretical bite force.

TABLE 2. Average maximum bite force (N) \pm standard error for *S. tiburo* in each testing condition

Variable	Restrained	Stimulated	Theoretical
Anterior BF	$14.2 \pm 1.2^*$	17.3 ± 2.1	$20.0 \pm 1.4^*$
Posterior BF	$53.1 \pm 5.2^{**}$	64.6 ± 8.3	$77.4 \pm 5^{**}$
Max anterior BF	20.3	25.3	25.7
Max posterior BF	79.2	91.1	107.9

Maximum bite forces are the single largest force for any of the sharks. Restrained and theoretical testing conditions were significantly different for both anterior and posterior bite force. * $P = 0.017$; ** $P = 0.014$.

TABLE 3. Comparison of absolute bite force and size removed bite force residuals among fishes

Species	Common name	Mass (g)	Anterior Bite Force (N)	Residual Bite Force
<i>Chilomycterus schoepfi</i> ⁴	Striped burrfish	180	380	1.92
<i>Lachnolaimus maximus</i> ²	Hogfish	209	290	1.65
<i>Archosargus probatocephalus</i> ¹	Sheepshead	581	186	0.89
<i>Heptranchias perlo</i> ⁸	Sharpnose sevensgill	1614	245	0.68
<i>Carcharhinus limbatus</i> ^{6,8}	Blacktip shark	9833	423	0.35
<i>Heterodontus francisci</i> ^{5,8}	Horn shark	2948	206	0.30
<i>Hydrolagus colliei</i> ⁷	Spotted ratfish	870	106	0.30
<i>Halichoeres bivittatus</i> ²	Slippery dick	19	11	0.19
<i>Chiloscyllium plagiosum</i> ⁷	White-spotted bamboo shark	870	106	0.07
<i>Halichoeres garnoti</i> ²	Yellowhead wrasse	21	10	0.07
<i>Thalassoma bifasciatum</i> ²	Bluehead wrasse	7	5	0.00
<i>Sphyrna mokarran</i> ⁹	Great hammerhead	580598	2432	-0.04
<i>Negaprion brevirostris</i> ⁷	Lemon shark	1219	79	-0.06
<i>Carcharhinus leucas</i> ⁹	Bull shark	140341	1023	-0.11
<i>Halichoeres maculipinna</i> ²	Clown wrasse	18	5	-0.41
<i>Squalus acanthias</i> ³	Spiny dogfish	1065	19.6	-1.05
<i>Sphyrna tiburo</i>	Bonnethead shark	2240	25.7	-1.16
<i>Etmopterus lucifer</i> ⁸	Black belly lanternshark	48	3.1	-1.18
<i>Etmopterus spinax</i> ⁸	Velvet belly lanternshark	349.1	1.6	-2.47

Highlighted species have a predominately durophagous diet. Compiled from ¹Hernandez and Motta ('97); ²Clifton and Motta ('98); ³Huber and Motta (2004); ⁴Korff and Wainwright (2004); ⁵Huber et al. (2005, ⁶2006, ⁷2008, ⁸2009); ⁹Huber and Mara, unpublished data.

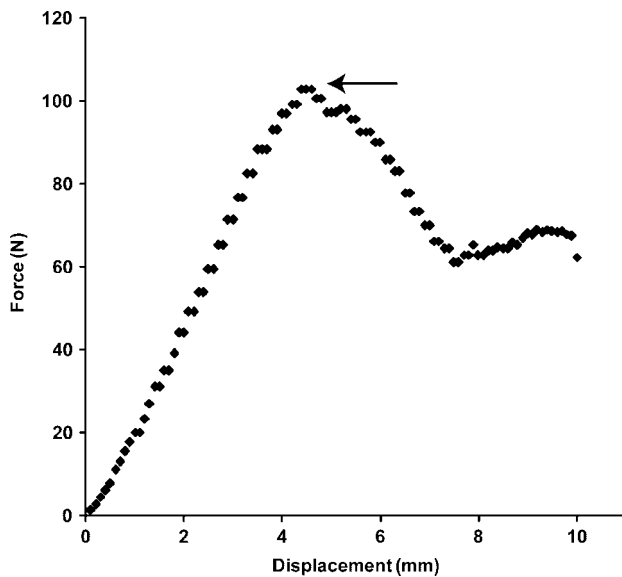


Fig. 3. Representative crushing force curve for a 40.5 mm CL, 67.5 g *C. sapidus* crushed at a loading rate of ~370 mm/sec using jaws removed from a 78.4 cm PCL *S. tiburo*. Force increases to a maximum where failure occurs (black arrow). N, Newtons.

