

Correlates of bite force in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*

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Abstract Bite force is a whole-animal performance measurement that can potentially provide valuable information regarding the biology of an organism. However, there have been few studies that directly measured bite force in sharks. We examined involuntary (obtained using jaw musculature stimulation) and voluntary bite force in Atlantic sharpnose sharks, *Rhizoprionodon terraenovae*, and considered the effects of size, sex, season, gape, and capture method on bite force in that species. Additionally, we considered the relationship between bite force and general head measurements and the position along the jaws used to apply the bite (anterior vs. posterior). We found that there were no significant differences in voluntary or involuntary bite force and no significant differences in bite force between sexes. Atlantic sharpnose sharks, ranging between 55.1 and 105.5 cm total length, had an anterior bite force between 4.4 and 60.2 Newtons (N) and a posterior force between 20.9 and 102.8 N. Anterior bite force was found to be lowest in the summer months and highest in the spring and fall and paralleled seasonal changes in shark condition as evidenced by hepato-somatic index. As gape increased, the anterior bite force increased, with the greatest force found between 60 and 80 % of maximum gape. A best-fit multiple regression using jaw length, mouth width, head length and head width explained 80.9 % of the variation in anterior bite force. Longline-captured Atlantic sharpnose

sharks produced significantly lower bite force when compared to hook-and-line-captured animals. Using published data and data from this study, we examined the body size-to-bite force relationship for nine shark species which provided a bite-force estimate of 123,876–179,219 N for the extinct megatooth shark, *Carcharodon megalodon*.

Introduction

Interspecific comparisons of jaw-cranial form and function inform our understanding of the evolution of vertebrate musculoskeletal systems (Sakamoto et al. 2010) and species community assemblages (Dayan et al. 2005). If cranial architecture is evolutionarily labile, for example in response to selection to take advantage of novel dietary items, adaptation in the form of dietary specialization can occur (e.g., in slender-snouted crocodilians; Erickson et al. 2012). However, if the size and shape of skulls is constrained by preexisting adaptation to diet, locomotion or social system, tooth structure, post-cranial musculoskeletal anatomy and/or foraging behavior may change over time such that some species may occupy unique feeding niches (Mori and Vincent 2008). Grubich et al. (2008) found that the jaw mechanics of the barracuda, *Sphyrna barracuda*, only predicted moderate force production, but coupled with razor-sharp teeth, barracudas are able to produce sufficient pressure to slice prey. In another example of compensation, the komodo dragon, *Varanus komodoensis*, feeds using bites supplemented by a variety of pulling forces including back-pedaling and pressing prey against a substrate to compensate for a relatively low bite force (D'Amore et al. 2011). The estimated force generated by the jaws of vertebrates is often used to indicate the likely foraging abilities of extinct taxa, as well as of extant species that are rare

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or difficult to observe (Wroe et al. 2005). Head width or head size has been found to be a significant predictor of bite-force production (e.g., Herrel et al. 2005; Lappin et al. 2006) because a wider or larger head can accommodate greater jaw muscle mass and, in turn, capacity for greater cross-sectional area. Raadsheer et al. (1999) found that in humans the physiological cross-sectional area of the masseter muscle played a greater role in bite-force magnitude than did other craniofacial factors. Bats have greater bite force than one would predict relative to their body sizes and tend to have shorter rostra and mandibles, higher skulls and a larger amount of muscle fibers attached to each tendon (Nogueira et al. 2009). Because measurements of relevant cranial variables can be readily collected from specimens in museums (e.g., Thomason et al. 1990; Thomason 1991; Wroe et al. 2005), bite force is typically estimated by mathematically modeling the functional anatomy of jaws (e.g., Thomason 1991; Wroe et al. 2005) rather than measuring bite force empirically in vivo (e.g., Anderson et al. 2008; Lappin and Jones 2014). Theoretical modeling studies of shark bite force have included Huber and Motta (2004), Huber et al. (2006, 2008, 2009), Wroe et al. (2008), Ferrara et al. (2011) and Habegger et al. (2012). Such modeling studies have been particularly insightful in comparative studies of mammalian taxa to explain, for example, the relative strength of adaptation and phylogenetic constraint in determining species bite force (Sakamoto et al. 2010).

