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Determinants Of Bite Force In Four Species Of Sharks From The Gulf Of Mexico With An Emphasis On The Atlantic Sharpnose Shark, Rhizoprionodon Terraenovae

Kyle Walter Rice
University of Mississippi

DETERMINANTS OF BITE FORCE IN FOUR SPECIES OF SHARKS FROM THE GULF OF MEXICO WITH AN EMPHASIS ON THE ATLANTIC SHARPNOSE SHARK, *RHIZOPRIONODON TERRAENOVAE*

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KYLE W. RICE

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ABSTRACT

Bite force can provide valuable information regarding the physiological ecology of an organism. However, there have been few studies wherein bite force in sharks has been considered. Herein I report on a study of the bite force of four species of sharks with particular emphasis on that of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Among the four species examined, blacktip shark, *Carcharhinus limbatus* bite force was significantly higher than that of sharpnose, *Rhizoprionodon terraenovae.* There was no significant difference between the bite force of those species compared with the same for finetooth shark, *C. isodon* and spinner shark, *C. brevipinna*. Within Atlantic sharpnose sharks, I examined both voluntary and involuntary (obtained using jaw musculature stimulation) bite force measurements, and I investigated differences in bite force between size, sex, season, gape, and capture method. Additionally, I examined bite force differences between anterior and posterior positions in the jaw, and considered correlations between various head morphometrics and anterior bite force. Sharpnose sharks, ranging between 55.1 - 105.5 cm, had an anterior bite force between 4.4 - 60.2 N, and a posterior force of 20.9 - 102.8 N. There was no significant difference between the different methods used to determine bite force. Adult females had a greater anterior force than adult males, but there was no difference in posterior force. Anterior force was found to be weakest in the summer months and highest in the spring and fall. As gape increased the anterior bite force increased, with the greatest force found between 70 - 80% of maximum gape. Longlining captured sharks produced significantly lower bite force when compared to hook and line capture.

LIST OF ABBREVIATIONS AND SYMBOLS

1 α-OHB	1 alpha-hydroxycorticosterone
AMC	Adductor manibulae complex
cos Ø	Cosine of angle of fiber pinnation
CSA	Cross-sectional area
FL	Fiber length
HH	Head height
HW	Head width
I_h	Hepato-somatic index
JL	Jaw length
JW	Jaw width
PBL	Pre-branchial length
P_O	Theoretical bite force

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TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

The force generated by the jaws of an organism can provide valuable information regarding physiological state, diet, intraspecific dominance hierarchies, jaw function, and ontogenetic shifts, and can also provide information regarding the evolution of the jaw-cranial musculoskeletal system (Anderson et al., 2008). An organism's jaws and associated musculature are adapted for handling specific prey. There are a variety of variables that have an influence on the amount of force the jaws' of an organism can produce. The three main variables are tooth morphology, the pinnation and the amount of mass in the jaw adductor muscles, and the degree to which the jaw is opened (gape).

The degree to which an organism can open its jaw and the angle at which optimum force is generated, can significantly influence feeding behavior and diet (Williams et al., 2009). For those animals thus far examined, there is a negative relationship between the amount of force produced and the gape angle of the jaws. Animals that normally use smaller gape angles can produce higher bite forces due to an increase in the density of muscle fibers in the cranial area with a larger cross-sectional area of muscles leading to an increase in the mechanical advantage of the jaw muscles, i.e., the ratio of force produced to the effort applied (Herrel et al., 2008; Nogueira et al., 2009; Williams et al., 2009). Raadsheer et al. (1999) found that in humans the masseter muscle cross sectional area (CSA) played a greater role in bite force magnitude than did various craniofacial factors. Bats have greater bite force than one would predict based on their body sizes and tend to have shorter rostrums and mandibles, higher skulls and a larger amount of

muscle fibers attached to each tendon (Nogueira et al., 2009). Christiansen and Adolfssen (2005) found that in carnivores, canids had some of the lowest bite forces because of their long jaw lengths. In most animals, large gapes correlate with less force because of the need to stretch muscle fibers past their optimal lengths to produce the most force output (Dumont & Herrel, 2003). In order to alleviate this problem in large carnivores, evolution has favored larger temporalis muscles over masseter muscles, which are found in animals that produce large forces at small gapes (Dumont & Herrel, 2003; Williams et al., 2009). Bourke et al. (2008) found that in the dingo, *Canis lupus,* the optimal gape angle to generate the most force was between 25° and 35°, but that stress load tended to increase on the mandible as the angle decreased. Williams et al. (2009) also observed that bite force peaked at 36% of maximum gape and decreased as gape widened in *Peromyscus maniculatus*.

Differences in bite forces have evolved among similar organisms due to the type, availability, and competition for resources and are good indicators of feeding ecology (Herrel et al., 2005; Van der Meij & Bout, 2004; Christiansen & Wroe, 2007). Christiansen and Wroe (2007) found that carnivores that fed on large prey items or tough, fibrous plant material had higher bite forces compared to animals that consumed smaller prey or were omnivorous. This has also been observed in orangutans that incorporate bark and tough vegetation into their diets. Anapol and Lee (1994) found morphological differences among platyrrhine primates based upon their dietary differences. Primates that were omnivorous had greater leverage in their temporalis muscles then in their masseter muscles, while vegetarians had the opposite. Herrel et al. (2008) found in the Italian wall lizard, *Podarcis sicula*, which were introduced to a new island that over a period of 36 years the lizards' head width and bite force increased because of a shift towards the consumption of plant material in their diet.

Tooth morphology plays an important role in the amount of force an organism may generate during a bite. Teeth are composite structures with their shape and material determining their function. Large loads can potentially cause tooth failure (Whitenack et al., 2010). Grubich et al. (2008) found that jaw mechanics of the barracuda (*Sphyraena barracuda*) only predicted moderate force production, but coupled with razor sharp teeth, barracudas are able to produce sufficient pressure to slice prey. The force needed to penetrate teleost prey is only on the order of tens of Newton's (Whitenack et al., 2011). American alligators (*Alligator mississippiensis*) on the other hand begin life with sharp and slender teeth but a morphological shift occurs with age towards more conical teeth that require more force in order to penetrate prey (Erickson et al., 2003). In the spotted hyena (*Crocuta crocuta*), bite force increased with age because of a change from weaker deciduous teeth to permanent teeth, a trend that continued to increase with muscle mass growth even when there was no change in jaw dimensions (Binder & Van Valkenburgh, 2000). Ruminant species, on the other hand, have molariform teeth that are able to withstand higher amounts of pressure during mastication. Sharks, similar to the barracuda, have razor sharp teeth and the vast majority of species have a piscivorous diet.

Terrestrial animals can be easy test subjects, but due to the concealing nature of the oceanic environment and the difficulty of sampling and handling sharks, there is a lack of knowledge concerning much of their biology. The work that has been conducted has only examined computer modeled *in situ* and *in vivo* bite force of captive sharks in relation to their size and jaw muscle mass. It has been assumed that bite force increases by $Mass^{0.67}$ (Huber et al., 2005; Wroe et al., 2008), but size is not always the best indicator of bite force because it ignores the feeding ecology of the animal (Freeman & Lemen, 2008). The cranial geometry and dentition of an organism has an influence on its diet and the amount of bite force generated

(Huber et al., 2006). Sharks have laterally compressed teeth along the anterior edge of the jaw used for grasping and penetrating soft flesh. This type of tooth design is unable to withstand large force generation compared to other animals of the same mass with conical teeth (Wroe et al., 2008). Durophagus species have wider teeth in the posterior position of their jaws in order to crush hard, shelled prey. This however, does not mean that they can produce a greater bite force. Huber et al. (2005) observed a series of compressive bites in the bonnethead shark (*Sphyrna tiburo*) when consuming hard prey items and concluded that the way in which force is applied can offset a low absolute magnitude of force. The cranial geometry of an individual will also play a role in the amount of force generated. Taller and wider heads are capable of accommodating larger muscles and are able to produce greater force because total force is directly proportional to the cross sectional area of the muscle mass (Huber and Motta, 2004). Herrel et al. (2005) theorized that the width of the head in Darwin's finches plays a greater role in the increase of bite force than the dimensions of the beak, which evolved to withstand the increase in force. Sharks jaws are a class III lever system with the fulcrum at one end, the load or object being bitten at the other, and the muscles providing the force between these two points (Huber and Motta, 2004). The length of the jaw also determines the amount of force applied, with shorter jaws being able to generate more force than longer ones.

