# Is Extreme Bite Performance Associated with Extreme Morphologies in Sharks?*

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## ABSTRACT

As top predators in many oceanic communities, sharks are known to eat large prey and are supposedly able to generate high bite forces. This notion has, however, largely gone untested due to the experimental intractability of these animals. For those species that have been investigated, it remains unclear whether their high bite forces are simply a consequence of their large body size or the result of diet-related adaptation. As aquatic poikilotherms, sharks can grow very large, making them ideal subjects with which to investigate the effects of body size on bite force. Relative bite-force capacity is often associated with changes in head shape because taller or wider heads can, for example, accommodate larger jaw muscles. Constraints on bite force in general may also be released by changes in tooth shape. For example, more pointed teeth may allow a predator to penetrate prey more effectively than blunt, pavementlike teeth. Our analyses show that large sharks do not bite hard for their body size, but they generally have larger heads. Head width is the best predictor of bite force across the species included in our study as indicated by a multiple regression model. Contrary to our predictions, sharks with relatively high bite forces for their body size also have relatively more pointed teeth at

the front of the tooth row. Moreover, species including hard prey in their diet are characterized by high bite forces and narrow and pointed teeth at the jaw symphysis.

## Introduction

Sharks are top predators in oceanic communities (Moss 1977; Cortes 1999; Motta and Wilga 2001) and have intrigued both scientists and the general public for over 2,000 years (Hamlett 1999). Larger species are known to include large and/or hard prey, such as marine mammals, sea turtles, sea birds, and other elasmobranchs, in their diet (Cortes 1999; Wetherbee and Cortes 2004) and consequently are assumed to have a high absolute bite force (Huber et al. 2006). Fossil forms have even been reported to bite large protostegid turtles and archeocetes (Purdy 1996; Shimada 1997; Shimada and Hooks 2004). However, whether the ability of these large sharks to consume such large prey is a consequence of their overall body size or the result of selection on bite-force capacity independent of body size (changes in head shape, feeding mechanics, etc.) is not known. Being aquatic poikilotherms, sharks can attain very large body sizes (Fig. 1), making them ideal subjects in which to investigate the effects of body size on bite force. Given that the force-generating capacity of muscle is proportional to its cross-sectional area, bite force will increase with length to the second power in isometrically growing organisms. Thus, larger animals will be able to bite relatively hard for their head or body length (Hill 1950; Herrel and Gibb 2006).

In other groups of vertebrates, body-size-independent increases in bite-force capacity are often associated with changes in head shape because taller or wider heads, for example, can contain more muscle and allow for more favorable muscular orientation (e.g., Herrel et al. 1999, 2001*a*, 2001*b*, 2007; Huber et al. 2006). Some of the constraints on bite force may also be released by changes in tooth shape because tooth shape probably has an important effect on the interaction between the jaws and the prey (Lucifora et al. 2001; Whitenack et al. 2004). For animals consuming relatively soft prey, teeth that facilitate better penetration of their prey for a given magnitude of bite force may be selected for (Evans and Sanson 1998). Sharp, pointed teeth optimize penetration of the teeth into the soft prey as they concentrate force onto a small surface area (Frazzetta 1988). Animals specializing in hard prey with stiff and/or tough exoskeletons (i.e., durophagous species eating crustaceans, mollusks, etc.) will probably have more blunt teeth with a lower aspect ratio and higher surface area to prevent fracture (Reif 1976; Nobiling 1977). However, given that con-