our sample are capable of crushing. Based on the range of maximum posterior bite force from our analyses (50.3 N, 62.5 cm PCL–107.9 N, 60.0 cm PCL), the largest blue crab that *S. tiburo* of 55.2–68.7 cm PCL are capable of crushing range between 32.3 mm CL (62.8 mm CW) and 37.5 mm CL (73.9 mm CW) (Fig. 5).

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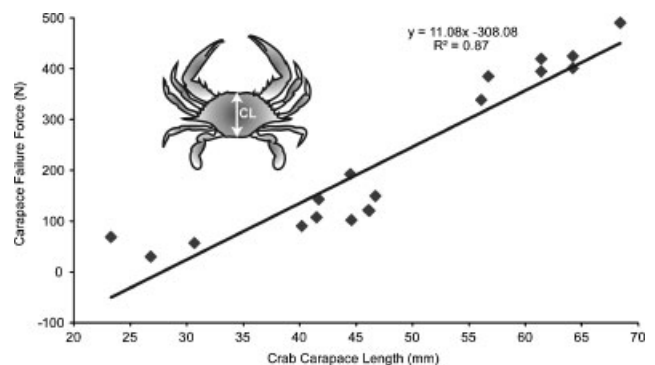


Fig. 4. Blue crab, *C. sapidus*, crushing results from fracture experiments on live crabs. Failure forces ranged from 30.0 to 490.0 N and exhibited a linear relationship to CL ($y = 11.07x - 308$, $R^2 = 0.87$). Scaling analyses indicated that failure force scaled isometrically with carapace width and length. However, failure force scaled with positive allometry with carapace depth and mass. N, Newtons.

DISCUSSION

Feeding biomechanics and bite force

The bonnethead shark *S. tiburo* differs from other durophagous chondrichthyan and teleost fishes by having relatively low bite force and a lack of: robust jaws, hypertrophied feeding muscles, and fused jaw symphysis (Summers, 2000; Summers et al., 2004; Huber et al., 2005). During closing, the lower jaw of *S. tiburo* acts as a third class lever system with relatively high force

TABLE 4. Scaling of log transformed crab carapace properties with respect to length, width, depth, and mass

Dependent variable	Independent variable	Isometric slope	Slope	y-Intercept	r ²	t (0.05(2), 16)	t critical
Failure force (N)	Carapace width	2	2.38	-2.28	0.87	1.63	2.12
	Carapace length	2	2.51	-1.95	0.86	2.03	2.12
	Carapace depth*	2	2.63	-1.48	0.83	2.12	2.12
	Crab mass*	0.67	0.87	0.71	0.85	2.22	2.12

Failure force scaled with positive allometry to carapace depth and crab mass.

*P ≤ 0.05.