Unfortunately, model-based estimates of bite force ignore how non-gustatory functions of jaws, proximate physiological factors, and ontogenetic and seasonal shifts in prey may affect the adaptive interpretation of bite force. Jaws are not just used for feeding; they are important in sexual selection (Husak et al. 2005). Biting is often used in intrasexual competition; the large heads that males of the gecko, *Hemidactylus frenatus*, needed for fighting are so important to reproductive success, for example, that males must accept a trade-off in their ability to flee from predators (Cameron et al. 2013). In addition, a variety of taxa including some male sharks, salamanders, mammals and birds bite their mates before or during copulation. Bite force can be dependent on energetic state and behavioral motivation (reviewed by Anderson et al. 2008), is affected by testosterone levels in some species (Husak et al. 2007) but not in others (Huyghe et al. 2010), and can be age-dependent in a manner independent of muscle size (Chazeau et al. 2012). Lappin and Husack (2005) found that bite force is a better predictor of mating success than either body length or body weight. The proximate effects of energetic condition and endocrine levels are likely seasonally dependent. Bite force may also vary with seasonal or ontogenetic changes in diet, prey hardness, the gape size necessary to feed on diet items of different sizes (Williams et al. 2009) and the position along the jaws used to deliver the bite (Lappin and

Jones 2014). In most animals, large gapes correlate with less force because the muscle fibers are extended beyond their optimal lengths for force production (Dumont and Herrel 2003).

The availability of pressure cell transducers (Anderson et al. 2008; Lappin and Jones 2014) has allowed investigators to collect in vivo bite-force measurements and observations of feeding behavior to complement cranio-muscular force modeling (Mori and Vincent 2008). However, only two studies (Huber et al. 2005; Mara et al. 2009) were identified by Lappin and Jones (2014), among the 99 vertebrate in vivo bite-force studies they reviewed, wherein bite-force performance was reliably quantified. It is surprising that the sharks, a group notorious for its bites, have rarely had their bite forces measured in vivo and the proximate factors affecting bite force are virtually unknown.

The abundance and ease of capture of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, have previously provided baseline data (Hoffmayer and Parsons 2003; Parsons and Hoffmayer 2005) that make the species particularly amenable to the experimental investigation of methodological, anatomical and physiological impacts on bite-force measurements. The Gulf of Mexico harbors about 65 species of shark, where they are exposed to both natural (e.g., changes in water temperature and oxygen availability) and anthropogenic (e.g., pollutants and fisheries) stressors.

Our objectives for this study were to examine the bite force of the Atlantic sharpnose shark to (1) determine whether voluntary bites and electrically induced involuntary bites provide equivalent measures of bite force, (2) examine the influence of head/jaw morphometrics on bite force, (3) compare anterior and posterior bite force across the entire size range, (4) assess the effect of gape size on bite force and (5) identify size, seasonal, stress and sex effects on force generation. Additionally, we determined the relationship between bite force and body size across shark species using a combination of our results and those from other species from the literature.

Materials and methods

Sharks were collected by hook-and-line and longline off the coast of Mississippi in the Mississippi Sound and surrounding waters. Longlining was conducted in offshore waters south of the Mississippi coast with assistance from the Gulf Coast Research Laboratory, the National Marine Fisheries Service, and the Dauphin Island Research Laboratory, with sampling conducted during the summer and fall months from early morning to late evening. Longline fishing lasted approximately 2 h, 1 h for the hooks to “fish” and another for retrieval. Collecting via hook-and-line was

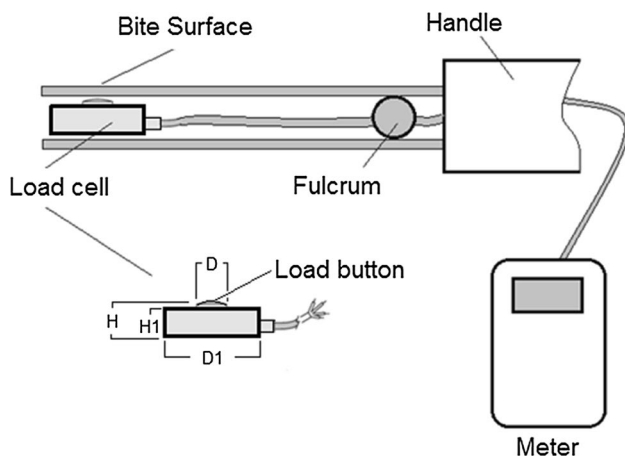


Fig. 1 A diagram of the bite-force meter designed for this study. A force transducer placed between two plates provided a biting surface for bite-force measurement. Metal plates that form the biting surface measure 8.5×2.5 cm ($D = 5$ mm, $D1 = 19$ mm, $H = 6$ mm and $H1 = 5$ mm)

accomplished using hooks typically baited with cut fish (*Brevoortia sp.*), squid (*Loligo sp.*) or whole cigar minnows (*Decapterus punctatus*). Sharks taken on hook-and-line were landed and their bite force measured within 3–5 min of capture.