Precaudal Length

1 m

*Sphyrna mokarran*

*Carcharhinus leucas*

*Carcharhinus limbatus*

*Heterodontus francisci*

*Chiloscyllium plagiosum*

*Heptranchias perlo*

*Negaprion brevirostris*

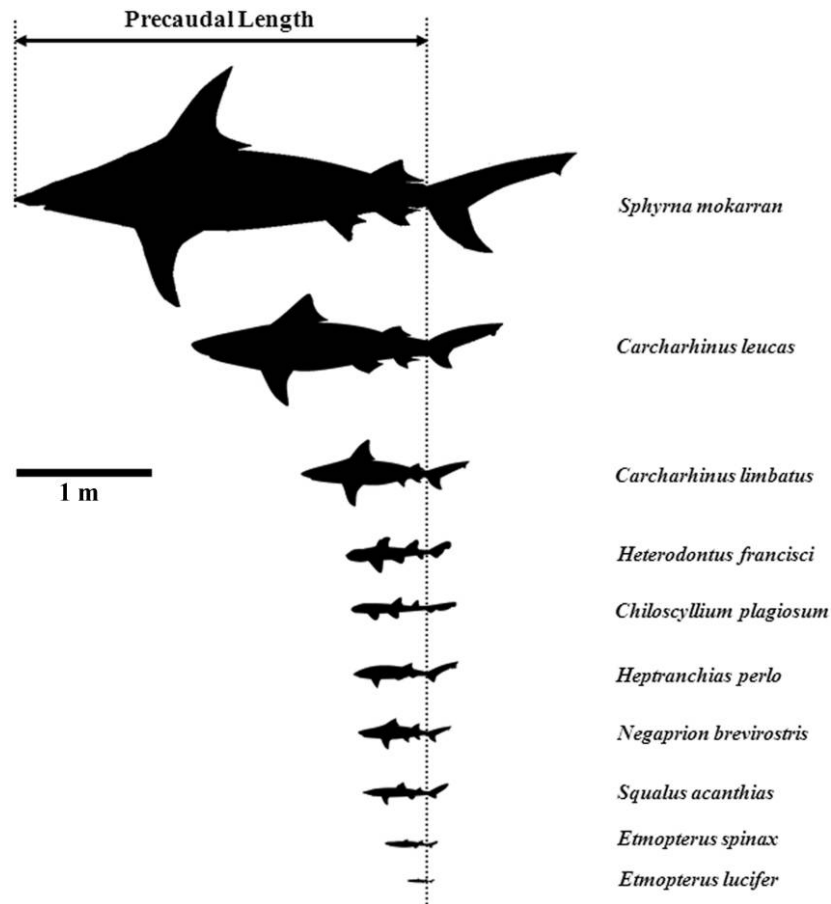*Squalus acanthias*

*Etmopterus spinax*

*Etmopterus lucifer*

Figure 1. Outlines of the different species of sharks included in our study to illustrate the great size range encompassed by these species.

tinuous tooth replacement is characteristic of sharks (Strasburg 1963), tooth breakage may not represent a significant constraint on their feeding performance. In some sharks, the dentition is heterodont and may function differently depending on their position along the jaw. This may allow them to efficiently exploit functionally different prey types (e.g., both hard/stiff and soft/fibrous prey).

Interestingly, the evolution of durophagous feeding habits has occurred independently several times among cartilaginous fishes and is often associated with one or more morphological specializations of the feeding mechanism (Huber et al. 2005, 2008; Dean et al. 2007a). These specializations may include a molariform or pavementlike dentition, hypertrophy of the jaw adductor muscles, and a high-leverage jaw-adducting mechanism (Summers 2000; Summers et al. 2004; Huber et al. 2005, 2008). Although high bite forces may be achieved by hypertrophy of the jaw muscles or allometric changes in biomechanical characteristics of the feeding mechanism relative to body or head size (Huber et al. 2005, 2006, 2008), an alternative strategy may be to increase overall body or head size (Herrel and O'Reilly 2006). Larger animals will by definition have a greater muscular cross-sectional area and will thus be able to bite harder (Herrel et al. 2005). Similarly, animals with relatively larger heads will be able to bite harder as well (Herrel et al.

1999, 2001a, 2001b). For very large predators, selection on bite-force capacity is likely to be relaxed as a larger proportion of their potential prey will be unable to withstand their high bite forces (Aguirre et al. 2003). Thus, larger/harder prey often make up a bigger proportion of the diet in larger individuals and species of sharks and other vertebrates (Cortes 1999; Simpfendorfer et al. 2001; Adnet and Martin 2007).

In this study, we explore the scaling of bite force and head shape across 10 species of sharks to test whether larger species do indeed have relaxed selection on bite force (Fig. 1). If so, we expect bite force to scale isometrically (i.e., being a consequence of geometric growth) or with negative allometry relative to body size. Second, we test which morphological traits related to head and body size are the best predictors of bite force across species. Given the importance of tooth shape, we explore whether a simple indicator of this parameter is correlated with bite force. We predict that species with relatively sharper, pointed teeth will have relatively lower bite forces because having more pointed teeth likely facilitates penetration of soft prey. Species with blunter teeth are likely to be hard-prey specialists and are expected to have relatively greater bite forces. Finally, we test whether species that include hard prey in their diet differ in head size, bite force, and tooth shape from nondurophagous species.

Table 1: Overview of the data

| Genus and Species | N | Diet[a] | Tooth Index | Standard Length (cm) | Mass (g) | Prebranchial Length (cm) | Head Width (cm) | Head Height (cm) | Anterior Bite Force (N) | Bite-Force Method[b] |
|---|---|---|---|---|---|---|---|---|---|---|
| *Carcharhinus leucas*[g] | 2 | 0 | .81 | 170.00 ± 41.01 | 95,224 ± 63,806 | 37.35 ± 7.42 | 32.35 ± 6.15 | 31.70 ± 6.08 | 833.50 ± 267.99 | 1 |
| *Carcharhinus limbatus*[d] | 6 | 1 | .5 | 90.25 ± 24.96 | 6,415 ± 2,694 | 23.93 ± 7.32 | 17.37 ± 7.23 | 12.20 ± 4.88 | 186.50 ± 146.68 | 1 |
| *Chiloscyllium plagiosum*[e] | 8 | 1 | .65 | 55.29 ± 6.42 | 1,172 ± 315 | 9.93 ± .95 | 7.20 ± .63 | 5.40 ± .98 | 61.63 ± 16.48 | 1–4 |
| *Etmopterus lucifer*[f] | 2 | 0 | 2.1 | 15.50 ± 4.95 | 31.50 ± 23.33 | 3.25 ± 1.77 | 2.10 ± .71 | 1.45 ± .49 | 1.95 ± 1.63 | 1 |
| *Etmopterus spinax*[f] | 8 | 0 | 1.78 | 32.53 ± 3.80 | 288 ± 89 | 6.98 ± .80 | 4.35 ± .65 | 3.93 ± .53 | 1.01 ± .36 | 2 |
| *Heptranchias perlo*[e] | 4 | 1 | .43 | 54.03 ± 6.58 | 1,240 ± 452 | 10.28 ± 1.97 | 6.08 ± 1.11 | 6.88 ± 1.33 | 130.00 ± 77.52 | 1 |
| *Heterodontus francisci*[g] | 10 | 1 | .7 | 55.50 ± 4.14 | 2,604 ± 595 | 11.55 ± 1.56 | 9.45 ± .18 | 8.42 ± .52 | 159.30 ± 33.24 | 1–4 |
| *Negaprion brevirostris*[e] | 9 | 1 | .58 | 49.56 ± 3.61 | 1,403 ± 211 | 10.62 ± .18 | 7.28 ± .48 | 6.28 ± .97 | 43.22 ± 25.65 | 1–4 |
| *Sphyrna mokarran*[c] | 1 | 0 | .6 | 300.00 | 580,598 | 70.00 | 48.00 | 68.50 | 2,432.00 | 1 |
| *Squalus acanthias*[h] | 8 | 0 | 1.86 | 48.29 ± 5.70 | 892 ± 277 | 10.36 ± .69 | 3.81 ± .92 | 7.39 ± .06 | 12.92 ± 4.43 | 1, 4 |