The jaws of a shark are an important body part, used for everything from feeding to mating. Mating in elasmobranchs consists of male sharks biting and holding onto females in order to insert their claspers. During mating season, females may bear mating marks or scars on their bodies, usually on the fins or flanks. In some sharks (*Prionace glauca*, *Carcharhinus plumbeus*) it has been shown that females have significantly thicker skin than males of the same size (Pratt & Carrier, 2001). This possibly serves as a defensive adaptation in order to minimize

the risk of infection or blood loss as biting by males may be needed in order to stimulate female's acceptance of their claspers (Pratt & Carrier, 2001).

Ellis and Shackley (1995) found that after maturation, male small-spotted catsharks (*Scyliorhinus canicula*) had longer and narrower mouths and also have longer teeth then females. This sexual dimorphism during the mating season is believed to be related to mating behavior and the need for males to penetrate the thicker skin of females (Pratt & Carrier, 2001). Jones et al. (2013) found that polygamous pinniped males had larger bite forces then monogamous males due to the competition for mates. Thus, it is also possible that males will have greater bite force generation associated with mating.

Aside from gender differences, the time of year of sampling can also influence tooth morphology and bite force generation. Some species, such as the Atlantic stingray (*Dasyatis sabina*), exhibit dentition that changes seasonally (Pratt & Carrier, 2001). Dentition and mating may not be the only thing that affects bite force. In their natural environment sharks experience a multitude of stimuli that could induce stress and have an impact on force generation.

Sharks use their jaws as a means to capture food, sense their environment, and defend themselves against conspecifics and other organisms. However, despite their importance the effects of stress on a shark's ability to generate bite force has not been examined. The stress response in fish is an adaptive reaction to any acute stressor in order to mediate and maintain a consistent homeostatic state (Barton, 2002). There are a multitude of stressors in an aquatic environment. They can be as small as minute water quality changes, such as salinity, or as large as a predator-prey interaction. The primary response in fish to a stressor is a quick neuroendocrine release of catecholamines followed by the activation of the hypothalamus-pituitary axis producing glucocorticoids (Reid et al., 1998). Once in circulation, these hormones

help to negate the detrimental effects that stress can elicit in the organism, such as acidosis. They also can help in increasing heart and respiration rate and in the mobilization of energy stores in the "fight or flight response" (Reid et al., 1998). Glucocorticoid secretion and detection in the circulatory system has an approximate 5 minute latency period from first contact with the organism and has been the dominant stress hormone measured in a fish's stress response (Barton, 2002). Hoffmayer and Parsons (2001) used hook and line captured sharks to establish a baseline stress response against which comparisons can be made.

Cortisol is the main glucocorticoid in teleost fish, but elasmobranchs synthesize a different hormone in their interrenal tissue, 1 α-hydroxycorticosterone (1 α-OHB). This corticosteroid is multifunctional and is both a glucocorticoid and a mineralcorticoid (Nunez & Trant, 1999). Glucocorticoids cause an increase in plasma glucose levels through gluconeogenesis, and mineral corticoids play a role in osmoregulation affecting the function of the rectal gland in elasmobranchs (Nunez & Trant, 1999). Unfortunately, there is no known reference steroid or antigen in order to perform an assay of 1 α-OHB to determine concentration levels in the plasma. As a consequence little is known about the stress levels of sharks, skates, and rays. Only basic hematological parameters have been monitored in stressed sharks, but this involves the serial bleeding of individuals, which in itself elevates the stress level (Hoffmayer & Parsons, 2001).

Freeman & Lemen (2008) observed in small mammals that a bite was elicited when the animals felt that there was an opportunity for escape, and out of multiple bites the strongest force produced was used as the maximum for that individual. When bite force is measured on a live organism, the effort level or motivation by the organism may affect the results. If individuals within a species and among species show different levels of willingness to bite, it is not possible

to make comparisons of voluntary bite force (Freeman & Lemen, 2008). In order to negate the willingness of an organism to bite, studies have used induced muscle tetanus through electrical stimulation. Dechow and Carlson (1983) used unipolar needle electrodes inserted unilaterally into the masseter muscle of monkeys and found that it took between 20V to 60V at multiple stimuli to induce a tetanus plateau.

Our objectives for this study were to: (1) examine the bite force of the Atlantic sharpnose shark, *Rhizoprionodon terranovae*, and compare it to bite force of other shark species, (2) examine the bite force of various shark species, (3) assess the effect of gape size on bite force, (4) identify seasonal, stress and sex effects on force generation, (5) compare voluntary and involuntary bite force and (6) compare those bite force measurements against that estimated from the cross sectional area of the jaw musculature of sharks.

MATERIAL AND METHODS

Sharks were collected by hook-and-line off the coast of Mississippi in the Mississippi Sound and surrounding waters using the University of Mississippi's 18 ft skiff. Longlining and gill netting was conducted with the assistance from the Gulf Coast Research Lab, the National Marine Fisheries Service, and the Dauphin Island Research Lab, with sampling conducted during the summer and fall months from early morning to late evening. Collecting via hook-and-line was accomplished using hooks typically baited with cut fish, squid or whole cigar minnows.

A bite force gauge constructed for this project (Fig. 1)[1], 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 Plug and Play, TEDS IEEE 1451.4; Precision Measurement Systems, Temecula, CA), placed between two thin metal plates. These plates were inserted into a polyvinyl chloride handle. Sharks were captured using hook and line and brought into the boat as quickly as possible, typically within approximately three minutes. While on the boat the shark was held as loosely as possible in order to induce a voluntary bite force. 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 mouth for posterior measurements. To determine involuntary bite force we used the *TENs Muscle Stimulator* set to deliver 100±5 V at a current of 20 µA which induced tetanus in the adductor muscles. This was accomplished by placing two

[1] All figures are found in the appendix.

electrode pads externally near the jaw musculature. 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. In order to reduce muscle fatigue the shark was only stimulated three times each for anterior and posterior force measurement, and only the largest of the three measurements was used for analysis.

Theoretical bite force was determined by using the methods of Huber and Motta (2004). Shark heads were collected, placed on ice, and then dissected at the University of Mississippi in order to determine the unilateral cross-sectional area (CSA) of the adductor manibulae complex (AMC) which is comprised of four divisions of the quadratomandibularis and the preorbital muscles. CSA was measured based on Powell's (1984) method. With this method the AMC was removed and for each muscle section the average angle of the muscle fiber pinnation from the central tendon (cos Ø), the average fiber length (FL) within the muscle, and the dry and wet weight of the muscle was measured. These data along with the muscle density of fish (1.05 g/cm^3) were used to determine CSA which was calculated using the equation:

$$(\text{CSA} = (\text{muscle mass}) * (\cos Ø\ \text{FL}) * (\text{muscle density}))$$

Theoretical bite force (P_o) was calculated using the equation:

$$(P_o = \text{CSA} * \text{specific tension})$$

where specific tension of vertebrate muscle is 20 N/cm^2. Estimates of P_o were then doubled to simulate bilateral muscle contraction.

The hepato-somatic index (I_h) was calculated using the equation:

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

with liver and body weight measured in grams.