A bite-force gauge (Fig. 1) constructed for this project was used to measure force at both the anterior and posterior positions in the jaw. The bite-force gauge was constructed from a force transducer (Smart Sensor Indicator Load Cell Meter, Precision Measurements Systems) placed between two hinged aluminum plates inserted into a polyvinyl chloride handle. The plates were 8.5×2.4 cm and were inserted into a 20-cm-long handle. The force transducer was attached to the plate using epoxy. The aluminum plates were covered with two layers of vinyl tape to soften the bite surface because the biting surface may be important in voluntary bites (Lappin and Jones 2014). Force applied to the plates was recorded by a load-cell meter. Laboratory calibration of the bite-force gauge revealed the gauge provided an accuracy of ± 0.15 %. While on the boat, the shark was held as loosely as possible to induce a voluntary bite but firm enough to prevent lateral movement during bite-force measurements. The bite-force gauge was placed at the anterior-most position in the jaw for anterior bite-force measurement, and at the corner of the jaw (near the articulation of the Meckel's and palatoquadrate cartilages) for posterior measurements. To determine involuntary bite force, we used a *TENs Muscle Stimulator* set to deliver 100 ± 5 volts (V) at a current of 20 microamperes (μ A), which induced tetanus in the adductor muscles. This was accomplished by placing an electrode pad on either side of the head on the skin surface. The pads, placed posterior

to the eye, were near the dorsal insertion of the adductor mandibulae muscle. Similar to voluntary force determination, the bite-force gauge was presented at the front of the jaw for anterior and the corner of the jaw for posterior force measurement before each stimulation. Prior to bite stimulation, the jaws were positioned directly over the force transducer. For each involuntary bite-force measurement, anterior or posterior, an individual shark received only three electrical stimuli. Only the largest of the three measurements was used for analysis. Use of a single individual for a single bite-force measurement was necessary to reduce the possibility of muscle fatigue. Individual sharks were not used repeatedly for multiple experimental comparisons (e.g., different individuals were used to compare voluntary and involuntary bite force, but also not used for comparing anterior and posterior transducer placement).

As an indicator of shark condition, the hepato-somatic index (HSI) was calculated using the equation:

$$\text{HSI} = (\text{liver weight/body weight}) * 100$$

with liver and body weight measured in grams (Hoffmayer et al. 2006).

To examine the bite-force/gape relationship, the height of the bite-force meter transducer was adjusted by placing premeasured spacers over the transducer. The spacers consisted of aluminum blocks wrapped in two layers of vinyl tape. These materials were the same as those used for bite-force meter construction. After bite force was measured, maximum gape, total length, mouth width (MW), jaw length (JL), head width (HW), head height (HH), head length (HL), sex and maturity were recorded. The maximum gape of each individual was measured as the distance between the symphysis of Meckel's cartilages and that of the palatoquadrate cartilages after opening the mouth carefully to its maximum by hand. Spacer placement provided bite-force measurements at gapes varying from 30 to 95 % of the animal's maximum gape, depending upon animal size.

Total length was measured with the caudal fin in a natural position as a straight line measurement along the body axis from the tip of the snout to a line perpendicular to the tip of the caudal fin. Mouth width was measured as the distance between the corners of the mouth where Meckel's cartilage articulates with the palatoquadrate. Jaw length was measured perpendicularly from the above articulation to the tip of the jaw. Head width was measured as the distance across the head between the first gill slits. Head height was measured at the first gill slit as the vertical distance from the top to the bottom of the head and head length was measured from the tip of the snout to the first gill slit.

Data analysis was accomplished using SPSS 22.0 (IBM Corp., Armonk, NY) and Microsoft EXCEL spread

sheet add-ins, and all values were considered significant at $p \leq 0.05$. A Shapiro–Wilk Test was used for normality testing. A nonparametric Kruskal–Wallis ANOVA on ranks was used to detect differences in the voluntary and involuntary methods of determining anterior bite force. We likewise used Kruskal–Wallis to examine the effect of season on anterior bite force followed by Mann–Whitney U post hoc testing. An ANOVA was used to examine the effect of season on hepato-somatic index (HSI) followed by Tukey’s post hoc. An ANCOVA was used to determine whether there was a significant difference between the slopes of the regression lines for anterior and posterior bite force regressed against total length. We used linear regression to describe the relationship between head/jaw morphometrics and bite force. Additionally, we used best-fit multiple regression to construct a model that provided the best predictor of bite force using head morphometrics. To investigate the effect of gape on bite force, we expressed gape as a percentage of maximum gape, grouped into categories (30–40, 40–50 %, etc.) and used Kruskal–Wallis to analyze sharks in the 75–85 cm TL size class. A significant Kruskal–Wallis test was followed by Mann–Whitney U post hoc testing. Because shark size availability varied with season, it was not possible to conduct a single comprehensive multivariate analysis that controlled for body size effects. Finally, to examine the relationship between size and bite force for various shark species, we obtained bite force and total length from the literature for nine different species of adult sharks, in addition to data from this paper, and used a polynomial regression to describe the relationship. This regression was then used to estimate the bite force for the extinct megatooth shark, *Carcharodon megalodon*, of maximum estimated size.

