

Comparative Analysis of Methods for Determining Bite Force in the Spiny Dogfish *Squalus acanthias*

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ABSTRACT Many studies have identified relationships between the forces generated by the cranial musculature during feeding and cranial design. Particularly important to understanding the diversity of cranial form amongst vertebrates is knowledge of the generated magnitudes of bite force because of its use as a measure of ecological performance. In order to determine an accurate morphological proxy for bite force in elasmobranchs, theoretical force generation by the quadratomandibularis muscle of the spiny dogfish *Squalus acanthias* was modeled using a variety of morphological techniques, and lever-ratio analyses were used to determine resultant bite forces. These measures were compared to in vivo bite force measurements obtained with a pressure transducer during tetanic stimulation experiments of the quadratomandibularis. Although no differences were found between the theoretical and in vivo bite forces measured, modeling analyses indicate that the quadratomandibularis muscle should be divided into its constituent divisions and digital images of the cross-sections of these divisions should be used to estimate cross-sectional area when calculating theoretical force production. From all analyses the maximum bite force measured was 19.57 N. This relatively low magnitude of bite force is discussed with respect to the ecomorphology of the feeding mechanism of *S. acanthias* to demonstrate the interdependence of morphology, ecology, and behavior in organismal design. *J. Exp. Zool.* 301A:26–37, 2004. © 2004 Wiley-Liss, Inc.

The complexity of the vertebrate cranium lies in its integration of numerous mechanical and neurological systems that have influenced its morphology throughout evolutionary time. The mechanical demands of the feeding mechanism may be the most influential of these because the loading regimes associated with feeding are the greatest in magnitude of those experienced by the cranium (Demes, '82). However, cranial design must be optimized to both withstand these loading regimes and efficiently exploit food resources necessary for survival (Alexander, '92; Herrel et al., 2001b). Knowledge of both the magnitude and the mechanism by which force generated by the cranial musculature is transmitted to the jaws during feeding is critical to our understanding of the diversity of cranial form in gnathostomes (Ringqvist, '72; Raadsheer et al., '99; Ravosa et al., 2000) and their feeding ecology (Wainwright, '87; Hernandez and Motta, '97; Herrel et al., 2001a, b). Elasmobranchs (sharks, skates, and rays) are an ideal system in which to investigate the relationship between these forces, cranial morphology, and behavior in relation to resource exploitation, i.e. prey capture (Norton,

'91), because: (1) they arguably possess a greater diversity of feeding mechanisms than any other vertebrate group containing so few species (Moss, '77), and (2) they have a relatively simple feeding apparatus composed of few kinetic elements. Recently, numerous studies on the descriptive morphology (Motta and Wilga, '95, '99; Motta et al., '97), cranial movement patterns (kinematics) (Tricas and McCosker, '84; Frazzetta and Prange, '87; Motta et al., '91, '97; Wu, '94; Ferry-Graham, '98; Wilga and Motta, '98, 2000), and motor activity patterns (Motta et al., '91; Wilga and Motta, '98, 2000; Wilga et al., 2001) of shark feeding mechanisms have been conducted. However, little is known about the biomechanical function of these mechanisms, especially in comparison to that known for bony fish (Lauder and Shaffer, '85; Motta and Wilga, '99).

The vast majority of research conducted on force generation by the cranial musculature has

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concentrated on mammalian mastication. Primarily focusing on the relationships between these forces and cranial design, these studies have found the relative hypertrophication of various cranial dimensions (Ringqvist, '72; Hylander and Johnson, '97), degree of mandibular symphyseal fusion (Greaves, '88b; Hylander et al., '98, 2000; Summers, 2000), and design of cranial sutures (Herring and Mucci, '91) to be related to the forces generated by the cranial musculature during feeding. Studies that have utilized theoretical modeling techniques have determined optimal muscle orientations and jaw morphologies and the mechanical limits of cranial structures (Hylander, '85; Greaves, '88a, 2000, 2002; Throckmorton and Dechow, '94). However, most of these studies have used proxies of the forces generated during feeding (electromyography of jaw musculature, bone strain patterns) in lieu of direct measures.

Bite force in particular, which is one of the least investigated aspects of feeding in sharks (Motta and Wilga, 2001), is an informative measure of ecological performance¹ because successful prey capture and processing are critical to an animal's existence (Wainwright and Reilly, '94; Binder and Van Valkenburgh, 2000; Herrel et al., 2001a). Bite force has been shown to affect the timing of ontogenetic diet shifts (Hernandez and Motta, '97; Clifton and Motta, '98), breadth of dietary diversity (Wainwright, '87, '88; Clifton and Motta, '98), niche diversification (Kiltie, '82; Herrel et al., 2001b), exemplify patterns of sexual dimorphism (Herrel et al., '99), and has been used to indicate the functional effects of morphological transitions in muscle placement throughout evolution (Dechow and Carlson, '83; Thomason and Russell, '86). In all cases, the magnitude of generated bite force was a limiting factor on resource utilization.