The maximum gape of each individual was measured using a small ruler. The mouth was opened gently to the maximum gape by hand and then measured. Based on this measurement the height of the bite force meter transducer was adjusted approximately to 25%, 50% and 75% of the animal's maximum gape. The bite force meter's height was adjusted by sliding premeasured blocks of wood wrapped in tape over the transducer. After bite force was measured, total length, jaw width, jaw length, head width, head height, pre-branchial length, sex and maturity were recorded. Jaw width (JW) was measured from the corners of the mouth of the shark. Jaw length (JL) was measured perpendicularly from the corner of the jaw to the tip of jaw. Head width (HW) was measured as the distance across the head between the first gill slits. Head height (HH) was the measurement from the first gill slit vertically, and pre-branchial length (PBL) was measured from the tip of snout to the first gill slit.

All data were $\log_{10}$ transformed and then analyzed using SPSS 22.0 (IBM Corp., Armonk, NY), and all values were considered significant if $P \leq 0.05$. A non-parametric Kruskal-Wallis ANOVA on ranks was used to examine if there was any difference in voluntary, involuntary, and the CSA methods in determining anterior bite force. If no significant difference was found then voluntary and involuntary data were combined for the rest of the tests. I used a one-way ANOVA to compare the difference in anterior bite force between species, followed by a Tukey's post-hoc test to separate significant means. An ANCOVA was used to determine if there was a significant difference between the slopes of the regression lines for anterior and posterior bite force regressed against total length. A Student's t-test was used for comparing the means of anterior bite force between hook and line and longlining samples, along with comparing the means of anterior and posterior force for adult male and female sharpnose sharks. A non-parametric Kruskal-Wallis ANOVA on ranks was used to examine if there was any

difference in voluntary, involuntary, and the CSA methods in determining anterior bite force. A backwards Multiple Regression was used to determine which head morphometric was the best predictor of anterior bite force. A one-way ANOVA followed by a Tukey's post-hoc test to separate significant mean values was used to compare anterior bite force between seasons. A one-way ANOVA was used to compare the hepato-somatic index between seasons followed by a Tukey's post-hoc to separate out significant means. Gape was compared using a one-way ANOVA followed by a Tukey's post-hoc to determine if there was any significant difference between the different percentages of maximum gape for each size class.

RESULTS

There was no significant difference (non-parametric ANOVA $x^2_2 = 4.461$, p = 0.107) between voluntary and involuntary bite force, and between those measurements when compared with the cross sectional area (CSA) method of estimation. Anterior bite force based on the CSA provided the largest force ($\overline{X}$ = 31.0 N ± 2.49, n = 12) followed by involuntary ($\overline{X}$ = 27.2 N ± 1.09, n = 81) and then voluntary ($\overline{X}$ = 23.7 N ± 3.35, n = 22).

A total of 105 *R. terranovae* (55.1 – 105.5 cm), 13 *C. limbatus* (67 -108.3 cm), 6 *C. brevipinna* (88 – 106 cm), and 4 *C. isodon* (96.2 – 101.6 cm) were captured by hook and line during the study (Fig. 2). Only specimens that were 80 cm or larger were used in the comparison of bite force between species. The only significant difference in anterior bite force was between *R. terranovae* ($\overline{X}$ = 33.8 N ± 1.47) and *C. limbatus* ($\overline{X}$ = 45.4 N ± 4.4; ANOVA: F(3, 68) = 2.755, p = 0.049), and there was no significant difference (ANOVA: F(2,22) = 1.862, p = 0.179) in posterior bite force between the species.

Total length for hook and line captured *R. terraenovae* ranged from 55.1 - 105.5 cm (n = 105), with an anterior bite force between 4.4 – 60.2 N and posterior bite force between 20.9 and 102.8 N. When anterior and posterior bite forces were regressed against total length, there was a significant difference (ANCOVA: F(1,96) = 80.21, p < 0.0001) in the slopes of the regression lines (Fig. 3).

Sampling using both hook and line and longlining resulted in a total of 132 sharpnose sharks ranging from 55.1 - 105.5 cm. Since longlining is biased towards larger specimens, only the upper size class (82.5-105.5 cm) was used for comparison (Fig. 4). There was a significant

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 N ± 1.48, n = 41) were compared against longline captured sharks (mean bite force= 11.85 N ± 2.9, n = 27).

Examining head morphometrics (Fig. 5), the length of the jaw and width of the head were the best predictors of anterior bite force (ABF). The multiple regression model provided a positive relationship (log ABF = 0.617*logJL + 0.694*logHW + 0.376; $R^2 = 0.5$, F(2, 67) = 33.437, $p < 0.001$).

Immature males and females (n = 62) were more commonly caught in the Sound, with only 35 adult males (TL 78.4 - 96.3 cm) and 8 adult females captured (87.2 - 105.5 cm; Fig. 6). Sharks ranging between 87.2 - 105.5 cm were compared and a significant difference (Student's t-test: t(28) = 2.18, p = 0.038 two-tailed) was observed between anterior bite force of adult males ($\overline{X}$ = 31.9 N ± 1.83, n = 22) and females ($\overline{X}$ = 41.1 N ± 4.29, n = 8). When posterior bite force was compared there was no significant difference (Student's t-test unequal variance: t(10) = -0.18861, p = 0.85 two-tailed) between adult male ($\overline{X}$ = 64.7 N ± 3.7, n = 12) and females ($\overline{X}$ = 65.6 N ± 7.8, n = 8; Fig. 7).

The largest number of sharks were caught in summer (n= 56) followed by fall (n = 30) and spring (n = 19). There was a significant difference (ANOVA: F(2, 102) = 5.901, p = 0.009) in anterior bite force between spring ($\overline{X}$ = 32.8 N ± 2.3) and summer ($\overline{X}$ = 25.4 N ± 1.2, p = 0.018), but not between these seasons and fall ($\overline{X}$ = 28.6 N ± 2.3; Fig. 8). The hepato-somatic index differed between the three seasons with fall ($\overline{X}$ = 4.9% ± 0.7, n = 7) being highest and summer the lowest ($\overline{X}$ = 3.7% ± 0.54, n = 9; Fig. 9). There was a significant difference (ANOVA: F(2,16) = 10.758, $p < 0.001$) between fall and summer (p = 0.006), and spring ($\overline{X}$ = 4.6% ± 0.25, n = 3, p = 0.01) and summer, but not between fall and spring.

Maximum anterior bite force at varying gapes was divided into three different size classes; size class one (55.1 – 67.9 cm), size class two (73.3 – 85 cm), and size class three (85.1 – 105.5 cm). Size class one had an average maximum gape of 5.12 cm and was divided into five gape sizes of 40%, 55%, 70%, 80% and 95% maximum. There was no significant difference (ANOVA: $F(4, 24) = 2.527$, $p = 0.067$) found between the force generated at the different gape sizes. Size class two had an average maximum gape of 6.1 cm with five different gape sizes (35%, 45%, 57%, 70% and 80%). There was a significant difference (ANOVA: $F(4, 47) = 7.246$, $p < 0.001$) between the force generated at 35% ($\overline{X}$ = 24.1 N ± 1.42; n = 20) and 57% ($\overline{X}$ = 30.9 N ± 1.93, n = 14, p = 0.029), 35% and 70% ($\overline{X}$ = 39.6 N ± 4.03, n = 5, p = 0.001), and also between the 35% and 80% ($\overline{X}$ = 35.0 N ± 2.61, n = 11, p = 0.001). The maximum average gape for size class three was 6.7 cm and was divided into six different gape sizes (31%, 52%, 63%, 74%, 84% and 95%). No significant difference (ANOVA: $F(5, 46) = 1.253$, $p = 0.301$) in force generated was found between any of the gape sizes (Fig. 10)

DISCUSSION

Species and Gender Differences in Bite Force

Bite force has been measured for very few species of sharks and at the present time, it has only been published for twelve shark species. A cubic regression provided a significant relationship between size and bite force (Fig. 11) in these species. This obviously suggests that bite force is a conservative characteristic, at least among closely related species. However, it is worth noting that the durophagous horn shark and the deep water seven gill both fall above the regression line. This was not surprising since the former preys upon a variety of hard shelled organisms and the latter includes marine mammals in its diet (Ebert 1991), both of which necessitates a more powerful bite force.