Results

Among adult Atlantic sharpnose sharks (85.0–108.3 cm, $\bar{X} = 91.5 \pm 1.1$ SE), there were no differences (Kruskal–Wallis, $H(1, 103) = 4.461$, $p = 0.107$) between anterior voluntary and involuntary bite force. Involuntary, anterior bite force averaged 27.2 Newtons (N) (± 1.09 SE, $N = 81$), and voluntary averaged 23.7 N (± 3.35 SE, $N = 22$). We examined anterior and posterior bite force across the full size range of Atlantic sharpnose sharks. Anterior bite force ranged from 4.4 to 60.2 N and posterior bite force from 20.9 to 102.8 N. When anterior and posterior bite forces were regressed against total length, a significant difference (ANCOVA: $F(1,96) = 80.21$, $p < 0.0001$, Fig. 2) in the slopes of the regression lines was found. Because anterior, involuntary bite force was logistically easier to obtain, we used this measurement in all subsequent studies.

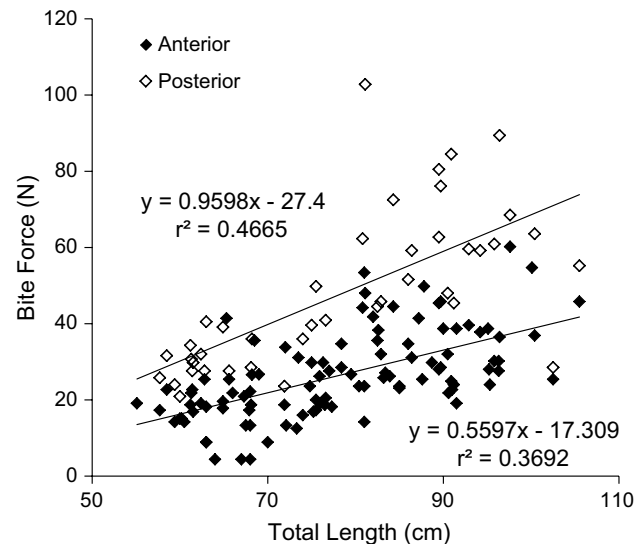


Fig. 2 Comparisons of anterior and posterior bite force for Atlantic sharpnose sharks in relation to total length (cm) revealing differing slopes (ANCOVA: $F(1,96) = 80.21$, $p < 0.0001$) of the regressions

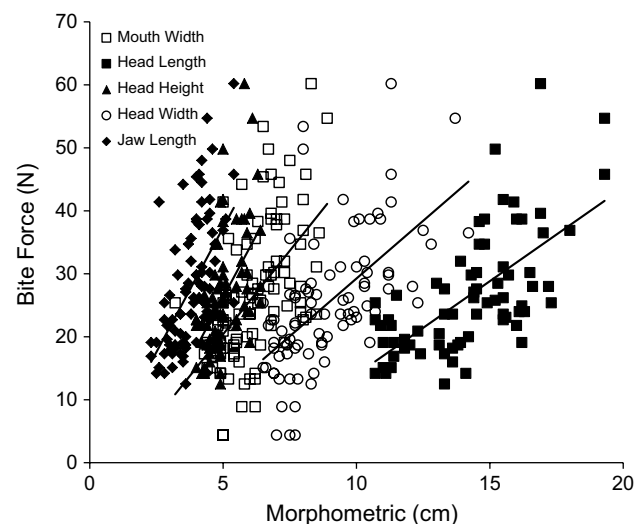


Fig. 3 Linear regressions of various head morphometrics against anterior bite force. The equations and correlation coefficients are as follows: bite force = $7.71(\text{jaw length}) + 3.44$, $r^2 = 0.695$; bite force = $3.50(\text{head length}) - 22.4$, $r^2 = 0.604$; bite force = $3.614(\text{head width}) - 6.06$, $r^2 = 0.487$; bite force = $5.47(\text{mouth width}) - 4.29$, $r^2 = 0.428$; bite force = $5.27(\text{head height}) - 3.54$, $r^2 = 0.352$

In considering head/jaw morphometrics, all measures provided a significant fit to bite-force data (Fig. 3). However, best-fit multiple regression analysis resulted in the equation:

$$\text{BF} = \text{JL}(-6.98) + \text{MW}(11.52) + \text{HL}(2.90) + \text{HW}(-3.62) - 27.55$$

where BF = bite force in Newtons, and JL, MW, HL and HW are jaw length, mouth width, head length and head width, respectively, in centimeters. This regression ($df = 4, 21$; $F = 18.0$, $p < 0.0001$) explained 80.9 % of the variation in bite force. Head height, when included in the regression, did not improve the correlation coefficient and was excluded from the regression equation.