[a] 0 = eats only soft prey; 1 = includes hard prey in diet (see Compagno 1984a, 1984b, 2001; Compagno et al. 2004).

[b] 1 = morphology; 2 = voluntary; 3 = restrained; 4 = stimulation.

[c] D. R. Huber and K. Mara, unpublished manuscript.

[d] Huber et al. 2006.

[e] Huber 2006.

[f] J. M. Claes and J. Mallefet, unpublished manuscript.

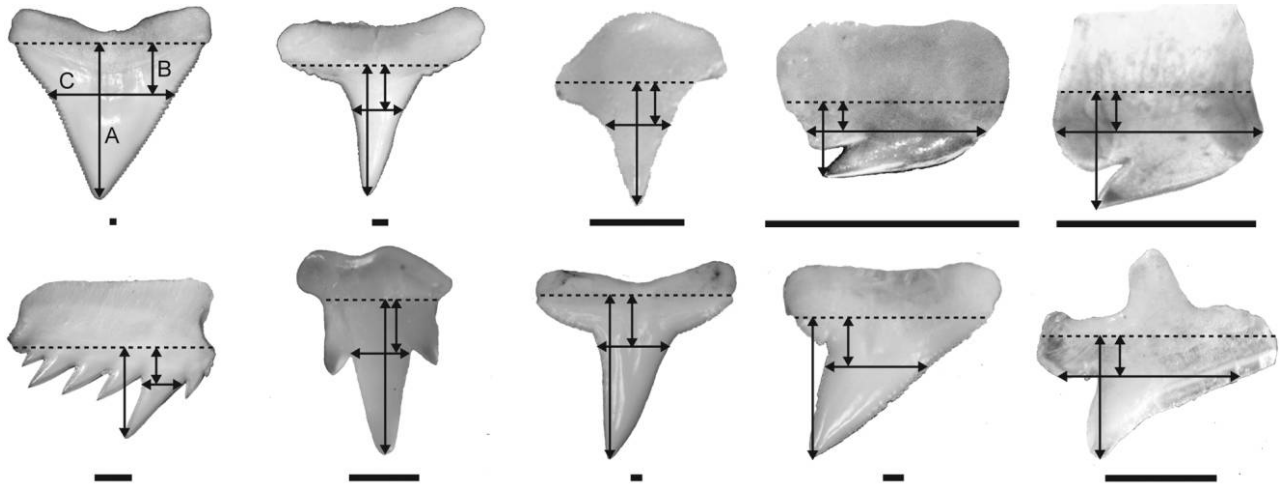[g] Huber et al. 2005.

[h] Huber and Motta 2004.

Figure 2. Images of anterior teeth from all species included in the analysis. From left to right, the upper row shows *Carcharhinus leucas*, *Carcharhinus limbatus*, *Chiloscyllium plagiosum*, *Etmopterus lucifer*, and *Etmopterus spinax*. From left to right, the lower row shows *Heptranchias perlo*, *Heterodontus francisci*, *Negaprion brevirostris*, *Sphyrna mokarran*, and *Squalus acanthias*. All teeth are shown in frontal view, and the scale bar below each tooth indicates 1 mm. All teeth are from the anterior margin of the upper jaw except for *E. lucifer*, *E. spinax*, and *H. perlo*, which are from the anterior margin of the lower jaw (see "Material and Methods"). Our tooth shape index was calculated by dividing the width of the tooth (*C*) at one-third of the crown height (*B*) by the total crown height (*A*). Thus, a smaller tooth index indicates narrower, more pointed teeth (higher aspect ratio).

## Material and Methods

### Morphological Data

Standard (precaudal) length, body mass, prebranchial length, head width, and head height at the first gill slit were measured directly for most species (Table 1). For one species, morphometric data were estimated based on specimens of similar size (*Squalus acanthias*), and for one species, these data were obtained from equations available in the literature (*Etmopterus spinax*; Gennari and Scacco 2007). Only adults were used in our analyses. Tooth shape was quantified by calculating a tooth index representative of a tooth's aspect ratio in which the width of the tooth crown at one third of the crown height was divided by the total crown height. The tooth index was calculated for anterior teeth of either the upper or lower jaw (Fig. 2). For a given species, those teeth with a higher aspect ratio (upper or lower) were selected for analysis because they better represent mechanical constraints on tooth shape during prey capture. Anterior teeth were chosen for this analysis because bite forces were measured and calculated at the anterior margin of the jaws.