The bite force for the Atlantic sharpnose shark was similar to the predicted value (Fig.11) and when compared to the other species included in this study, was only significantly different from the blacktip shark. There is a dietary difference between these two species that may account for this disparity in bite force. Blacktip sharks mainly feed upon teleosts and small elasmobranch species, while sharpnose feed on a combination of teleost and small crustaceans (Castro, 1996; Gelsleichter et al., 1999). Hoffmayer and Parsons (2003) found that 66.2% of the stomachs sampled containing food in sharpnose sharks contained teleost species and 36.8% had crustaceans with the most common being soft-shelled Panaeid shrimp and *Squilla empusa*, and for blacktips 94% contained bony fish and only 6% had crustaceans. Bethea et al. (2004)

observed that blacktip sharks ingested larger prey items compared to similarly sized sharpnose sharks. I suggest that the greater force production in the blacktip shark would be beneficial in order to successfully obtain larger prey items. Additionally, since greater bite force provides increased jaw closing speed, this could likewise benefit the blacktip shark in obtaining elusive, pelagic, teleost prey items.

Adult sharpnose sharks segregate by sex with adult males staying in near-shore water and females moving off-shore (Parsons and Hoffmayer, 2005). In this study mature females had a higher anterior bite force (41.1 N ± 4.29) than males (31.9 N ± 1.83). It is very uncommon to catch adult females inside the Sound and all adult females were collected on a single day in May. The majority of the sampling was done throughout the summer months when the sharks are most physiologically stressed, and it is possible that seasonal differences in bite force may explain the gender differences observed. It is also possible that the increased bite force may reflect the highly competitive nature of the offshore environment where females spend almost the entirety of their adult lives. The increased bite force in females could provide a selective advantage their ability to successfully utilize resources and defend themselves against predators.

Stress and Capture Method

Longline fishing has a dramatic effect on stress in fish, because of the extended period of time that the animals spend on the hook. In this study, it was not possible to determine the length of time the shark was on the hook although in all cases it was at least one hour. When sharpnose were initially caught by hook-and-line, they were quite active and in as little as five minutes were already fatigued. When the sharks were released the majority would lethargically

swim away. Fish muscle is composed of white muscle mass that fatigues easily and is conducive for short bursts of activity (Skomal, 2007). Hoffmayer and Parsons (2001) found an increase in blood glucose, lactate, plasma osmolality and a decrease in blood pH over a 60 minute time frame in Atlantic sharpnose sharks. These parameters are a good indication of a secondary stress response in fish and have an impact on the condition and performance of the organism (Barton, 2002; Skomal, 2007). There have been relatively few studies that examined bite force and its relation to stress. Freeman and Lemen (2008) observed a 31% decrease in the bite force of the white-footed mouse (*Peromyscus leucopus*) that were exposed to a cold mist while in the traps, and Huber et al. (2008) noted a 85% decrease in spotted ratfish (*Hydrolagus colliei*) and a 50% decrease in spiny dogfish (*Squalus acanthias*) bite force due to tetanic muscle fatigue.

Stress levels in the Atlantic sharpnose shark fluctuate seasonally (Hoffmayer et al., 2006). Hoffmayer et al. (2012) observed the highest *un-stressed* baseline for plasma glucose, lactate, osmolality, and hematocrit during the summer. Additionally, when sharpnose sharks were subjected to a standardized stress protocol, the highest secondary stress response was observed in summer. These results point to one conclusion; that the summer months are a stressful time of year for Atlantic sharpnose sharks.

To investigate how this seasonal effect on stress may alter bite force, I examined the hepato-somatic index in sharpnose sharks during spring, summer and fall and compared this with bite force in the same months. The lowest average anterior bite force (25.4 N ± 1.2) and hepato-somatic index (3.7% ± 0.54) were observed during summer in this study. Hoffmayer et al. (2006) found a similar trend in adult male sharpnose sharks, with the largest livers being recorded in spring and autumn and the lowest during summer. The lowest Fulton's condition factors were also recorded by Parsons and Hoffmayer. (2005) during the summer months for

sharpnose. These results help to support the idea that stress has a negative impact on bite force**.** Freeman and Lemen (2008) found, by accident, that stressed white-footed mice had a 31% lower bite force than non-stressed individuals. If a correlation between bite force generated and stress levels are found, then bite force can be used as a simple noninvasive procedure to determine stress level in sharks. This information could be a useful tool in the conservation of declining shark populations (Baum et al. 2003).

Morphometrics and Bite Force

Multiple regression indicated that the best predictive morphological features were head width and jaw length. Huber et al. (2006) also found that blacktip head width was the best predictive feature, and this was also observed by Habegger et al. (2012) for bull sharks. This increase in the width of the head allows for the hypertrophication of the jaw muscles which enables a greater production of force. Huber et al. (2006) also found that prebranchial length of the head was an indicator of force production, but in their study they only examined head width, height, and prebranchial length. Instead of head length we found that jaw length was more influential. Sharks jaws are third class lever systems and by increasing the length of the out-lever, it decreases the mechanical advantage at the anterior most point of the system, which decreases force and increases closing velocity. This likewise explains the significant result in the ANCOVA in the slopes of the regression lines of anterior and posterior forces. As you increase the length of the jaw, the difference between the anterior and posterior bite force increases. Dumont et al. (2009) found that in wrinkle face bats, short jaws and wide skulls allowed for a high bite force, even at relatively large gaps.

For Atlantic sharpnose sharks the highest bite force generated was at 70% (46º) to 80% (49.8º) of the maximum gape. Similar results have been observed in the great white (*Carcharodon carcharias*) and sandtiger (*Carcharias taurus*) sharks with maximum anterior force produced at the 45º - 55° gape angle (Ferrara et al., 2011). This is a larger optimum gape than has been observed in studies on mammals. 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 as the gape angle increased there was a decrease in force (Dumont and Herrel, 2003). It is possible that *R. terranovae*'s ability to produce a large force at higher gapes is due to the feeding ecology of the species. Atlantic sharpnose are ram feeders that attack prey with mouths open to some degree. In order to be efficient predators, a larger force produced at wider gapes would be beneficial for admitting the largest possible prey item. Ferrara et al. (2011) found in white and sandtiger sharks that as gape increased the angle of the muscles pinnation to the jaw reached a more optimal configuration to produce higher forces. It is important to note that a third class lever system favors closing velocity over force production. In the Atlantic sharpnose and other shark species, the widest effective gape may be that which provides the fastest closing speed. This coupled with the protrusion of the palatoquadrate during jaw closure may increase the effectiveness of the feeding mechanism.

Involuntary and Voluntary Bite Force

Bite force can be a very difficult measurement in sharks, because when an unknown object is presented to them they have the tendency to bite tentatively to obtain tactical cues. For these reasons similar to Huber and Motta (2004), involuntary force was induced through the use of stimulating electrodes to cause tetanus in the jaw adductor muscles. During sampling the willingness of the organism to corporate was a major factor in obtaining data. When handled or left freely to themselves, only a small percentage would willingly bite the force transducer. Rather than bite, the most common action was an opening of the mouth and lateral shaking of the head in an attempt to slash objects with their teeth instead of producing a penetration. There was no significant difference between the three methods used to estimate bite force, but voluntary force had the lowest average (23.7 N ± 3.35). When voluntary bite force was successfully measured, sharks of similar size where able to produce the same bite force of those that were recorded during electrical stimulation. This suggests that the external stimulation used in this study was an accurate method for the determination of bite force.

Conclusions

Despite the difficulties and inherent risk to the researcher in measuring bite force in wild organisms, bite force measurement of wild organisms can be a useful tool for gauging the condition of an organism and for providing insight into various ecological aspects of a species. These data can provide information regarding an organism's diet or its defense strategies. The elasmobranch bite force data that has been gathered to date suggests a lower bite force when

compared to other carnivorous species of similar mass. It is likely that these differences are related to the ram feeding strategy of these organisms. Organisms deal with stress in their environment daily. These stimuli, varying in magnitude from water chemistry to predator-prey interactions, can be harmless or can have a negative impact on their health. The results in this report indicate that over time stress inhibits the amount of force that can be generated by the jaw muscles. Bite force then may be used as a noninvasive tool to make informed managerial decisions, help in the reduction of by-catch in longlining, or a parameter to determine the condition of a shark.