We assessed the effect of gape on bite force (Fig. 4) in sharks collected during summer months (to eliminate seasonal effects) and those ranging from 75 to 85 cm TL (to eliminate size effects). There was a significant difference (Kruskal–Wallis: $H(5, 44) = 21.13$, $p < 0.001$) in bite force observed across gape with a peak in bite force observed at 60–70 % of maximum gape. Mann–Whitney U (two-tailed) post hoc testing revealed that, in general, gapes less than 60 % were different from those greater (Fig. 4).

We examined the bite force and HSI of sharks during spring, summer and fall. When sharks ranging in size from 85.1 to 105.5 cm were examined, there was a significant difference (Kruskal–Wallis: $H(2, 53) = 6.17$, $p = 0.0129$) in anterior bite force between seasons. Post hoc testing revealed a difference in bite force between spring and summer (Mann–Whitney $U = 88.5$; $N_1 = 12$, $N_2 = 32$; $p = 0.0066$; two-tailed) and between summer and fall (Mann–Whitney $U = 107.5$; $N_1 = 32$, $N_2 = 12$; $p = 0.026$; two-tailed), but not between spring and fall (Fig. 5). An ANOVA revealed an effect of season ($F(2,16) = 10.758$, $p < 0.001$) on HSI with fall ($\bar{X} = 4.9\% \pm 0.7$ SE, $N = 7$) being highest and summer the lowest ($\bar{X} = 3.7\% \pm 0.54$ SE, $N = 9$). Tukey's post hoc revealed a significant difference in HSI between fall and summer, and spring and summer, but not between fall and spring (Fig. 5).

We compared the bite force of sharks captured by hook-and-line with those captured using longline. Since longlining typically takes larger specimens, only sharks ranging in size from 82.5 to 105.5 cm total length were used for comparison. We observed a difference (Student's T test: $t_{(66)} = -6.80$, $p < 0.0001$) in anterior bite force when hook-and-line-captured sharks (mean bite force = $33.5 \text{ N} \pm 1.48$ SE, $N = 41$) were compared against longline-captured sharks (mean bite force = $11.85 \text{ N} \pm 2.9$ SE, $N = 27$). Additionally, only a single shark captured on hook-and-line produced a bite force below 20 N, whereas 70 % of longline-captured sharks produced a bite force of 10 N or less. Because of these differences, longline-captured sharks were excluded from all analyses.

We compared bite force between similarly sized (78.4–105.5 cm, mean = 89.2 ± 1.3 SE) male ($n = 23$) and female ($n = 11$) Atlantic sharpnose sharks captured in spring and winter (to eliminate seasonal effects) and found no difference (Student's T test: $t_{(32)} = 1.0059$, $p = 0.32$). We likewise compared the ratio of mouth width to total

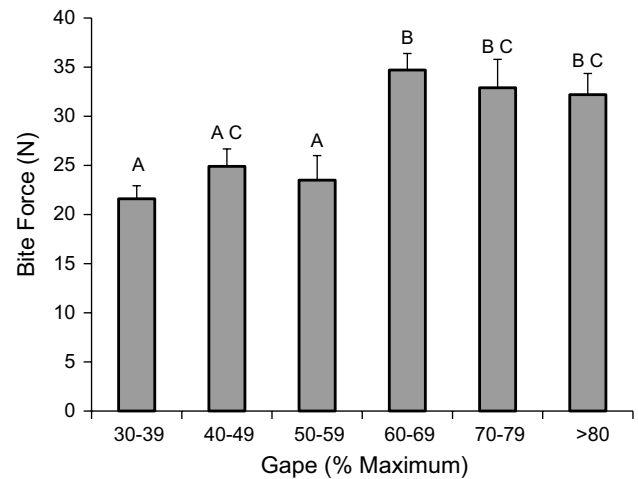


Fig. 4 Anterior bite force for Atlantic sharpnose sharks by percentage of maximum gape for sharks 75.0–85.0 cm TL captured in summer months. Means and standard errors are shown. Letters not in common indicate values that are significantly ($p < 0.05$) different from each other

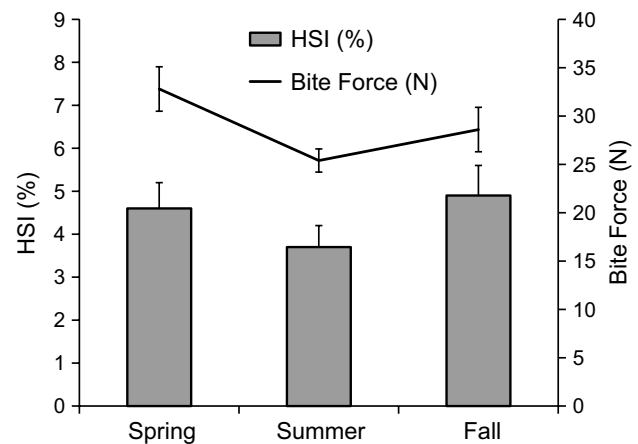


Fig. 5 Mean anterior bite force and hepato-somatic index for Atlantic sharpnose sharks by season. Vertical lines are standard errors

length and found that females larger than 85 cm TL had larger mouth widths than males of similar size (Kruskal–Wallis: $H(28, 58) = 4.85$, $p = 0.028$). Female ratios ranged from 0.072 to 0.11 and males from 0.071 to 0.092 (Fig. 6).