Previously, the only bite forces measured from sharks were obtained using a gnathodynamometer in which forces were estimated from the depths of indentations made by metal ball bearings in an aluminum core when sharks bit an outer plastic sleeve. However, much error was associated with these measurements because individual bites could not be differentiated nor the region of the jaw where the bite took place identified (Snodgrass and Gilbert, '67; Evans and Gilbert, '71). Additional qualitative inferences of bite force have been based on observations of morphological

characteristics such as the relative hypertrophy of the adductor musculature associated with the feeding mechanism (Moss, '77; Motta and Wilga, '99), robustness of jaws to resist compressive forces (Nobiling, '77; Wilga and Motta, 2000), and dental morphology (Nobiling, '77; Frazzetta, '88; Wilga and Motta, 2000).

The goals of this study are to determine an estimate of the maximum bite force generated by the spiny dogfish *Squalus acanthias*, and to determine an accurate morphological proxy for estimating bite force in sharks. In addition, we relate these measures to the feeding ecology and behavior of this shark to demonstrate the interdependence of morphology, ecology, and behavior in organismal design (Bock, '80; Motta and Kotrschal, '92).

MATERIALS AND METHODS

Experimental animals

Squalus acanthias were collected in July and August, 2001, by otter trawl off the coast of Friday Harbor and Orcas Islands in the San Juan Islands, Washington, USA, and housed at 11°C in a 4.0m diameter holding tank with a flow-through seawater circulation system. Experimental animals were maintained in accordance with the institutional animal care and use guidelines of the Friday Harbor Laboratories (University of Washington) on spot prawns *Pandalus platyceros*, sand lance *Ammodytes hexapterus*, and tubenout *Aulorhynchus flavidus* every two to three days. One group of eight individuals deceased upon collection (37.0–45.1cm SL) was used for morphological analysis and a second group of nine (46.5–53.3cm SL) for muscle stimulation experiments, which were conducted within two weeks of capture (sex undetermined for both groups).

Morphological analysis

In *S. acanthias* the quadratomandibularis is a parallel fibered muscle made up of four divisions (anterior, posterior, superficial, and ventral) (Fig. 1), each of which generates force along a line of action consistent with its fiber direction relative to the jaws (Wilga and Motta, '98). Together with the preorbitalis muscle they comprise the adductor mandibulae complex, the primary elasmobranch jaw adductor (Moss, '72; Motta and Wilga, '95; Motta et al., '97). Unilateral theoretical estimates of maximum tetanic tension (P_O) for the left quadratomandibularis (all divisions included)

¹Performance is the measured level of a characteristic related to an action/behavior, which can be determined by the design of the structure involved in the action/behavior (Domenici and Blake, 2000).

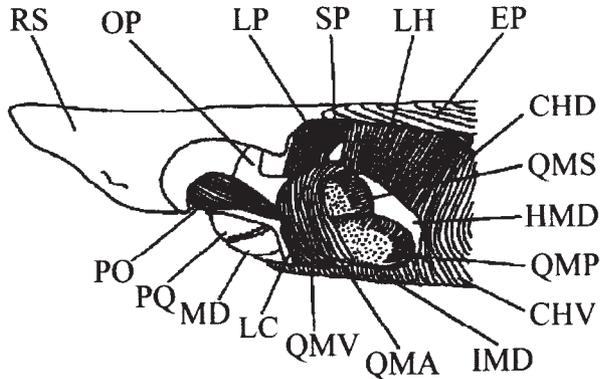


Fig. 1. Left lateral view of the head of a 74.5 cm total length female *Squalus acanthias* with the skin and eye removed and muscle fiber direction indicated. Skin over the rostrum and cranium is left intact. Myosepta only of the epaxialis muscle are indicated. Raphes overlying quadratomandibularis are indicated by stippling. CHD, constrictor hyoideus dorsalis; CHV, constrictor hyoideus ventralis; EP, epaxialis; HMD, hyomandibula of suspensorium; IMD, intermandibularis; LC, labial cartilages; LH, levator hyomandibularis; LP, levator palatoquadrate; MD, mandible or lower jaw; OP, orbital process of palatoquadrate; PO, preorbitalis; PQ, palatoquadrate or upper jaw; QMA, quadratomandibularis anterior; QMP, quadratomandibularis posterior; QMS, quadratomandibularis superficial; QMV, quadratomandibularis ventral; RS, rostrum; SP, spiracularis (from Wilga and Motta, '98).

of each individual were obtained by multiplying its cross-sectional area (CSA) by the specific tension of vertebrate muscle (20 N/cm^2) (Powell et al., '84; Wainwright, '88):

$$P_O = \text{CSA} * \text{specific tension}$$

Estimates of P_O were doubled to determine theoretical maximum force from symmetrical, bilateral contraction of *S. acanthias*' quadratomandibularis muscles.