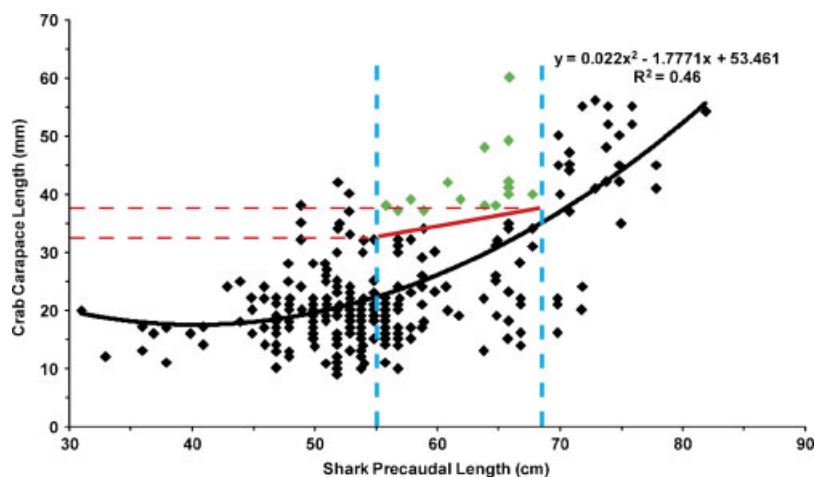


Fig. 5. Occurrence of blue crabs, *C. sapidus*, in the stomachs of *S. tiburo* from Cortés et al. ('96). Highlighted box (dashed blue vertical lines) indicates the size range of sharks used in this study. Red solid line is the range of maximum size crab *S. tiburo* of 55.2–68.7 cm PCL is capable of crushing (32.3–37.5 mm CL, dashed red lines) based on the maximum and minimum bite force. The majority of *C. sapidus* ingested by sharks can be crushed. However, crabs consumed that fall above the solid red line (~21%, green points) cannot theoretically be crushed by sharks of this size range and would require other processing methods.

efficiency at the back of the jaws (posterior mechanical advantage = 0.88). However, the mechanical advantage of the bonnethead shark is not particularly large as force amplifying second class lever systems, with mechanical advantages greater than 1.0, have been found in other durophagous fishes, including chondrichthyan (*H. francisci* and *Hydrolagus colliei*) and teleost oral and pharyngeal jaws (black drum, *Pogonias cromis* and striped burrfish, *Chilomycterus schoepfi*) (Korff and Wainwright, 2004; Huber et al., 2005; Grubich, 2005; Huber et al., 2008). In fact, even nondurophagous fishes, such as the euryphagous blacktip shark, *Carcharhinus limbatus* (post. MA = 1.09), have jaw adducting mechanisms with posterior mechanical advantage exceeding 1.0 (Huber et al., 2006). It should be noted that second class lever systems cause joint reaction forces to switch from compression to tension at the jaw joint resulting in greater chance for dislocation (Huber et al., 2008). The anterior mechanical advantage of *S. tiburo* (0.24) is comparable to those of numerous teleosts possessing low to

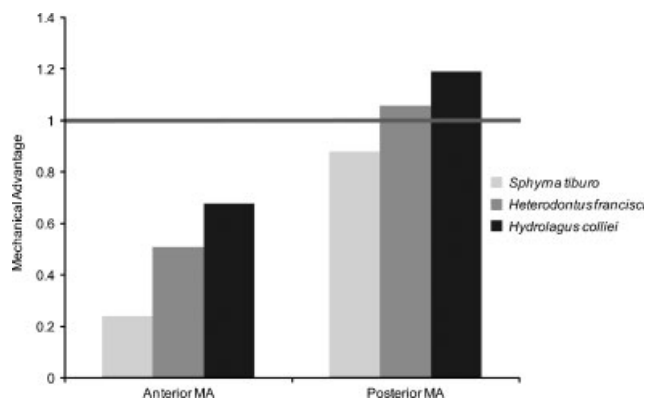


Fig. 6. Anterior and posterior mechanical advantages for durophagous chondrichthyans studied to date. Dark line at mechanical advantage = 1 is the point where the lever system switches from a third class lever system to a force amplifying second class lever system. *S. tiburo* consumes hard prey without the advantage of a second class lever system.

intermediate jaw leverage (wrasses (0.13–0.41) gray triggerfish *Balistes capriscus* (0.25–0.27)), and considerably lower than those of other durophagous fishes (horn (0.51), chimaera (0.68),

parrotfish (0.45–1.04), etc.) (Durie and Turingan, 2001; Wainwright et al., 2004; Westneat, 2004). Furthermore, when only durophagous chondrichthyans are considered, *S. tiburo* has lower anterior and posterior mechanical advantages (Fig. 6).

Mass-specific bite force measurements are an indicator of the relative feeding performance of vertebrates. Durophagous taxa, such as the striped burrfish, *C. schoepfi* (1.92, Table 3), typically have high mass-specific bite forces owing to relatively hypertrophied jaw adductors and high mechanical advantage of the feeding mechanism (Korff and Wainwright, 2004). Although *S. tiburo* has an almost exclusively durophagous diet, it surprisingly has the third lowest mass-specific bite force (–1.16) of any fish that has been studied. This includes soft prey specialists such as the spiny dogfish *Squalus acanthias* and nondurophagous piscivores such as the lemon shark *Negaprion brevirostris* and blacktip shark *C. limbatus* (Table 3) (Huber and Motta, 2004; Huber et al., 2005, 2008). The mass-specific bite force for *S. tiburo* places it above *E. lucifer* and *E. spinax*, both of which are deepwater lantern sharks whose diet consists of small fishes, squid, and some crustaceans (Compagno et al., 2005).