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APPENDIX

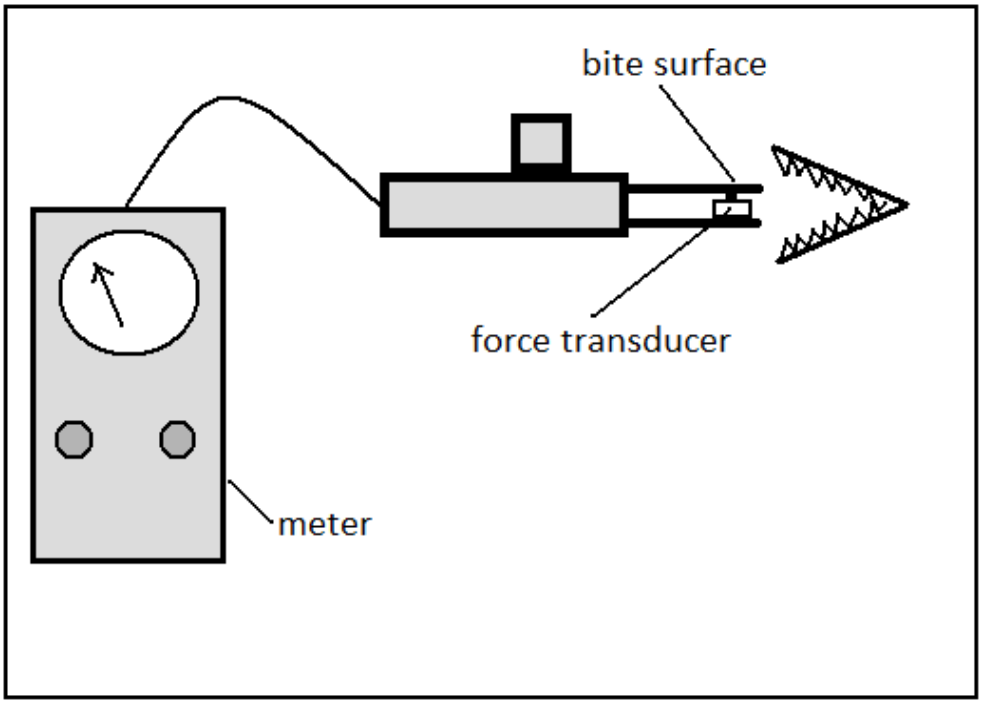

Figure 1. A diagram of the shark bite force meter constructed for this project.

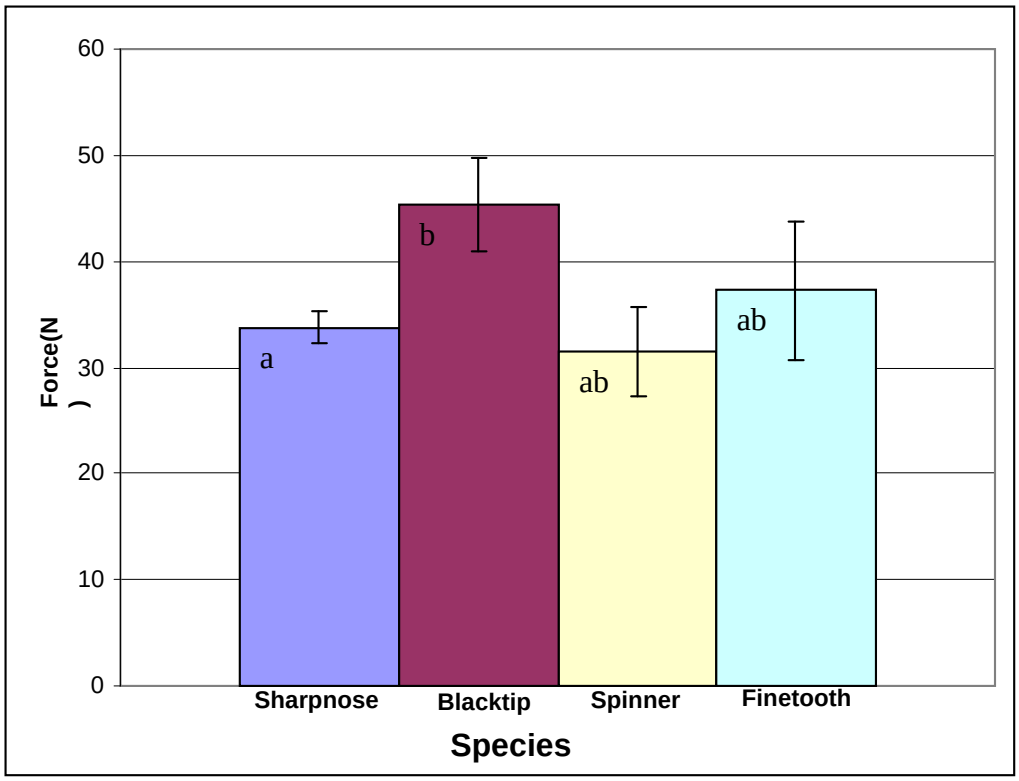

Figure 2. Mean anterior bite force for sharpnose, blacktip, spinner and finetooth sharks caught by H&L. Vertical lines are standard errors. Letters not in common indicate values are significantly different ($P < 0.05$) from each other.

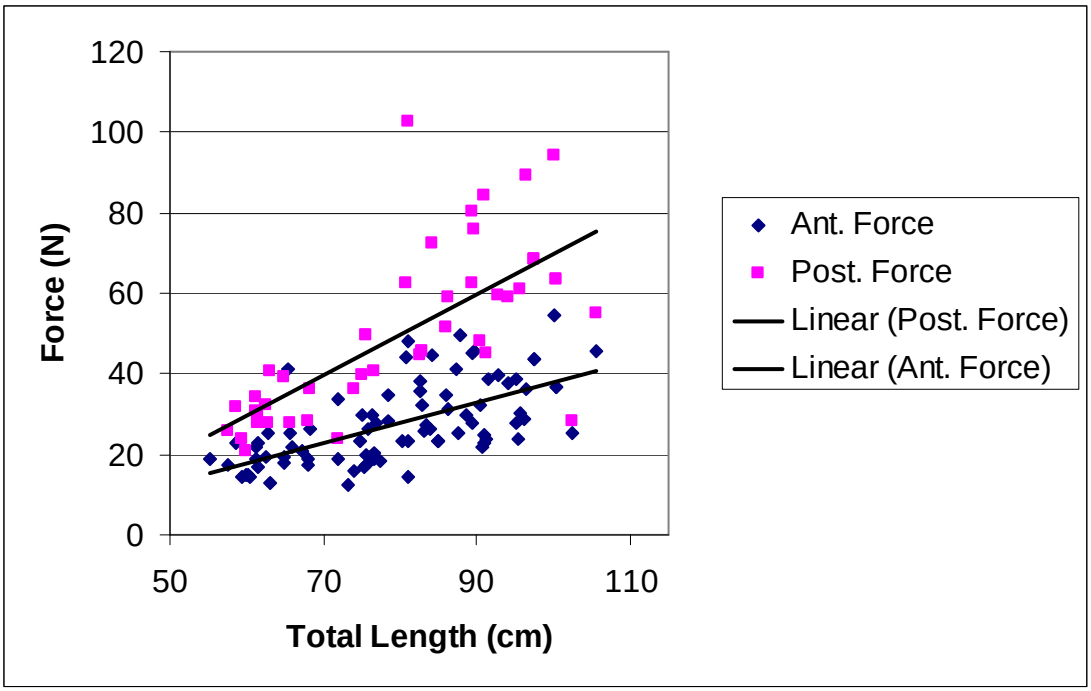

Figure 3. Anterior and posterior bite force for Atlantic sharpnose shark in relation to total length(cm). There was a significant difference between the slopes of the anterior and posterior bite forces.