Cross-sectional area for each muscle was determined both physiologically and morphologically. Physiological cross-sectional area was estimated in accordance with the method of Powell et al. ('84) using the following equation:

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

where ϕ is the average angle of muscle fiber pinnation from the muscle's central tendon, FL is the average fiber length within the muscle, and the density of fish muscle is 1.05 g/cm^3 (Lowndes, '55). ϕ was estimated as 0° because each of the four divisions of the quadratomandibularis muscle in *S. acanthias* is parallel fibered, i.e. they do not insert on a central tendon in the traditional pinnate sense (Liem and Summers, '99). Wet masses (g) were taken for each muscle upon

excision, and were then soaked in 95% ethanol for dehydration and allowed to air-dry until being reweighed to determine dry masses (g). The average of each muscle's wet and dry masses was used to determine cross-sectional area. Fiber lengths were measured at five points between the dorsal, medial, and ventral portions of the quadratomandibularis using digital calipers, and the averages of these measurements were used in calculations of cross-sectional area. Fiber length was assumed to be that of the muscle in a given region because the parallel fibers within each division of the quadratomandibularis are stacked end on end, making the effective fiber length that of the muscle and obviating the need to enzymatically digest the surrounding perimysium to measure individual fibers (Biewener and Full, '92; Adriaens et al., 2001). In four individuals the physiological cross-sectional area was determined for the intact quadratomandibularis, whereas the quadratomandibularis of the other four experimental animals was separated into its four divisions (anterior, posterior, superficial, and ventral), and the physiological cross-sectional area of each division was determined. These areas were then summed for the total physiological cross-sectional area of the four divisions.

Morphological cross-sectional area was determined on the same eight individuals by bisecting the entire quadratomandibularis in the transverse plane through its center of mass perpendicular to the principle fiber direction and taking digital images of the cross-sections with a Nikon Coolpix 950 digital camera mounted in a Nikon SMZ800 dissecting microscope with a 0.5 objective lens. Cross-sectional areas were then measured from the images with NIH Image 1.62 Software. As in measurement of physiological cross-sectional area, morphological cross-sectional area was determined for four intact and four separated (anterior, posterior, superficial, and ventral divisions) quadratomandibularis muscles. Center of mass (intact or individual division) was estimated by allowing a muscle to freely hang from a pin with which it had been pierced. From this pin a weighted (plumb) line was hung, and the line it made along the muscle was traced. After repeating this from another point, the intersection of the two line-tracings indicated the center of mass of the muscle.

In order to determine the theoretical maximum bite force at the anterior margin of the jaws of *S. acanthias*, estimates of the perpendicular component of the theoretical maximum tetanic tension

($\perp P_O$) of each quadratomandibularis were determined via trigonometric analysis:

$$\perp P_O = \sin \theta * P_O$$

where θ is the angle between the lower jaw (Meckel's cartilage) and the line of action of the quadratomandibularis, because only the component of a muscle force vector perpendicular to the lower jaw generates motion about that jaw in a rotating system such as the feeding mechanism of *S. acanthias* (Fig. 2). Lines of action were determined by analyzing the superficial fiber architecture of each muscle in relation to its center of mass. Bilateral values of $\perp P_O$ (the in-lever force or force applied to the lower jaw) were multiplied by their respective mechanical advantage ratios for jaw closing, the jaw's in-lever length (L_I) divided by its out-lever length (L_O) to determine the theoretical maximum bite force of each experimental animal (Westneat, '94; Wainwright and Richard, '95; Cutwa and Turingan, 2000) (Fig. 2):

$$\text{Force}_{\text{Out-lever}} = \text{Force}_{\text{In-lever}} * (L_I/L_O)$$

Mechanical advantage ratios indicate the relative trade-off between force and velocity in a lever system, with values closer to one indicating force amplification and those closer to zero indicating velocity amplification for a class III lever system such as the shark jaw (Westneat, '94; McGowan, '99; Wainwright, '99). In-lever distances were measured from the center of rotation of the articulations between the upper (palatoquadrate) and lower jaw cartilages to the centers of mass of the intact quadratomandibularis or its divisions for each respective method. Out-levers were

measured from the center of rotation of the jaw joints to the tip of each tooth in the functional tooth row. Those measured to the anterior most tooth in the functional row were used for comparisons of theoretical maximum bite force between methods.