### Bite Forces

Bite forces were taken from the literature or estimated by (1) calculating bite force based on muscle and jaw geometry (Huber and Motta 2004; Huber et al. 2005, 2006; Huber 2006; J. M. Claes and J. Mallefet, unpublished manuscript; D. R. Huber and K. Mara, unpublished manuscript), (2) measuring in vivo voluntary bite forces of free-ranging animals (Huber et al. 2005; Huber 2006; J. M. Claes and J. Mallefet, unpublished manuscript), (3) measuring in vivo bite forces in restrained animals (Herrel et al. 1999; Huber et al. 2005; Huber 2006), and (4) tetanic electrical stimulation of the jaw adductors (Huber and Motta 2004; Huber et al. 2005; Huber 2006). When estimates were available based on multiple methods, the highest bite force was retained for each individual (Table 1). All data collected specifically for this study were obtained according to the guidelines of the Institutional Animal Care and Use Committees of the University of South Florida and the Catholic University of Louvain (protocol 1882).

### Analyses

All data were $\log_{10}$ transformed before analysis. Species means were calculated for all morphological variables and maximal bite force. All analyses were conducted based on the raw data as well as using phylogenetically informed methods (Felsenstein 1985; Harvey and Pagel 1991). To take into account the historical relationships among species included in the analysis, we constructed a tree based on previously published articles including both morphological and molecular evidence (Shirai 1996; Winchell et al. 2004; Compagno 2005; Iglesias et al. 2005; Fig. 3). For the analyses, all branch lengths were set to unity because no information is available for divergence times between all taxa included in our analysis. Independent contrasts were calculated using the PDAP package (Garland et al. 1999)

First, we regressed cranial dimensions and bite force against standard length to explore scaling relationships across species (Table 2). Regressions on independent contrasts were forced through the origin (Garland et al. 1999). To test whether slopes were different from predictions of geometric similarity, we used two-tailed *t*-tests (Sokal and Rohlf 1995). Residual data were extracted and used as input for a multiple regression model.
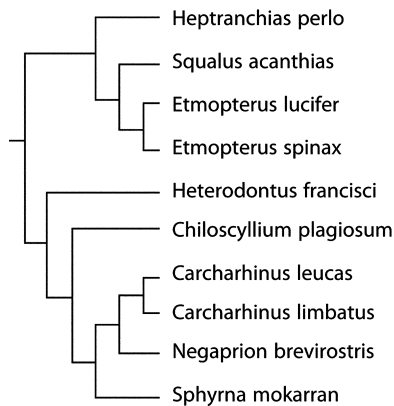
Figure 3. Composite cladogram depicting the relationships between the species used in our analyses. The tree is a consensus of both morphological and molecular studies (see "Material and Methods").

In the model, bite force was set as the dependent variable and morphological data as the independent variables to explore which morphological traits best explained variation in bite force. Next, residual bite force was correlated with the residual tooth index to test whether tooth shape covaries with relative bite force across species.

Finally, ANCOVAs were run with standard length as covariate to test whether durophagous species differ in cranial morphology, bite force, and tooth shape from nondurophagous ones (Table 1). In our dietary categorization, we combined all species that include some hard prey in their diet into one group and those completely lacking hard prey into another (based on Compagno 1984a, 1984b, 2001; Compagno et al. 2004). Although we realize that this is an over simplification of biological reality, it may allow us to detect interesting trends that could be explored in more detail in future studies. Simulation analyses were performed using the PDSIMUL and PDANOVA programs (Garland et al. 1993). In the PDSIMUL program, we used Brownian motion as our model for evolutionary change and ran 1,000 unbounded simulations to create an empirical null distribution against which the F value from the original data

could be compared. In the PDANOVA program, morphological traits and bite force were entered as independents, diet was entered as factor, and standard length was entered as covariate. We considered differences among categories significant if the original F value was higher than the $F95$ value derived from the empirical distribution based on the simulations.

## Results

### Scaling of Morphology and Bite Force

Our data set spans five orders of magnitude in body sizes ranging from the 30 g blackbelly lantern shark *Etmopterus lucifer* to the nearly 600 kg great hammerhead shark *Sphyrna mokarran* and is thus particularly appropriate for scaling analyses (Table 1). Conventional and phylogenetically informed analyses on the independent contrasts give identical results. Both analyses suggest a significant positive allometry in the scaling of head height (Table 2). Thus, larger sharks have relatively taller heads. Both types of analyses also suggested a negative allometry in the scaling of standard length relative to mass, suggesting that larger sharks are relatively more robust (i.e., have a greater body mass for their length). Bite force scaled as expected with a slope not different from 2 in both the conventional and the independent contrast analyses, suggesting no additional selection on bite force relative to body size (Table 2; Fig. 4).