Discussion

Involuntary/voluntary bite force

The literature on bite force is replete with different methodologies and contexts for measurement. The diversity of methodological approaches makes it difficult to know whether interspecific comparisons are valid. The advantages

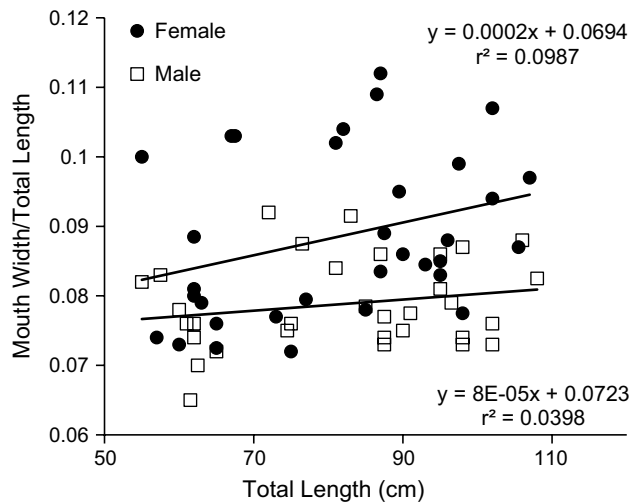


Fig. 6 Ratio of mouth width to total length for male and female Atlantic sharpnose sharks

of using electrical stimulation to induce an involuntary muscle tetanus are that the investigator is not dependent on the study subject's motivation to bite (Freeman and Lemen 2008), and the measurement location can be carefully standardized between individual subjects. Even electrical stimulation studies, however, vary in the method of stimulation. For example, Dechow and Carlson (1983) used unipolar needle electrodes inserted unilaterally into the masseter muscle of monkeys and found that it took between 20 and 60 V at multiple stimuli to induce a tetanus plateau. Alternatively, superficial electrode placement, identical to the method used in this study, can be used to induce muscle tetanus in bite-force studies (Manns et al. 1979; Hylander and Johnson 1993) and is perhaps more amenable to data collection under field conditions. Although there was no difference between bite force obtained using voluntary and involuntary methods, mean voluntary force was generally lower. One observation relevant to this discussion is that although mean voluntary bite force was lowest, there were sharks that voluntarily produced bite forces as large as those measured involuntarily. This suggests that the problem with voluntary bite-force measurement in this species and the low values obtained might be one of motivation, a problem faced by many researchers in this field (Anderson et al. 2008). Upon reviewing videotape of our voluntary bite-force measurement efforts, we observed that, rather than bite down while being handled, the Atlantic sharpnose shark is more likely to open its mouth wide and move the head and body in a lateral motion, seemingly in an attempt to inflict a slashing wound, and was successful on one occasion. This behavior could make repeatable voluntary bite-force measurement problematic in this species and reinforces the use of involuntary measurements.

Involuntary stimulation using external electrodes may provide a reproducible method for future in vivo bite-force studies, at least in small sharks. While bite-force estimates from theoretical models of mechanics can be insightful, shark bite-force measurements made in the field can provide information that may not be obtainable by other means.

Morphometrics and anterior/posterior bite force

Morphometric analysis indicated that jaw length, head length, and head width were the best predictors of bite force in Atlantic sharpnose sharks. Similarly, best-fit multiple regression analysis revealed that head height alone failed to improve the correlation coefficient and was excluded from the equation. Huber et al. (2006) found that blacktip shark head width was the best predictive feature of bite force, and this was also asserted by Habegger et al. (2012) according to theoretical predictions for bull sharks. This increase in the width of the head may reflect hypertrophy of the jaw muscles, thus enabling greater force production. Huber et al. (2006) also found that prebranchial length of the head was a significant predictor of force production. In a similar fashion, we found that head length in the Atlantic sharpnose shark was the single best predictor of bite force explaining 60 % of the variation. However, a multiple regression that included all morphometrics except head height described more (80.9 %) of the variation in bite force.