Muscle stimulation

In vivo bite force measurements were taken from nine additional *S. acanthias* (46.5–53.3 cm SL) for comparison with the theoretical estimates of maximum bite force generation determined from physiological and morphological measurements of cross-sectional area. After being anesthetized in a 0.04 g l⁻¹ seawater solution of tricaine methanesulfonate (MS-222), experimental animals were strapped ventral side up to an operating table, where they remained for the duration of the experiment, and the anterior divisions of the left and right quadratomandibularis muscles of each individual were implanted with 0.002 cm diameter stainless steel electrodes via 25 gauge hypodermic needles. Tetanic fusion of the quadratomandibularis muscles was accomplished by burst stimulation with a Grass stimulator at 90Hz and 20V with a 3ms pulse width. Force production was measured via a Millar Mikro-Tip catheter pressure transducer sealed within rubber surgical tubing and placed between the upper and lower jaws at their respective symphyses and a Millar TCB-600 Transducer Control Unit. Pressure data from each individual were acquired via a National Instruments DAQpad 6020E data acquisition board in three five-bite series with a two-minute rest period between series. These data were then converted into force measurements (N) using Matlab 6.0 R12 software. The pressure transducer was calibrated at the onset of each animal's measurements by placing it between the jaw symphyses and resting standard weights on a platform attached to the lower jaw to mimic force applied to the transducer during biting. During the rest periods and intermittently throughout calibrations, *S. acanthias* were perfused with an aerated 0.04 g l⁻¹ seawater solution of MS-222 to reduce the effects of fatigue on the muscle and to maintain a constant level of anesthesia, and were out of water for no more than fifteen minutes total. The means of the maximum forces from each of the three five-bite series were used in statistical analyses. Upon completion of bite force trials, individuals were returned to the holding tank and manually ventilated until able to swim autonomously.

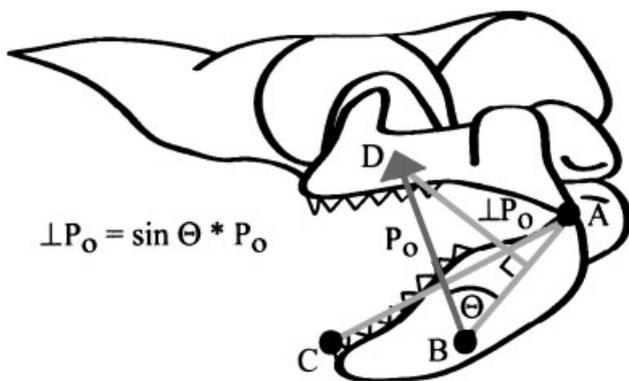


Fig. 2. Schematic diagram of the jaws of *Squalus acanthias* indicating jaw-closing lever arms and force vectors. Line AB, in-lever; AC, out-lever; BD, muscle force vector; P_O , maximum tetanic tension; $\perp P_O$, component of P_O perpendicular to the in-lever; θ , angle between the in-lever and muscle force vector.

Statistical analyses

All cross-sectional area, maximum bilateral tetanic tension, and maximum bite force values were regressed against standard length to eliminate the effects of size and residuals were used for statistical comparisons in SigmaStat 2.03 (SPSS Inc., 1997). One-way analysis of variance was performed to identify significant differences between (a) cross-sectional area of the quadratomandibularis, (b) maximum bilateral tetanic tension determined using the Powell et al. ('84) method, and (c) theoretical maximum bite force values resolved using lever ratio analysis. The data comprising these three variables were grouped into four treatments: (1) Morphological cross-sectional area, maximum bilateral tetanic tension, and theoretical maximum bite force comprised of data from both whole and divided muscles; (2) Physiological cross-sectional area, maximum bilateral tetanic tension, and theoretical maximum bite force comprised of data from both whole and divided muscles; (3) Intact muscle cross-sectional area, maximum bilateral tetanic tension, and theoretical maximum bite force comprised of data from both morphological and physiological measurements, and (4) Divided muscle cross-sectional area, maximum bilateral tetanic tension, and theoretical maximum bite force comprised of data from both morphological and physiological measurements. These are subsequently referred to as the Morphological, Physiological, Intact, and Divided methods of determining bite force in *S. acanthias*. Maximum theoretical bite force values from each of these four groups were then compared to the in vivo maximum bite force measures taken with the pressure transducer by means of a Kruskal-Wallis analysis of variance on ranks to identify significant differences between theoretical and in vivo maximum bite force measurements. This non-parametric analysis of variance was used due to a lack of equality of variance between these data as determined by the Levine Test in SigmaStat ($P=0.003$). Force values from the above four groups and in vivo bite force measures were also regressed against standard length through the origin (0,0 on a Cartesian plane) to standardize the values for comparison, and the resulting linear equations were evaluated at the average standard length of all experimental animals ($SL=45.3\text{cm}$) to compare the average percent differences among these methods. From morphological analyses a distribution of theoretical maximum bite forces

around the lower jaw of a *S. acanthias* of the average standard length of those animals sampled ($SL=45.3\text{cm}$) was determined as well.

RESULTS

No differences were found in (a) cross-sectional area ($P=0.999$), (b) maximum bilateral tetanic tension calculated using the method of Powell et al. ('84) ($P=0.999$), or (c) theoretical maximum bite force measurements from lever analyses ($P=0.999$) as determined by the four treatments of measuring cross-sectional area for the quadratomandibularis (see methods for description) (Table 1). Data obtained using the Morphological method of determining cross-sectional area, and subsequently maximum bilateral tetanic tension and theoretical maximum bite force, demonstrated a stronger relationship with standard length than did that of the Physiological method. Furthermore, bite force values determined by summing the areas of the divisions of the quadratomandibularis (Divided) were more accurately predicted by standard length than using the method of measuring the whole muscle (Intact) (Table 2, Fig. 3). Thus, the Physiological and Intact groups of data (see methods) were not included in Figure 3.