To investigate which morphological traits best explain bite force, we ran a multiple regression analysis with raw data and a significant model with head width as the only predictor was retained ($r = 0.90$; $P < 0.001$; Fig. 4). A similar model using the independent contrasts as input retained a significant model with head width as well ($r = 0.82$; $P = 0.004$). Thus, the evolution toward increased bite force in these sharks has gone hand in hand with an evolution of wider heads.

### Tooth Shape and Diet

Our residual tooth shape index (Table 1) is significantly correlated with residual bite force across species (Pearson correlation, $r = -0.71$; $P = 0.02$; Fig. 5) indicating that sharks with

Table 2: Results of scaling analyses

|  | Intercept | Slope | r | P |
|---|---|---|---|---|
| Conventional analysis: | | | | |
| Standard length ∼ mass | .79 | .294[a] | .99 | <.001 |
| Standard length ∼ prebranchial length | −.76 | 1.050 | .99 | <.001 |
| Standard length ∼ head width | −1.10 | 1.141 | .97 | <.001 |
| Standard length ∼ head height | −1.38 | 1.285[a] | .99 | <.001 |
| Standard length ∼ anterior bite force | −3.07 | 2.695 | .91 | <.001 |
| Independent contrast analysis: | | | | |
| Standard length ∼ mass | | .290[a] | .99 | <.001 |
| Standard length ∼ prebranchial length | | 1.039 | .99 | <.001 |
| Standard length ∼ head width | | 1.017 | .96 | <.001 |
| Standard length ∼ head height | | 1.369[a] | .99 | <.001 |
| Standard length ∼ anterior bite force | | 2.071 | .82 | .004 |

[a] Slopes significantly different from predictions of geometric similarity (two-tailed t-test).
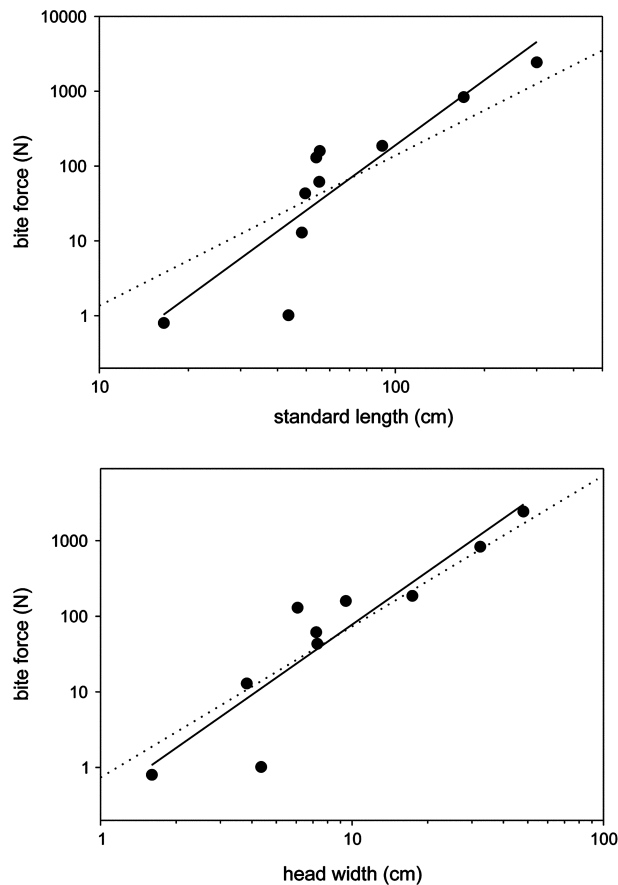
Figure 4. Graphs illustrating the scaling of bite force relative to standard length (*top*) and head width (*bottom*). Dashed lines indicate the expected slope of 2 under geometric similarity. Although the slope of the regression of bite force on standard length is slightly steeper, this is not significantly different from the expected slope of 2, suggesting that large sharks do not bite relatively harder than smaller sharks based on expectations of geometric similarity (see Table 2).

relatively larger bite forces had relatively narrower, pointier teeth. An analysis on the independent contrasts also suggested a relationship between residual bite force and residual tooth shape that was however, not significant (Pearson correlation, $r = -0.52$; $P = 0.15$).

Both conventional and phylogenetic ANCOVA testing for differences in head shape, tooth shape, and bite force between durophagous species and nondurophagous species indicated significant differences in bite force and the tooth index (Table 3). Durophagous species have relatively higher bite forces and relatively more pointed anterior teeth.

## Discussion

The isometric scaling of bite force across species observed here for sharks is different from intraspecific studies on other vertebrate groups, where positive allometric scaling of bite force is typically observed. This pattern differs from that observed for intraspecific scaling of cranial biomechanics and bite force in the blacktip shark *Carcharhinus limbatus* and spotted ratfish

*Hydrolagus colliei* as well (Huber et al. 2006, 2008). In blacktip sharks, bite force is hyperallometric owing to positive allometry of both muscle cross-sectional area and the mechanical advantage of the jaw system. Interestingly, positive allometry of bite force in this species is not correlated with an increase of hard prey in its diet over ontogeny, although relatively larger prey are taken by large blacktip sharks (Bethea et al. 2004; Huber et al. 2006). Positive allometry of mechanical advantage is responsible for hyperallometric bite force in the spotted ratfish and in alligators (Erickson et al. 2003; Huber et al. 2008).