Although mass-specific bite force allows for comparison of relative ability among species, comparison of absolute bite force permits ecological predictions to be made about diet. Forces required to crush prey must be generated independent of predator mass, and absolute bite force values determine the ability to consume a particular prey item (Huber et al., 2008). When comparing among species of similar size, the absolute bite force of *S. tiburo* is comparable to soft prey specialists such as *S. acanthias*, and an order of magnitude smaller than other durophagous species such as *H. francisci* (Table 3).

Although *S. tiburo* consumes hard-shelled prey, it does so in a manner that is biomechanically different than previously described in chondrichthyans. Animals that specialize on fast, agile, and elusive prey have speed-efficient jaw closing systems with low mechanical advantages (Turingan et al., '95). Previous studies have shown a tradeoff between bite force and the ability to capture elusive prey (Herrel et al., 2002b). The bonnethead shark feeding mechanism appears to be a compromise between adductive speed and force. Furthermore, the jaw adducting musculature in *S. tiburo* can be active in a cyclical manner that could aid in fracturing prey exoskeletons

(Wilga and Motta, 2000). This shark captures small, elusive blue crabs by ram feeding with a wide gape and fast jaw closure (Wilga and Motta, 2000) yet is constrained to smaller crabs by its limited bite force (see below).

Model verification

Numerous methods for measuring bite force have been employed (Anderson et al., 2008), although few have been quantitatively compared (Huber and Motta, 2004; Huber et al., 2005). Previous studies have shown some methods of recording bite force are accurate predictors of maximum tetanic bite force, whereas others are less so (Huber et al., 2005; Herrel et al., 2008). In previous studies of elasmobranch bite force, it has been shown that, in some cases, theoretically determined bite force accurately predicts those produced during in vivo voluntary testing (Huber et al., 2005). Furthermore, in bats, theoretical morphological models of bite force accurately predict bite force capacity (Herrel et al., 2008). However, other factors not accounted for in our model (e.g., inertial fluid forces, resistance of body tissues) may influence the accuracy of our theoretical predictions (see Van Wassenbergh et al., 2005).

Our data show that 55.2–68.7 cm PCL bonnethead sharks are capable of producing a maximum bite force of 107.9 N at the posterior molariform teeth (Table 2). In bonnethead sharks no differences were found between restrained and stimulated or stimulated and theoretical testing conditions. However, both anterior and posterior theoretical bite forces (20.0 and 77.4 N, respectively) were greater than restrained bite force (14.2 and 53.1 N, respectively). Both theoretical and stimulated testing conditions remove behavioral motivation as a potential variable. However, during restrained biting the animal can choose to perform less than maximally. Behavioral motivation, or lack thereof, can result in less than maximal performance (Irschick, 2002). During our testing we noted that restrained testing conditions elicited a reluctant bite from *S. tiburo*; the animal's teeth had to be prodded numerous times to elicit a bite. Furthermore, *S. tiburo* did not voluntarily bite the force transducer even when presented with food. These results are contrary to that of the horn shark, *H. francisci*, where the sharks vigorously bit the offered force gauge, and restrained bite force was the largest among the three testing conditions (Huber et al., 2005). In the bonnethead shark, theoretical and

stimulated bite force appear to be good indicators or performance, whereas voluntary bite force, under the conditions utilized here, is under representative of its biting capabilities.

Ecological performance

Although high bite force may facilitate a larger range of potential prey, it is often associated with dietary specialization because increased performance allows exploitation of prey resources unavailable to other species or available to only a small number of species (Hernandez and Motta, '97; Berumen and Pratchett, 2008). Thus, access to durophagous prey via high bite force has been shown to potentially reduce interspecific competition in fishes (Wainwright, '88; Grubich, 2005), lizards (Herrel et al., 2001b), and mammals (Christiansen and Wroe, 2007).