Although no differences were found among the different methods of estimating theoretical maximum bite force, the Morphological and Divided methods of determining cross-sectional area and subsequently theoretical maximum bite force of the quadratomandibularis muscle demonstrated the most linear relationships with standard length, indicating they should be used in conjunction when estimating the theoretical force generated by this muscle. During in vivo biting trials, the measured forces ranged from 0.77–19.57 N, and exhibited a positive relationship with standard length ($R^2=0.629$) (Fig. 3). No significant differences were found between these values and the theoretical maximum bite force values from each method of morphological analysis ($P=0.982$, Table 1). After standardization via regression through the origin, forces predicted at the anterior tip of the lower jaw of a 45.3cm *S. acanthias* from the Morphological and Physiological methods of estimating cross-sectional area were 0.9% and 10.93% different from the biting trial estimate of 8.23N respectively (Table 3). Forces from cross-sectional area measurements of Intact and Divided quadratomandibularis muscles were 38.85% and 12.77% different, corroborating the previous

TABLE 1. Results of ANOVAs of morphological and bite force variables as determined by the morphological, physiological, intact, divided, and pressure transducer methods of estimating bite force in *Squalus acanthias*

Variable	d.f.	F	H	P
Cross-sectional Area ¹	3	1.38E-29		0.999
Maximum Tetanic Tension ¹	3	1.18E-28		0.999
Theoretical Maximum Bite Force ¹	3	5.81E-29		0.999
Theoretical and in vivo Maximum Bite Force ²	4		0.416	0.982

¹Parametric One-Way ANOVA; ²Non-Parametric Kruskal-Wallis One-Way ANOVA on Ranks.

TABLE 2. Results of linear regressions (R^2) of cross-sectional area and maximum bilateral tetanic tension of the quadratomandibularis muscle and theoretical maximum bite force against standard length for each method of morphologically determining bite force in *Squalus acanthias*

Method	Cross-Sectional Area	Max. Bilateral Tetanic Tension	Bite Force at Tip of Jaw
Morphological	0.879	0.875	0.704
Physiological	0.806	0.806	0.593
Intact QM	0.179	0.179	0.575
Divided QM	0.797	0.795	0.932

indication that the Morphological and Divided methods should be used in conjunction. Calibrations with the sharks' weighted jaws determined that at forces greater than 1N (89% of measurements), the pressure transducer was 79.9–97.5% accurate.

Measurement of out-levers to each tooth in the functional row yielded a series of average theoretical maximum bite forces for a *S. acanthias* of the average standard length of the experimental animals (SL=45.3cm) ranging from 18.34 N at the posterior most tooth to 6.68 N at the anterior most (Fig. 4). These calculations were made under the assumption that the lower jaw of *S. acanthias* functions as a rigid plane subjected to symmetrical bilateral contraction of the quadratomandibularis muscles during jaw adduction about both jaw joints functioning as simple hinges with negligible energy lost to friction. Equivalence of sarcomeres, the assumption that all sarcomeres in a muscle are of equal size and shorten an equal amount, must be assumed as well because the force generated by a muscle is a function of the velocity and distance of sarcomere displacement (Gans et al., '85; Gans and Gaunt, '91; Galis, '92; Hernandez and Motta, '97). If these assumptions were invalid, potential

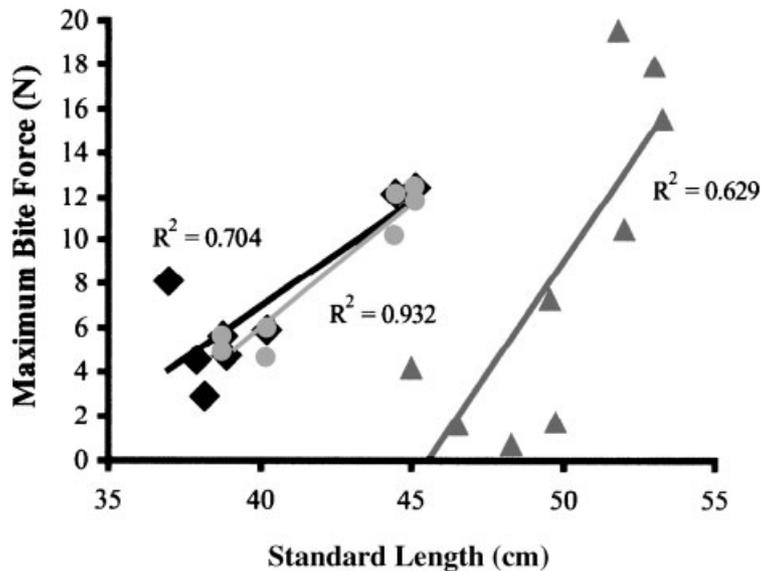


Fig. 3. Results of linear regressions of maximum bite force of *Squalus acanthias* from theoretical and in situ measurements versus standard length. ◆=theoretical bite forces from the Morphological method of determining cross-sectional area

of the quadratomandibularis; ●=theoretical bite forces from the Divided method of determining cross-sectional area of the quadratomandibularis; ▲=actual bite forces from in vivo bite force measurements.