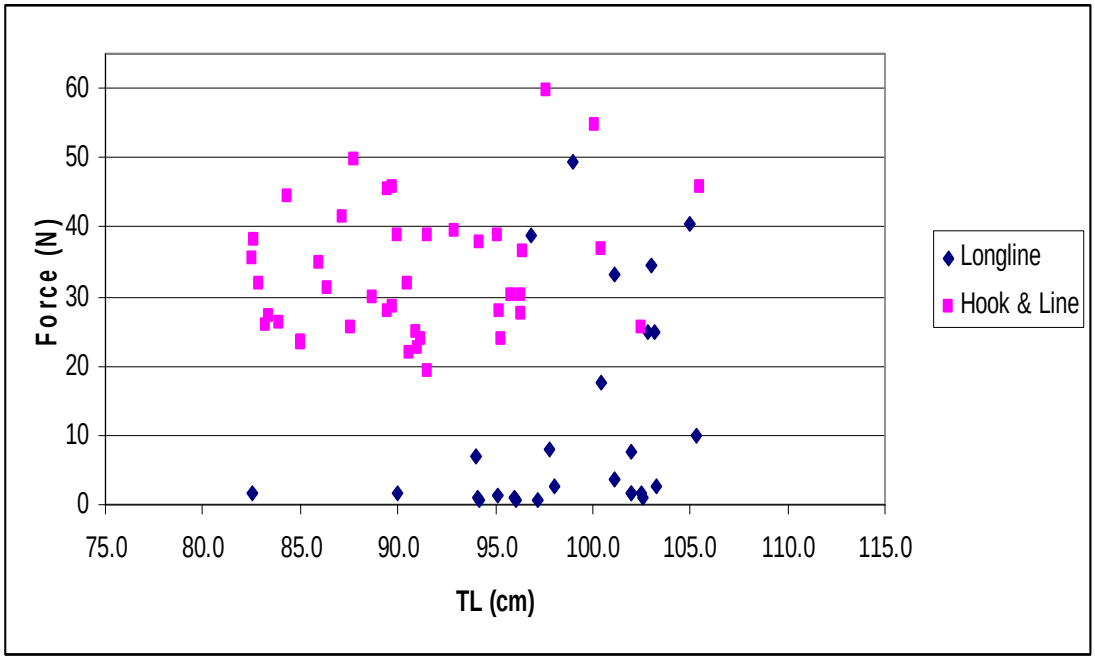

Figure 4. Anterior bite force for adult Atlantic sharpnose sharks (TL 82.5-105.5 cm) comparing longline versus hook and line.

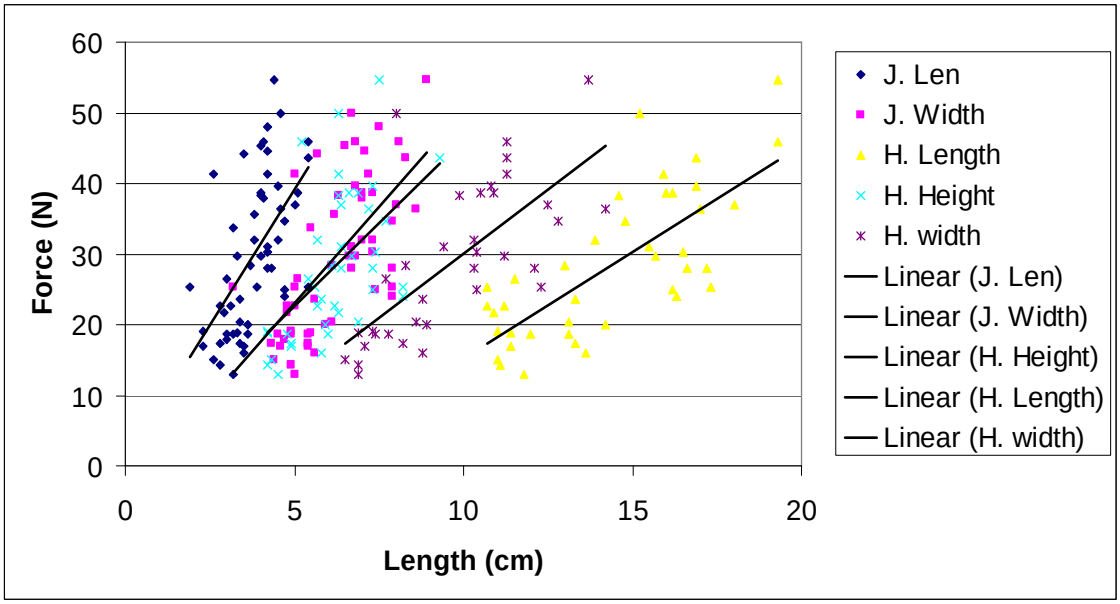

Figure 5. Length of head morphometrics against anterior bite force.

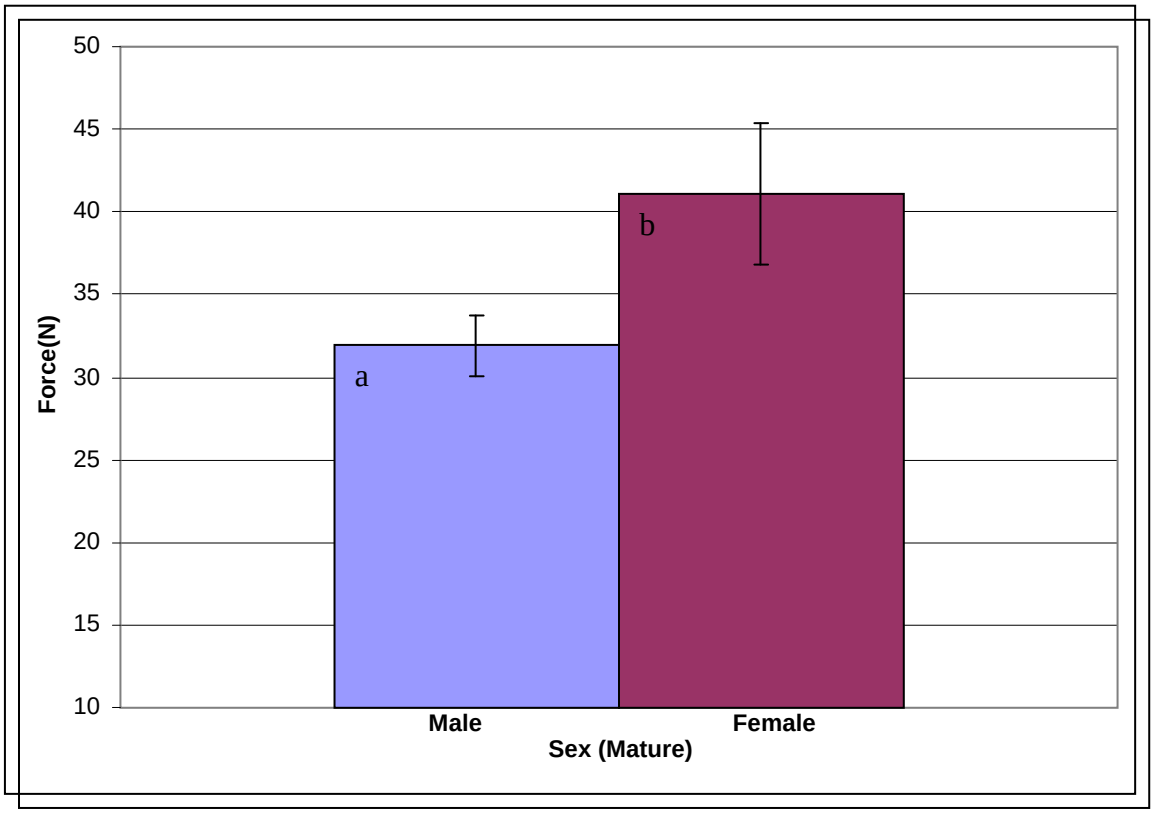

Figure 6. Mean anterior bite force for mature Atlantic sharpnose sharks by sex. Vertical lines are standard errors. Letters not in common indicate values are significantly different ($P < 0.05$) from each other.