Sharks jaws are third-class lever systems, and it is not surprising that jaw length and head length were the two best single predictors. By increasing the length of the out-lever, a decrease in the mechanical advantage at the anterior-most point of the system occurs with a corresponding decrease in force production (Lappin and Jones 2014; Groning et al. 2013). However, this increase in length can result in an increase in closing velocity. This likewise explains the significant difference in the slopes of the regression lines of anterior and posterior bite force (Fig. 3). As sharks increase in size, jaw muscle mass increases, which increases both anterior and posterior bite force, but the increase in jaw length acts to decrease anterior bite force. From a biological perspective, all things being equal, a longer jaw results in a trade-off between force production and gape. A larger gape would accommodate larger prey items, but without changes in jaw musculature, i.e., increased muscle mass or changes in muscle insertion, the accompanying reduction in force production could reduce a predators' effectiveness in prey capture or manipulation. Relevant to this discussion is the ontogenetic shift in diet that has been documented in Atlantic sharpnose sharks. Smaller individuals consume a larger percentage of invertebrate prey with adult Atlantic sharpnose sharks demonstrating a shift to potentially more elusive teleost prey as adults (Hoffmayer and Parsons 2003).

When the ratios of mouth width to body length were compared between males and females, females were found to have significantly larger mouths at body lengths larger than 75 cm. This was an interesting observation since a difference in bite force between males and females was not detected. Obviously, an increase in mouth width would allow female Atlantic sharpnose sharks to exploit larger prey items. Adult females spend almost the entirety of their lives in deeper offshore waters, while adult males migrate inshore and offshore with season (Parsons and Hoffmayer 2005). Perhaps the ability to process larger prey items provides female sharks with a selective advantage in the highly competitive offshore environment.

Gape and bite force

For Atlantic sharpnose sharks, the highest bite force generated was at 60–70 % of the maximum gape. Although not presented in this study, a similar nonsignificant pattern showing a bite force peak at approximately 70 % of maximum gape was also observed for the smallest and largest sharks collected. Similar results have been observed in the great white, *Carcharodon carcharias*, and sandtiger, *Carcharias taurus*, sharks with maximum anterior force produced at a gape angle of 45°–55° (Ferrara et al. 2011). In the same study, Ferrara et al. (2011) found that in white and sand tiger sharks, as gape increased, the angle of the muscles' pinnation to the jaw reached a more optimal configuration to produce higher forces. The optimum gape reported in this study is higher than the optima that have been observed in studies on mammals perhaps due to differences in jaw mechanics in this group. In the deer mouse, *Peromyscus maniculatus*, and northern grasshopper mouse, *Onychomys leucogaster*, maximum force was produced around 40 % of maximum gape (Williams et al. 2009), and in seven species of bats there was a rapid decrease in force with an increasing gape angle (Dumont and Herrel 2003).

A bite-force optimum at a large gape is unusual among vertebrates and may be related to the feeding ecology of the Atlantic sharpnose shark and perhaps sharks in general. Atlantic sharpnose sharks, like many other shark species, are ram feeders which attack prey with mouths open to some degree. To be effective predators, a larger force produced at wider gapes would be beneficial for admitting the largest possible prey item that could be successfully handled. However, it is generally recognized that sharks have low bite-force production when compared to other similarly sized vertebrate groups (Wroe et al. 2008). Some sharks are known to attack prey using burst speeds, with mouth agape and biting simultaneously. This ram feeding strategy takes advantage of

the sharks' forward momentum (Wilga et al. 2007) and would compensate for the relatively low bite force that is observed in sharks. This could work in conjunction with a bite-force optimum at an unusually large gape to produce an effective predator.

Stress and seasonal effects on bite force

There have been relatively few studies that have examined bite force and its relation to stress in organisms. Freeman and Lemen (2008) found, by accident, that stressed, white-footed mice had a 31 % lower bite force than non-stressed individuals. Huber et al. (2008) noted an 85 % decrease in the spotted ratfish, *Hydrolagus colliei*, and a 50 % decrease in spiny dogfish, *Squalus acanthias*, bite force due to tetanic muscle fatigue.

Body condition and the physiological response to applied stressors vary seasonally in the Atlantic sharpnose shark. Parsons and Hoffmayer (2005) used Fulton's condition factor to document a decline in Atlantic sharpnose shark condition during summer with minimum values reported in July. Similarly, Hoffmayer et al. (2006) observed parallel changes in hepato-somatic index with the largest livers recorded in spring and fall and the lowest during summer. Additionally, when Atlantic sharpnose sharks were subjected to a standardized stress protocol, the highest secondary stress response (Hoffmayer and Parsons 2001) and the highest baseline values for plasma glucose, lactate, osmolality and hematocrit were observed during the summer (Hoffmayer et al. 2012). In this study, the lowest average anterior bite force and hepato-somatic index were observed during summer. The correlation between decreased hepato-somatic index and decreased bite force is in support of the assertion that summer months in the shallow Gulf of Mexico is a stressful period of time for this species. It is important to note that the effect of season on bite force, although relatively subtle, may introduce unexplained variation in bite force in those studies where it is unaccounted for.