That bite force can determine diet is well known (Herrel et al., 2001b; Aguirre et al., 2003; Korff and Wainwright, 2004; Grubich, 2005). However, few studies relate bite force to characteristics of known prey species (Herrel et al., 2001b; Aguirre et al., 2003; Kolmann and Huber, 2009). In South Florida, the diet of *S. tiburo* consists of almost exclusively blue crabs and may represent specialization on prey that is unavailable to other nondurophagous species. However, maximum bite force imposes limits on the size of its preferred prey with the maximum size blue crab consumed by bonnethead sharks in the size range studied here to ~60.2 mm CL (Cortés et al., '96). Blue crabs reportedly reach a maximum size of 88.0 mm CL, leaving the upper 32% of the blue crab population unutilized by *S. tiburo* of this size range (Atar and Seçer, 2003). When dietary data is compared with maximum bite force, 57/72 crabs (~79%) consumed by bonnethead sharks in the size range sampled here are able to be crushed, indicating that the majority of crabs consumed by *S. tiburo* fall well below their performance limits (Fig. 5). Therefore, our data indicate that *S. tiburo* may be selecting blue crabs, in part based on some metric of size that relates to their ability to crush and consume them. Crabs falling outside of their performance limits would require dismemberment before consumption by lateral head shaking or other manipulation (Wilga and Motta, 2000; Matott et al., 2005). This is supported by many blue crabs found in the stomachs of *S. tiburo* being dismembered (E. Cortés, Personal Communication; K. R. Mara, Personal Observation). Behavior and prey properties could also help explain the

discrepancy between performance and diet. Electromyography data suggests that *S. tiburo* is capable of cyclical activity in the jaw adducting musculature which could aid in fracturing the carapace (Wilga and Motta, 2000). However, no study has quantitatively investigated this cyclical activity. Furthermore, individual variation in failure force could partially explain the 21% of crabs in the diet falling above the crushing ability of *S. tiburo*. Our results provide an upper estimate of the force *S. tiburo* must produce to crush blue crabs and further data is required to address the roles of behavioral and variation in prey properties play in durophagy in *S. tiburo*.

Durophagy is often assumed to relate directly to mechanical function, however an animal can maintain a durophagous diet without extensive modification of the feeding apparatus. It is known that the gastric pH of elasmobranchs can reach values as low as 0.4 (Papastamatiou and Lowe, 2005; Papastamatiou et al., 2007). Furthermore, chitinolytic enzyme activity has been previously demonstrated in elasmobranchs (Lindsay, '84). If bonnethead sharks have similar gastric pH values or chitinolytic enzymes, the hard shell of their prey can be broken down chemically by the stomach rather than mechanically by the feeding apparatus. In this instance durophagy is established through the means of physiological modifications rather than morphological modifications.

The apparent correlation between bite force and diet could also be explained by gape and processing time limitations. Independent of bite force, larger items may not be consumed because of the physical dimensions of the gape or because of the adductor muscles being stretched beyond their optimal range (Kiltie, '82; De Schepper et al., 2008). Furthermore, many studies have demonstrated an increase in processing time with increased prey size (Verwajen et al., 2002). The increased processing times required to consume very large crabs could make these crabs less cost effective to consume than smaller crabs with lower processing times. In addition large blue crabs may generate large crushing forces relative to other crabs which could result in serious injury to the cephalofoil, leading *S. tiburo* to avoid potentially dangerous large blue crabs (Schenk and Wainwright, 2001). However, the ability of *S. tiburo* to process large prey remains to be tested.

S. tiburo is unlike other durophagous chondrichthyan species. It has relatively low bite force and lacks hypertrophy of the feeding muscles and jaws. Furthermore, its posterior mechanical ad-

vantage is considerably lower than other species. In fact, the manner in which *S. tiburo* consumes hard prey is biomechanically different than previously described in chondrichthyans. When the bonnethead shark is compared with a broad range of chondrichthyan and teleost species, its mass-specific bite force is the second lowest of any species studied to date in spite of its predominantly durophagous diet. Bite force modeling is an accurate predictor of maximum biting capacities in *S. tiburo*. However, behavioral motivation was found to play a large role in in vivo bite force measurements. The bite force of *S. tiburo* constrains the size of its preferred prey, blue crabs, that it can consume. However, crabs that are larger than the maximum crushable size are consumed by *S. tiburo*. This independent evolution of durophagy without the morphological modifications seen in other durophagous taxa, indicates that durophagy can be accomplished in the absence of high mechanical advantage and high bite force.

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