The isometric scaling of bite force across species of sharks is also different from interspecific studies on other vertebrate groups, in which positive allometry of bite force is also typically observed (Aguirre et al. 2002; Herrel et al. 2002). Ontogenetic scaling patterns in other vertebrate groups generally indicate strong positive allometry of bite force with respect to body or head length as well (Meyers et al. 2002; Erickson et al. 2003; Herrel et al. 2005; Herrel and O'Reilly 2006). It is possible that the extremely large body sizes attained by some shark species, combined with specialized tooth morphologies, result in the capacity of these larger species to capture and reduce large and/ or hard prey into manageable pieces. In other words, the high absolute bite forces generated by these larger shark species allow them to overcome constraints set by prey durability, thereby eliminating the selective pressure for positive allometry of bite force at these large sizes. To this point, positive allometry of bite force has only been identified in small to medium-sized cartilaginous fishes (21–121 cm standard length; Huber et al. 2006, 2008). Intraspecific scaling patterns of bite force in the larger shark species and analyses of bite force in other large predatory animals are needed to thoroughly evaluate this hypothesis.

Our data suggest that head width is the best predictor of bite force across shark species, as was found in the blacktip shark (Huber et al. 2006). As argued previously, wider heads can either accommodate larger adductor muscles or are larger because of the geometric arrangement of the adductor muscles
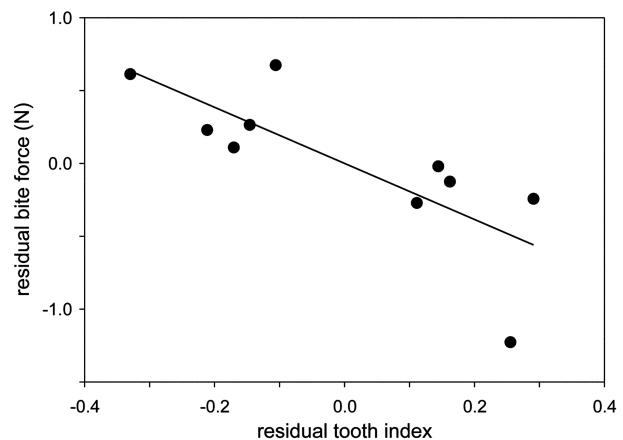


Figure 5. Graph illustrating the relationship between tooth shape and bite force. Sharks with relatively larger bite forces have relatively narrower, higher aspect ratio teeth (lower tooth index).

Table 3: Results of ANCOVA with standard length as covariate testing for differences in morphology and bite force for species differing in diet

| Variable | $F_{phylogenetic}$ | $F_{conventional}$ | $P$ |
|---|---|---|---|
| Prebranchial length | 5.09 | .27 | .65 |
| Head width | 6.85 | .44 | .56 |
| Head height | 5.39 | .15 | .73 |
| **Bite force** | 5.70 | 5.95 | .047 |
| **Tooth index** | 5.24 | 54.21 | <.001 |

Note. Variables in bold differ significantly between diet groups.

relative to the jaws (Huber et al. 2005, 2006; Herrel et al. 2007). This is especially the case in sharks, in which the low pullout strength of cartilage precludes tendinous point insertions, and the jaw adductors have broad surface insertions on the lateral faces of the upper and lower jaws (Liem and Summers 1999; Motta and Wilga 2001; Summers et al. 2003). Species with wider heads likely have larger jaw adductors and thus higher bite forces.

Our analyses indicated that tooth shape is indeed related to bite-force capacity, suggesting an important role for the interaction between tooth shape and bite force in the predatory behavior of sharks. Contrary to our expectations, however, sharks with relatively larger bite forces had narrower, more pointed anterior teeth, although this result was not significant in the independent contrast analysis. The fact that we specifically chose to quantify tooth shape for the anterior teeth used in the capture but not crushing of prey may explain this result. Although sharp, pointed teeth probably improve the penetration of tissues such as skin and muscle, they are also likely to break when encountering prey with mineralized reinforcements (large bones of marine mammals, turtle shells, invertebrate exoskeletons, etc.). Moreover, our indicator of tooth shape does not account for cusp direction, further complicating the interpretation of these results. Interestingly, the pointed teeth of the whitespotted bamboo shark *Chiloscyllium plagiosum* have been noted to change position passively in response to hard prey (i.e., lie flat along the jaws), allowing these sharks to crush hard objects without risking tooth fracture (Ramsay and Wilga 2007). Clearly, tooth-food interactions are highly complex, and our simple indicator of tooth shape does not capture the true complexity thereof.

It should also be noted that several of these species have an anatomically and/or functionally heterodont dentition with considerable overlap among high aspect ratio anterior teeth and flattened, molariform posterior teeth. Although individually narrow and pointy, collectively, the anterior teeth of species such as the horn shark *Heterodontus francisci* and whitespotted bamboo shark *C. plagiosum* form an imbricated dental battery, which may help resist tooth fracture by distributing food reaction forces over a considerable area (Reif 1976; Ramsay and Wilga 2007). These relatively sharp anterior teeth may allow hard-prey specialists to capture soft-bodied piscine prey in addition to benthic invertebrates, thereby broadening their

potential ecological niche. Additionally, there is some evidence to suggest that the loose acrodont dentition of sharks allows the teeth to shift about their basal connection to the jaws, dissipating food reaction forces while facilitating the slicing or sawing of prey with the lateral edges of the teeth (Frazzetta 1988; Powlik 1995). This phenomenon is further augmented by lateral head shaking, both of which may further release constraints on tooth shape in sharks (Motta and Wilga 2001). Thus, we would argue that heterodonty may have evolved from a primitively narrow and pointed homodont dentition (Motta 2004) in species that started to include hard prey in their diet and evolved high bite forces. By specializing the posterior teeth, which have a higher mechanical advantage for crushing hard prey, the anterior teeth of these species could have remained pointed and used for other functions.