TABLE 3. Accuracy of morphological methods of estimating bite force in *S. acanthias*

Method	Predicted Value (N) ¹	%Different than Bite Force Trials
Morphological	8.15	0.90
Physiological	7.42	10.90
Intact QM	5.95	38.85
Divided QM	9.28	12.77

¹Predicted bite force at the anterior tip of the lower jaws of an *S. acanthias* of the average standard length of all experimental animals (45.3cm).

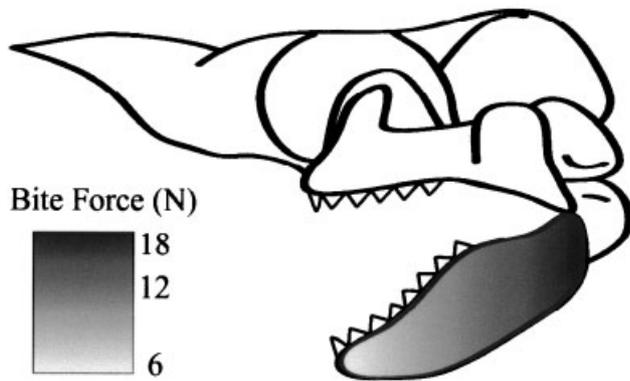


Fig. 4. Left lateral view of the head of *Squalus acanthias* of the average standard length of all experimental animals (45.3cm) with a gradient map along the lower jaw indicating the average maximum theoretical bite force measurements (6.68 — 18.34 N) for out-levers measured to each tooth in the functional row.

force calculations would deviate considerably from realized force generation.

DISCUSSION

The study of bite force has implications for our knowledge of both the ecology and evolution of gnathostomes. Detailed analysis of feeding mechanisms reveals the morphological and mechanical basis for trophic diversity amongst animals. This diversity is directly linked to the behavioral capacity (performance) of an organism to exploit the resources associated with its niche. Bite force as a performance measure has been shown to affect dietary diversity and niche overlap in both terrestrial and aquatic vertebrates (Kiltie, '82; Wainwright, '88; Herrel et al., 2001b). For example, the generated magnitude of bite force was shown to be the limiting factor on the size of barnacles consumed by an ontogenetic series of sheepshead *Archosargus probatocephalus*, with those individuals capable of greater bite forces

canalizing their diet to exploit a novel resource (large barnacles) that most other fish are incapable of consuming (Hernandez and Motta, '97). Therefore, bite force measurements can serve as estimates of the prey that an animal is physically capable of consuming and of an organism's fit to its environment, given that the selective pressures associated with the feeding mechanism are thoroughly understood. Additionally, by identifying the morphological characters to which different performance levels of bite force are associated, the effects that environmental pressures have had on the evolution of cranial design can be better understood. In doing so, the evolutionary trajectories that gave rise to various feeding mechanisms such as ram, suction, and biting in fish can be compared across taxa on a morphological, ecological, and behavioral basis.

Methodological comparison and ecological morphology

Despite the fact that no significant differences were found in cross-sectional areas, maximum bilateral tetanic tensions, and theoretical maximum bite forces using the four methods of analyzing the quadratomandibularis muscle, it was determined that the Morphological method of estimating cross-sectional area should be used in conjunction with the separation of the quadratomandibularis into its constituent divisions for the most accurate estimation of force production by this muscle. This finding was based on (1) the strong linear relationships that the Morphological and Divided methods exhibited with standard length (Table 2) and (2) the accuracy of these methods in estimating bite force as compared to the *in vivo* bite forces from the stimulation experiments (Table 3). This method calculates potential force by estimating cross-sectional area directly from the separate but summed divisions of the quadratomandibularis. This morphological procedure of determining bite force represents a relatively simple method for estimating bite force in light of the inherent difficulty and cost of maintaining sharks in captivity and measuring bite force *in situ* with force transducers. A further complication with *in situ* field measurements is a lack of behavioral motivation by the experimental animals associated with an artificial feeding situation, which may result in widely varying bite forces. This method of estimating bite force has direct military and civilian applications as well, as underwater cables and fishing gear are often

damaged by shark bites (Hurley et al., '87; Marra, '89). Using this methodology, an industry developing aquatic technology can assess the potential threat (bite force) posed by the sharks endemic to the region and design their products to resist such forces.