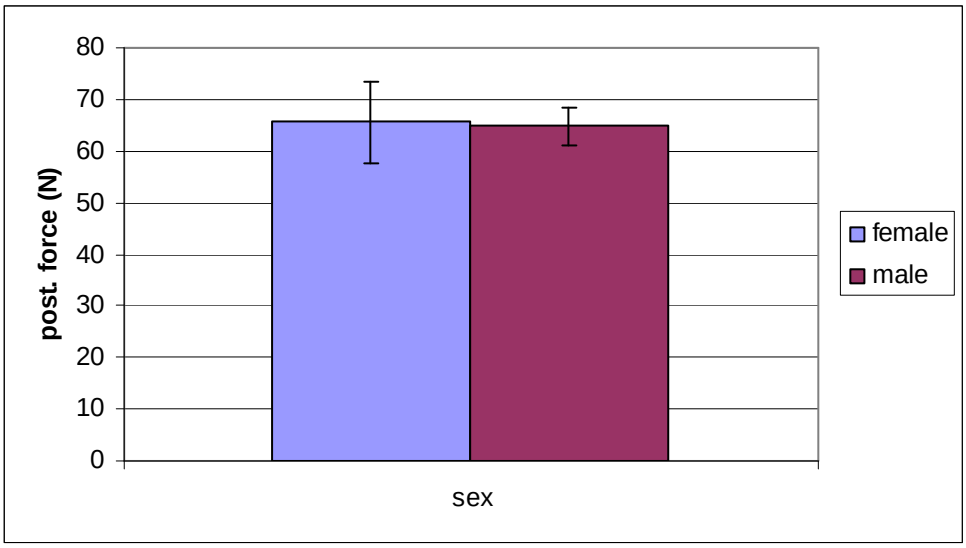

Figure 7. Posterior bite force between male and female adult sharpnose. Vertical lines represent standard errors. There was no significant difference between the sexes.

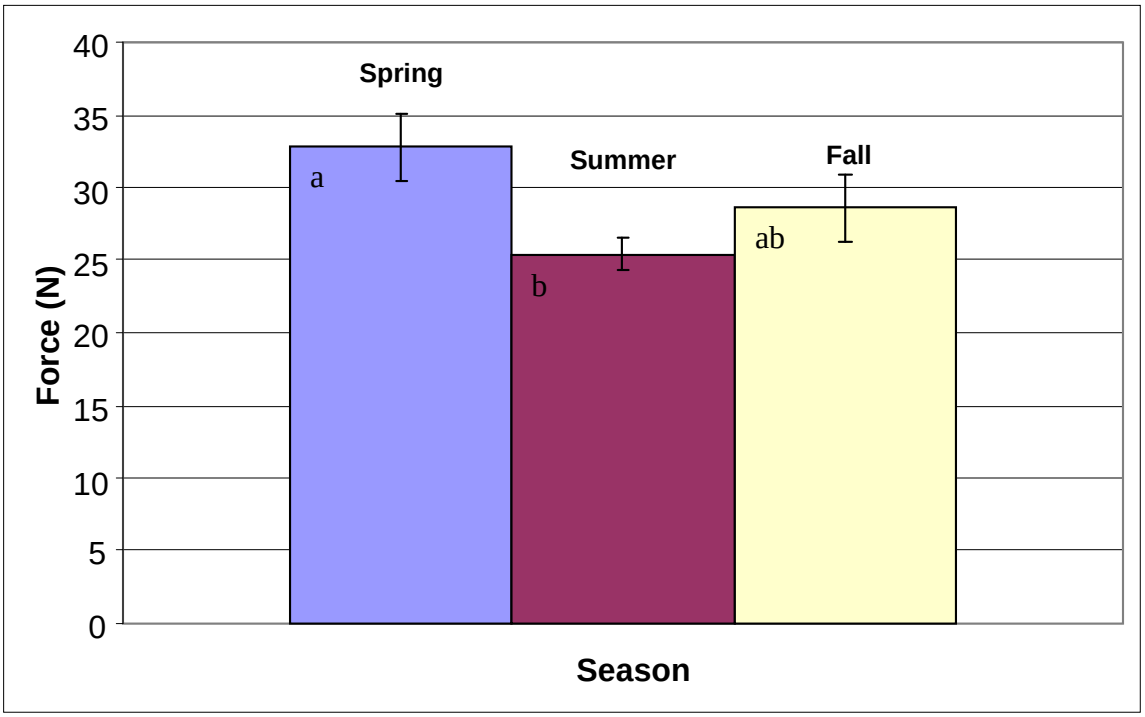

Figure 8. Mean anterior bite force for Atlantic sharpnose by season. Vertical lines are standard errors. Letters not in common indicate values are significantly different ($P < 0.05$) from each other.

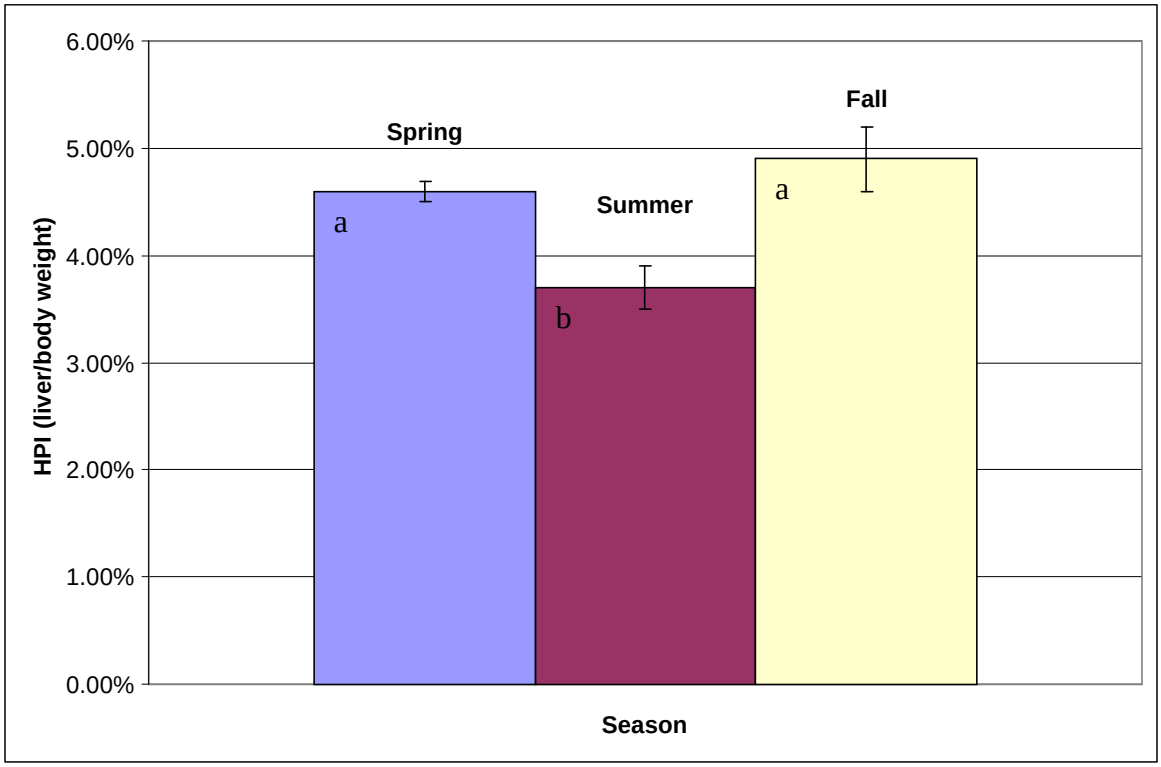

Figure 9. Mean hepato-somatic index (liver weight/body weight * 100) for Atlantic sharpnose by season. Vertical lines are standard errors. Letters not in common indicate values are significantly different ($P < 0.05$) from each other.