In summary, our results suggest that large sharks do not bite hard for their body size but attain large body size and consequently have large absolute bite forces. Bite force capacity is tightly correlated with head dimensions, with head width being a particularly good predictor of bite force across species. Species including hard prey into their diet have larger bite forces and show a tendency to have more narrow anterior teeth, although future analyses should include more highly resolved dietary and dental categorizations. While tooth shape is correlated with bite force, it remains currently unclear what the interaction between variables implies for the feeding strategies of these animals. Thus, integrative studies relating cranial mechanics, tooth shape and function, and diet are crucial to our understanding of the evolution of the cranial system in sharks and elasmobranchs in general (see Dean et al. 2007*b*).

## Acknowledgments

## Literature Cited

Adnet S. and R.A. Martin. 2007. Increase of body size in sixgill sharks with change in diet as a possible background of their evolution. Hist Biol 19:279–289.

Aguirre L.F., A. Herrel, R. Van Damme, and E. Matthysen. 2002.

Ecomorphological analysis of trophic niche partitioning in a tropical savanna bat community. Proc R Soc B 269:1271–1278.

———. 2003. The implications of food hardness for diet in bats. Funct Ecol 17:201–212.

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

Compagno L.J.V. 1984a. FAO Species Catalogue. Vol. 4. Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. Pt. 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis, no. 125. Food and Agriculture Organization of the United Nations, Rome.

———. 1984b. FAO Species Catalogue. Vol. 4. Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. Pt. 2. Carchariniformes. FAO Fisheries Synopsis, no. 125. Food and Agriculture Organization of the United Nations, Rome.

———. 2001. Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. Vol. 2. Bullhead, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes, no. 1. FAO Fisheries Synopsis, no. 125. Food and Agriculture Organization of the United Nations, Rome.

———. 2005. Checklist of living Chondrichthyes. Pp. 503–548 in W.C. Hamlett, ed. Reproductive Biology and Phylogeny. Vol. 3. Reproductive Biology and Phylogeny of Chondrichthyes. Science Publishers, Enfield, NH.

Compagno L.J.V., M. Dando, and S. Fowler. 2004. Sharks of the World. Harper Collins, London.

Cortes E. 1999. Standardized diet compositions and trophic levels of sharks. ICES J Mar Sci 56:707–717.

Dean M.N., E. Azizi, and A.P. Summers. 2007a. Uniform strain in broad muscles: morphological innovation in the jaw adductor of the chimaera, Hydrolagus colliei. J Exp Biol 210:3395–3406.

Dean M.N., J.J. Bizzarro, and A.P. Summers. 2007b. The evolution of cranial design, diet and feeding mechanisms in batoid fishes. Integr Comp Biol 47:70–81.

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

Evans A.R. and G.D. Sanson. 1998. The effect of tooth shape on the breakdown of insects. J Zool (Lond) 246:391–400.

Felsenstein J. 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

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

Garland T., Jr., A.W. Dickerman, C.M. Janis, and J.A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292.

Garland T., Jr., P.E. Midford, and A.R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. Am Zool 39:374–388.

Gennari E. and U. Scacco. 2007. First age and growth estimates in the deep water shark, Etmopterus spinax (Linnaeus, 1758), by deep coned vertebral analysis. Mar Biol, doi:10.1007/s00227-007-0769-y.

Hamlett W.C. 1999. Sharks, Skates and Rays: The Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore.

Harvey P.H. and M.D. Pagel. 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford.

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

Herrel A. and A.C. Gibb. 2006. Ontogeny of performance in vertebrates. Physiol Biochem Zool 79:1–6.

Herrel A. and J.C. O'Reilly. 2006. Ontogenetic scaling of bite force in lizards and turtles. Physiol Biochem Zool 79:31–42.

Herrel A., J.C. O'Reilly, and A.M. Richmond. 2002. Evolution of bite performance in turtles. J Evol Biol 15:1083–1094.

Herrel A., V. Schaerlaeken, J.J. Meyers, K.A. Metzger, and C.F. Ross. 2007. The evolution of cranial design and performance in squamates: consequences of skull-bone reduction on feeding behavior. Integr Comp Biol 47:107–117.

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

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

Herrel A., S. Van Wassenbergh, S. Wouters, P. Aerts, and D. Adriaens. 2005. A functional morphological approach to the scaling of the feeding system in the African catfish, Clarias gariepinus. J Exp Biol 208:2091–2102.

Hill A.V. 1950. The dimensions of animals and muscular dynamics. Sci Prog 38:209–230.

Huber D.R. 2006. Cranial Biomechanics and Feeding Performance of Sharks. PhD diss. University of South Florida, Tampa.