Our theoretical bite forces based on muscle morphology underestimated the maximum bite force measured at the tip of the jaws during stimulation (19.57N). Such theoretical measures of bite force based on morphology might underestimate bite force measurements taken from live, free-swimming sharks or restrained, electrically stimulated sharks for a variety of reasons. During eccentric muscle contraction, when a muscle is activated while being stretched, perhaps by an antagonist, the maximum force generated can exceed that produced during tetanic stimulation of static muscle (Askew and Marsh, '97; Josephson, '99). This phenomenon is thought to be due to high variability in sarcomere length, which develops during stretching, and is augmented by rapid lengthening of the muscle (Josephson, '99; Marsh, '99). Bite forces measured during stimulation might also underestimate the actual capability of *S. acanthias* because the preorbitalis muscle, which is developmentally linked to the quadratomandibularis in *S. acanthias* and plays a role in jaw closing and palatoquadrate protrusion (Wilga and Motta, '98), was not stimulated. However, these maximum bite forces were induced by electrical stimulation of the quadratomandibularis muscle using stimulation voltages several orders of magnitude higher than the stimulation voltages occurring within the vertebrate neuromuscular system (Basmajian and De Luca, '85), and may therefore be higher than those bite forces occur-

ring during natural, voluntary biting. Thus, the biological relevance of maximum bite force measurements from stimulation experiments is questionable as these experiments biomechanically indicate the strength of muscles, but do not account for the neurophysiological control that would accompany voluntary biting (Dechow and Carlson, '83).

Although oral jaw bite force has been measured in only a few vertebrates (Table 4), the values for *S. acanthias* measured in this study are substantially lower than those of the only other fishes investigated, *A. probatocephalus* (196.55 N) and the silky shark *Carcharhinus falciformis* (889 N) (Evans and Gilbert, '71; Hernandez and Motta, '97). All things being equal, bite force increases positively with animal size and hence muscle cross-sectional area (Schmidt-Nielson, '84; Gans and Gaunt, '91). Consequently, a two-meter long *C. falciformis* such as that studied by Evans and Gilbert ('71) is expected to generate substantially greater bite force than the *S. acanthias* examined in this study. However, the *A. probatocephalus* investigated were approximately two-thirds the size of the average *S. acanthias* used in this study. The difference in bite force is explained by the molluscivorous diet of adult *A. probatocephalus*. *Squalus acanthias* is a trophic generalist and consumes little if any durophagous prey (Alonso et al., 2002).

Maximum pharyngeal jaw biting force has been determined in a number of labrid fishes such as the Caribbean hogfish *Lachnolaimus maximus* (290.3 N) and the bluehead wrasse *Thalassoma bifasciatum* (4.5 N) (Wainwright, '88; Clifton and Motta, '98). Pharyngeal bite force within the labrids was also positively correlated with the

TABLE 4. Maximum bite forces for twelve animals

Species	Bite Force (N)	Reference
bluehead wrasse (bony fish) ¹	5	Clifton and Motta, '98
spiny dogfish	20	Huber and Motta, this work
laboratory rat	50	Robins, '77
Canary Island lizard	109	Herrel et al., '99
sheepshead (bony fish)	197	Hernandez and Motta, '97
Spanish hogfish ¹	290	Clifton and Motta, '98
rhesus monkey	500	Dechow and Carlson, '83
labrador dog	550	Strom and Holm, '92
human	680	Ringqvist, '72
silky shark	889	Evans and Gilbert, '71
spotted hyena	4500	Binder and Van Valkenburg, 2000
American alligator	13300	Paul, '88

¹Pharyngeal jaw bite force.

degree of durophagous prey in the diet and negatively correlated with dietary diversity, as often is the case with functional specialists such as the durophagous *L. maximus* (Wainwright, '88; Clifton and Motta, '98; Ferry-Graham et al., 2002). An ontogenetic increase in bite force generation in *S. acanthias* associated with allometric growth of the quadratomandibularis may be expected because at 60 cm (TL) a Patagonian population of *S. acanthias* undergoes an ontogenetic dietary shift from fish, squid, and ctenophores to primarily fish (Alonso et al., 2002).

Although the estimates of theoretical maximum bite force determined in this study may underestimate actual bite force generation by *S. acanthias*, these low maximum bite force values indicate that a mechanism other than force generation may be a critical factor in effective predation by this shark. The fine tips and cutting surfaces of shark teeth enable bite force to be concentrated over a small area, resulting in relatively high-pressure application. Fracture or rupture of material (prey) occurs when shear stresses arise in that material as it bulges around a compressive element (tooth) (Frazzetta, '88). When these stresses reach a critical level, the inter-atomic bonds of the material undergo catastrophic failure and rupture, the extent of which is proportional to the rate and magnitude of the applied pressure, and is augmented by the movement of the compressive element through the material (Frazzetta, '88; Martin et al., '98; McGowan, '99). Head-shaking by *S. acanthias* while grasping compliant teleost prey (Wilga and Motta, '98) augments this cutting action by dragging the non-serrated edges of the teeth across the prey. As *S. acanthias* swings its head from side to side, the laterally pointed oblique cusps on its teeth would concentrate stress on the tooth tips being driven into the prey resulting in their penetration (Frazzetta and Prange, '87; Wilga and Motta, '98). The laterally orientated arrangement of the hyomandibula (principal connection between the jaws and chondrocranium) relative to the chondrocranium in squaloid sharks provides a strong structural support for the feeding mechanism during this head-shaking behavior (Moss, '77). Thus, head-shaking in *S. acanthias* is a prime example of how behavior mediates the relationship between morphology and ecology. Additionally, as the teeth of *S. acanthias* increase in size towards the rear of its mouth, so does the functional cutting surface of each tooth. Thus, as lever mechanics dictate

that bite force increases caudally along the jaws of *S. acanthias*, functional differentiation may exist in the use of its pointier anterior teeth (piercing) and broader posterior teeth (slicing).