We also observed significantly reduced bite force in longline-captured Atlantic sharpnose sharks when compared to hook-and-line-captured specimens. Duration between capture and measurement for hook-and-line-captured sharks was consistently within 3–5 min. The longer soak time (1–2 h) used during longline capture likely placed these animals in a physiologically compromised state prior to they being landed, and this resulted in lowered bite force. The increased soak time may have led to heightened stress. An apparent association between lowered bite force and likely higher stress levels suggests that bite force may be used as a simple noninvasive procedure to determine condition in sharks.

Interspecific comparisons

There have been few direct measurements of bite force in sharks due to the difficulty in locating, capturing and handling these organisms. Additionally, the inherent risk involved in obtaining those measurements has likely discouraged research progress. At present, bite-force estimates have been published for only thirteen shark species and the majority of those were indirect estimates rather than direct measurements (Huber 2006; Huber et al. 2005, 2006, 2009; Wroe et al. 2008; Mara et al. 2009; Ferrara et al. 2011; Habegger et al. 2012). We observed a highly significant relationship ($r^2 = 0.988$) between total length and bite force across this diverse group of sharks, representing an order of magnitude difference in total length (Fig. 7). This was an interesting observation, and it suggests that bite force in this group may be a highly conservative characteristic. Additionally, this high correlation implies that there may be less inconsistency in bite-force measurement than was previously noted. The bite force of the horn shark, *Heterodontus francisci*, was higher than predicted from the general relationship. The horn shark is an extremely durophagous species (Huber et al. 2005), and it is not surprising that it produces a large bite force relative to other, more typical species.

While the perils of extrapolating outside of observed data are well known (Lindstedt and Schaeffer 2002), the apparently highly conservative nature of shark bite force across a diverse group of species suggests that this may not be unreasonable. We used the relationship in Fig. 7 to

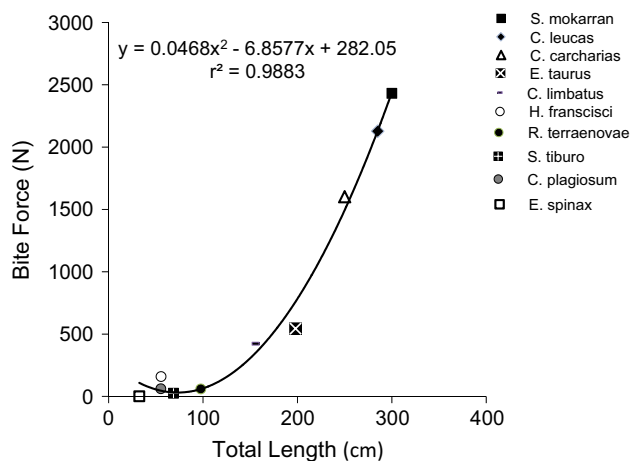


Fig. 7 A polynomial regression of maximum anterior bite force (ABF) on total length (cm) for 10 shark species. (*Etmopterus spinax*, *Sphyrna mokarran*, Huber et al. 2009; *Chiloscyllium plagiosum*, Huber 2006; *Heterodontus francisci*, Huber et al. 2005; *Sphyrna tiburo**, Mara et al. 2009; *R. terraenovae**, This study; *C. limbatus*, Huber et al. 2006; *C. taurus*, Ferrara et al. 2011; *Carcharodon carcharias* Wroe et al. 2008; *Carcharhinus leucas*, Habegger et al. 2012). (*Taxa measured in vivo)

predict the bite force of the extinct megatooth shark, *Carcharodon megalodon*. The maximum length of the megatooth shark has been estimated from tooth anatomy to be approximately 17 m (Portell et al. 2008) to 20.3 m (Gottfried et al. 1996). Based on the relationship established in this study, a 17- and 20.3-m shark would possess an anterior bite force of 123,876 (95 % CI 80,595–183,849) and 179,219 (95 % CI 112,251–247,843) N, respectively. Wroe et al. (2008) used computer modeling and estimated a bite force of 93,127 N for a 103,197-kg (20.3 m, Gottfried et al. 1996) megatooth shark. Our analysis suggests significantly higher bite force in this species. However, it is important to point out that the megatooth bite-force estimates presented here are based on the measurements of only 10 of the approximately 400 extant species of sharks. Clearly, the value reported here is only an estimate and additional adult bite-force data over a range of species are needed. The true bite force of this species will likely never be known, but as stated by Wroe et al. (2008) “*C. megalodon* is clearly one of the most powerful predators in vertebrate history.” In conclusion, while our results suggest that comparison of bite force across shark species can potentially detect diet-specific adaptations, consideration of the proximate factors affecting physiological state of individual study specimens is necessary when examining variation within a species.

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