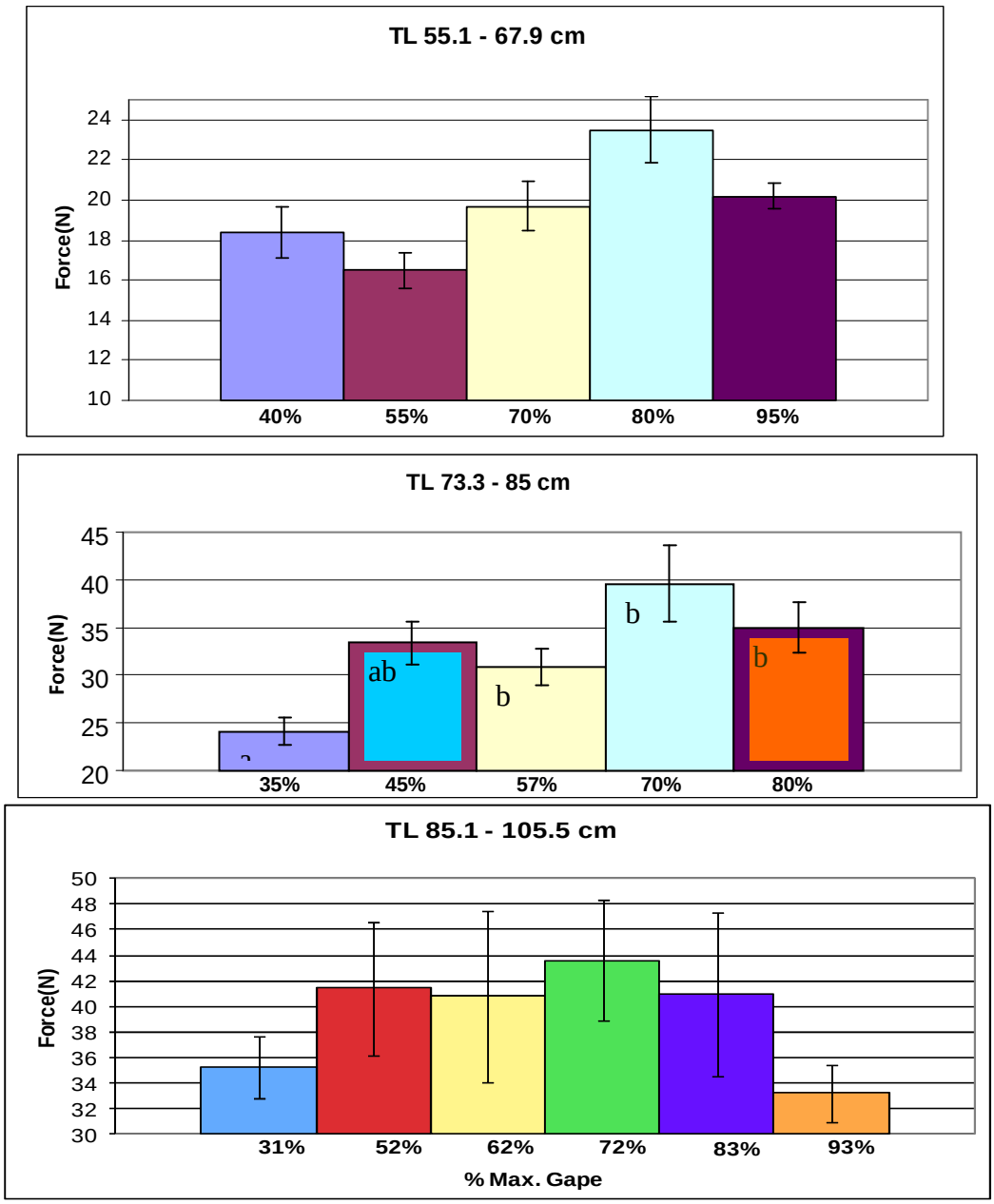

Figure 10. Anterior bite force for Atlantic sharpnose by percentage of maximum gape for three different size classes. Size class one (TL 55.1 – 67.9 cm), size class two (73.3 – 85.0 cm), and size class three (85.1 –105.5 cm). The vertical lines represent standard errors. Letters not in common indicate values are significantly different ($P < 0.05$) from each other.

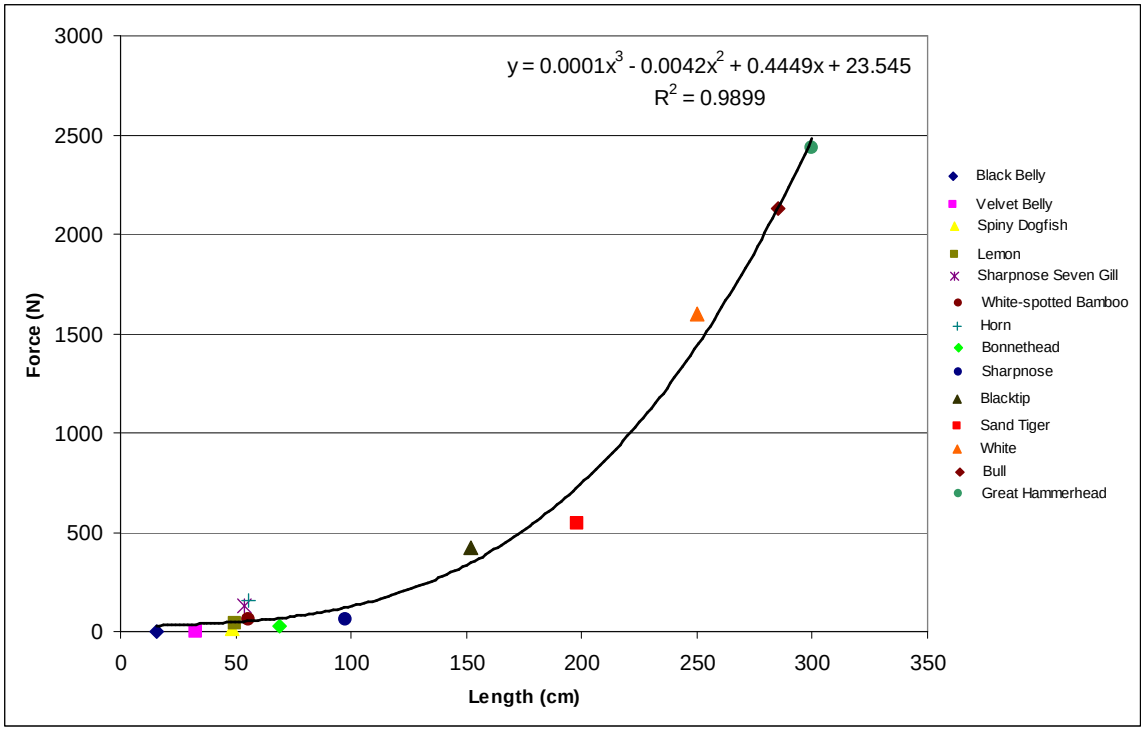

Figure 11. A comparison of maximum anterior bite force (ABF) of different shark species by length (cm).

VITA

EDUCATION:

2003	High School Diploma	Munster High School, Munster, IN
2007	Purdue University	Purdue University, West Lafayette, IN

RESEARCH EXPERIENCE:

2009-2013: Bycatch reduction device testing for shrimp trawling in the Gulf of Mexico. The Walton Fund for Marine Research. The World Wildlife Fund. The University of Mississippi

TEACHING EXPERIENCE:

2009-2014, Fall Semester	BISC 330 Human Physiology Lab	The University of Mississippi
2009-2014, Spring Semester	BISC 330 Human Physiology Lab	The University of Mississippi

PRESENTATIONS

2012 Rice, Kyle W. and Glenn R, Parsons. Examing the effects of stress, gape angle, and jaw muscle mass on bite force in sharks of the Gulf of Mexico. AFS Southern Chapter Meeting. Biloxi, MS. 2012