The rate at which pressure is applied to a prey item by the teeth of *S. acanthias* is augmented by the design of its jaw system. The mechanical advantage ratios for jaw closing in each specimen analyzed ranged from 0.13–0.28, indicating that velocity is amplified at the tip of the jaws, which move faster than the muscles causing the movement are shortening (Westneat, '94; Wainwright and Richard, '95). This range of mechanical advantage values for jaw closing corresponds to that found by Wainwright and Richard ('95) for 18 coral reef fishes employing ram or suction based feeding mechanisms, in which rapid jaw movements are essential to prey capture. These values were significantly lower than those found for 16 coral reef fishes employing biting mechanisms, in which force amplification is desirable (Wainwright and Richard, '95). The velocity of lower jaw elevation by *S. acanthias* (40.3 cm/s) is faster than both the horn shark *Heterodontus francisci* (24.7 cm/s) and the leopard shark *Triakis semifasciata* (25.1 cm/s), but slower than that of the bonnet-head shark *Sphyrna tiburo* (46.6 cm/s), all of which utilize rapid jaw movements for either ram or suction feeding (Ferry-Graham, '98; Wilga and Motta, '98, 2000; Edmonds et al., 2001). This rapidity of lower jaw elevation may impart substantial momentum to the jaws, augmenting penetration of a prey item by the teeth (Wassersug and Yamashita, 2001), and facilitate rapid jaw closure for capture of elusive prey.

The extensive palatoquadrate protrusion exhibited by *S. acanthias* aids in securing prey by reducing the time to jaw occlusion during the bite cycle and by reducing the gape by 51% at maximum protrusion (Wilga and Motta, '98), and in gouging prey by extending the palatoquadrate beyond the margin of the mouth, enabling it to excise pieces of a prey item larger than the mouth (Moss, '72, '77; Tricas and McCosker, '84; Frazzetta and Prange, '87). These characteristics of palatoquadrate protrusion assist force application by the lower jaws of *S. acanthias* in the cutting and processing of a prey item. Palatoquadrate protrusion in *S. acanthias* occurs faster (19.7 cm/s) than in any other shark investigated except *H. francisci* (31.3 cm/s), and reduces maximum gape considerably more than has been observed in any other shark (*S. tiburo* – 13%, *Negaprion brevirostris* – 26%, *T. semifasciata* – 33%,

H. francisci – 39%) (Motta et al., '97; Ferry-Graham, '98; Wilga and Motta, '98, 2000; Edmonds et al., 2001). This rapid movement of the palatoquadrate likely imparts substantial momentum to the bite as well (Wassersug and Yamashita, 2001).

Squalus acanthias is primarily a suction feeder (69% of prey captures, Wilga and Motta, '98) and is, therefore, relatively less reliant upon generating large bite forces in order to be an effective predator than ram-feeding or durophagous sharks. The coupling of an effective morphological design for suction feeding, rapid jaw adduction, and the ability to extensively protrude the palatoquadrate alleviate *S. acanthias*' need to generate large bite forces. Its versatile feeding mechanism, as evidenced by the ability of *S. acanthias* to modulate its feeding behavior with respect to the type of prey offered (Wilga and Motta, '98), is important to its effective predation at the higher trophic levels (Moss, '72; Cortes, '99), and may contribute to *S. acanthias* being one of the most abundant extant elasmobranchs (Compagno, '84).

In summary, other than direct measures of bite force from free-swimming sharks, the most simple and accurate method of morphologically estimating bite force in *S. acanthias*, or other sharks in which the jaw adductor musculature is parallel fibered within its constituent divisions, is to sum the cross-sectional areas of these divisions, determine the maximum tetanic tension of the adductors from these measurements, and use jaw lever-ratio analysis to resolve the output force generated by these muscles with respect to discrete positions along the lower jaw. Theoretical maximum bite force as determined by these methods is indicative of the potential ecological niche of an animal (Wainwright, '87, '88). When compared to the bite forces that the animal actually generates in nature (in situ bite force measurement), which are indicative of its realized ecological niche (Wainwright, '87, '88), behavioral and physiological constraints on the feeding mechanism as well as potential niche overlap between species can be identified. Lastly, comparison of potential and realized niches provides a potential yardstick for estimating the behavioral and ecological plasticity of animals and their feeding mechanisms.

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