Huber D.R., M.N. Dean, and A.P. Summers. 2008. Hard prey, soft jaws and the ontogeny of feeding mechanics in the spotted ratfish Hydrolagus colliei. J R Soc Interface 5:941–952.

Huber D.R., T.G. Eason, R.E. Hueter, and P.J. Motta. 2005. Analysis of the bite force and mechanical design of the feeding mechanism of the durophagous horn shark Heterodontus francisci. J Exp Biol 208:3553–3571.

Huber D.R. and P.J. Motta. 2004. Comparative analysis of methods for determining bite force in the spiny dogfish Squalus acanthias. J Exp Zool 301:26–37.

Huber D.R., C.L. Weggelaar, and P.J. Motta. 2006. Scaling of bite force in the blacktip shark Carcharhinus limbatus. Zoology 109:109–119.

Iglesias S.P., G. Lecointre, and D.Y. Sellos. 2005. Extensive paraphylies within sharks of the order Carchariniformes inferred

from nuclear and mitochondrial genes. Mol Phylogenet Evol 34:569–583.

Liem K.F. and A.P. Summers. 1999. Gross anatomy and functional morphology of muscles. Pp. 93–114 in W.C. Hamlett, ed. Sharks, Skates and Rays: The Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore.

Lucifora L.O., R.C. Menni, and A.H. Escalante. 2001. Analysis of dental insertion angles in the sand tiger shark, *Carcharias taurus* (Chondrichthyes: Lamniformes). Cybium 25:23–31.

Meyers J.J., A. Herrel, and J. Birch. 2002. Scaling of morphology, bite force, and feeding kinematics in an iguanian and a scleroglossan lizard. Pp. 47–62 in P. Aerts, K. D'Août, A. Herrel, and R. Van Damme, eds. Topics in Functional and Ecological Vertebrate Morphology. Shaker, Maastricht.

Moss S.A. 1977. Feeding mechanisms in sharks. Am Zool 17: 355–364.

Motta P.J. 2004. Prey capture behavior and feeding mechanics of elasmobranchs. Pp. 165–202 in J. Carrier, J. Musick, and M. Heithaus, eds. Biology of Sharks and Their Relatives. CRC, Boca Raton, FL.

Motta P.J. and C.D. Wilga. 2001. Advances in the study of feeding behaviors, mechanisms, and mechanics of sharks. Environ Biol Fish 60:131–156.

Nobiling G. 1977. Die Biomechanik des Kieferapparates beim Stierkopfhai (*Heterodontus portusjacksoni = Heterodontus philippi*). Adv Anat Embryol Cell Biol 52:1–52.

Powlik J.J. 1995. On the geometry and mechanics of tooth position in the white shark, *Carcharodon carcharias*. J Morphol 226:277–288.

Purdy R. W. 1996. Paleoecology of fossil white sharks. Pp. 67–77 in A.P. Klimley and D.G. Ainley, eds. Great White Sharks: The Biology of *Carcharodon carcharias*. Academic Press, San Diego, CA.

Ramsay J.B. and C.D. Wilga. 2007. Morphology and mechanics of the teeth and jaws of white-spotted bamboo sharks (*Chiloscyllium plagiosum*). J Morphol 268:664–682.

Reif W.-E. 1976. Morphogenesis, pattern formation and function of the dentition of *Heterodontus* (Selachii). Zoomorphology 83:1–47.

Shimada K. 1997. Paleoecological relationships of the late cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). J Paleontol 71:926–933.

Shimada K. and G.E. Hooks. 2004. Shark-bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama. J Paleontol 78:205–210.

Shirai S. 1996. Phylogenetic interrelationships of neoselachians (Chondrichthyes: Euselachii). Pp. 9–34 in M.L.J. Stiassny, L.R. Parenti, and G.D. Johnson, eds. Interrelationships of Fishes. Academic Press, San Diego, CA.

Simpfendorfer C.A., A. Goodreich, and R.B. McAuley. 2001. Diet of three commercially important shark species from Western Australian waters. Mar Freshw Res 52:975–985.

Sokal R.F. and F.J. Rohlf. 1995. Biometry. W.H. Freeman, New York.

Strasburg D.W. 1963. The diet and dentition of *Isistius brasiliensis*, with remarks on tooth replacement in other sharks. Copeia 1963:33–40.

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

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

Summers A.P., M.M. Koob-Emunds, S.M. Kajiura, and T.J. Koob. 2003. A novel fibrocartilaginous tendon from an elasmobranch fish (*Rhinoptera bonasus*). Cell Tissue Res 312: 221–227.

Wetherbee B.M. and E. Cortes. 2004. Food consumption and feeding habits. Pp. 225–246 in J.C. Carrier, J.A. Musick, and M.R. Heithaus, eds. Biology of Sharks and Their Relatives. CRC, Boca Raton, FL.

Whitenack L.B., P.J. Motta, and T.J. Koob. 2004. A preliminary analysis of selachian tooth performance. Integr Comp Biol 44:664.

Winchell C.J., A.P. Martin, and J. Mallat. 2004. Phylogeny of elasmobranchs based on LSU and SSU ribosomal RNA genes. Mol Phylogenet Evol 31:214–224.