



Mechanics of biting in great white and sandtiger sharks

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ABSTRACT

Although a strong correlation between jaw mechanics and prey selection has been demonstrated in bony fishes (Osteichthyes), how jaw mechanics influence feeding performance in cartilaginous fishes (Chondrichthyes) remains unknown. Hence, tooth shape has been regarded as a primary predictor of feeding behavior in sharks. Here we apply Finite Element Analysis (FEA) to examine form and function in the jaws of two threatened shark species, the great white (*Carcharodon carcharias*) and the sandtiger (*Carcharias taurus*). These species possess characteristic tooth shapes believed to reflect dietary preferences. We show that the jaws of sandtigers and great whites are adapted for rapid closure and generation of maximum bite force, respectively, and that these functional differences are consistent with diet and dentition. Our results suggest that in both taxa, insertion of jaw adductor muscles on a central tendon functions to straighten and sustain muscle fibers to nearly orthogonal insertion angles as the mouth opens. We argue that this jaw muscle arrangement allows high bite forces to be maintained across a wider range of gape angles than observed in mammalian models. Finally, our data suggest that the jaws of sub-adult great whites are mechanically vulnerable when handling large prey. In addition to ontogenetic changes in dentition, further mineralization of the jaws may be required to effectively feed on marine mammals. Our study is the first comparative FEA of the jaws for any fish species. Results highlight the potential of FEA for testing previously intractable questions regarding feeding mechanisms in sharks and other vertebrates.

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1. Introduction

Biomechanical analyses of the jaws of teleost fish (Osteichthyes) have shown that prey preference is strongly influenced by both jaw mechanics and dentition (Wainwright and Richard, 1995; Grubich et al., 2008). In contrast, few studies have examined such relationships in sharks (Nobiling, 1977; Summers et al., 2004). Hence, tooth shape has traditionally been used as an indicator of feeding behavior in chondrichthyans (Whitenack and Motta, 2010). Two classic examples of the relationship between tooth shape and prey selection are the lamniform sharks *Carcharodon carcharias* (great white) and *Carcharias taurus* (sandtiger). The great white is the most formidable extant species of predatory shark. The docile sandtiger (known as the grey nurse in Australia) was hunted to near extinction simply because it looked like a “man-eater”. This fierce appearance has made the species popular in public aquaria around the world (Compagno, 2001). The broad, serrated teeth of adult great whites are characteristic of shark species that gouge chunks of flesh from large prey (e.g., marine mammals), whereas the long,

awl-like teeth of the sandtiger typify piscivorous taxa that grab and swallow fast moving fish (Tricas and McCosker, 1984; Frazzetta, 1988; Powluk, 1995; Lucifora, 2001; Smale, 2005). The morphology of these teeth may also be an adaptive response to the stresses imposed during feeding on different prey types (Preuschoft et al., 1974): pliant soft-bodied prey for the sandtiger versus bone and other dense material (e.g., turtle shells) encountered by great whites (Long, 1996). Given that the relationship between jaw mechanics and diet is poorly understood in chondrichthyans, it remains to be determined whether prey capture proficiency in sharks is simply a matter of suitable dentition, or if additional adaptations of the jaws are required.

The link between morphological adaptation and ecology can be examined through analysis of a structure's performance, i.e., how well it executes certain tasks. The ability of a structure (e.g., the jaws) to perform certain behaviors (e.g., biting and capturing prey) is limited by morphology. Anatomical constraints will therefore affect species ability to exploit resources in its environment (Wainwright, 1994). The mechanical performance of the jaws affects prey capture via structural and behavioral attributes. In addition to resisting deflection upon prey contact, the jaws must also effectively transmit force from the musculature to the prey (Thomason, 1991; Huber et al., 2005; Wroe, 2008). Thus, bite force has been widely used as an

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indicator for prey capture in vertebrates, since the magnitude of bite force is determined by the morphology of feeding structures, and will therefore influence and limit prey choice (Thomason, 1991; Rayfield et al., 2001; Dumont and Herrel, 2003; Preuschoft and Witzel, 2005; Christiansen and Wroe, 2007; Bourke et al., 2008; Wroe, 2008; Dumont et al., 2009; Fry et al., 2009; Huber et al., 2009).

Direct investigation of bite force in sharks is limited by the relatively small number of species that can be observed in captivity, and difficulty in eliciting natural biting behaviors under controlled conditions (Evans and Gilbert, 1971; Huber and Motta, 2004; Huber et al., 2009). In addition, the effect of gape angle (i.e., how wide the jaws are open) on bite force remains difficult to examine experimentally. Hence, although gape angle is known to significantly influence bite force in some taxa (Dumont and Herrel, 2003; Bourke et al., 2008), its role in sharks is unknown (Powlik, 1995; Huber and Motta, 2004; Huber et al., 2005).

To examine biting performance in the great white and the sandtiger, we digitally constructed three-dimensional (3D) models of the jaws of both species using Finite Element Analysis (FEA). FEA of crania and jaws (e.g., Fig. 2) have been shown to be useful as performance indicators for feeding behavior in a range of vertebrate species (Rayfield et al., 2001; Wroe et al., 2007; Wroe, 2008; Fry et al., 2009). Our aim has been to examine the effect of gape angle on bite force and stress in the jaws of great white and sandtiger sharks, and to determine whether these results are consistent with diet in these species. Specifically, we examine: (1) whether maximum bite force in the sandtiger will occur at a shallower gape angle than the great white (which includes larger prey in its diet) and (2) if the shape of the great white's jaws is mechanically better suited to tolerate stresses associated with jaw adduction. In addition, the skeleton of the feeding apparatus of cartilaginous fish is composed of an outer mineralized layer of cartilage that surrounds a non-mineralized core of hyaline-like cartilage. The mineralized blocks (tesserae) of prismatic cartilage present in the outer layer are synapomorphic for chondrichthyans (Summers, 2000).

FEA offers several advantages over traditional lever system models, including simultaneous examination of multiple performance indicators (e.g., bite force and stress) in a single analysis, as well as examination of models with two or more material properties. The Finite Element Models (FEMs) assembled in the present study incorporate material properties specific for mineralized and non-mineralized elasmobranch cartilage and simulate 3D muscle geometry more realistically as a series of axially loaded truss elements (beam elements that can only transmit axial loading) rather than as single vectors for each muscle group (Fig. 1); this method utilizes multiple vectors, which have been shown to be more effective at modeling the complexity of muscle force distributions (Röhrle and Pullan, 2007). Although bite force remains a useful performance indicator, recent studies reveal that the magnitude of bite force alone cannot fully explain dietary diversity in sharks (Huber and Motta, 2004; Huber et al., 2005, 2009). FEA therefore permits analysis of how the jaws respond to muscular forces generated during biting and transmit these muscular forces into bite forces.

2. Materials and methods

Additional details for the following are found in the supplementary information section (Appendix A).

2.1. Model assembly

FEMs are based on computerized serial tomography (CT) scan data from the jaws of a great white that was 250 cm in total length (TL) and a sandtiger that was 198 cm TL. Segmentation was performed using MIMICS (v. 12.02) and CT attenuation data to

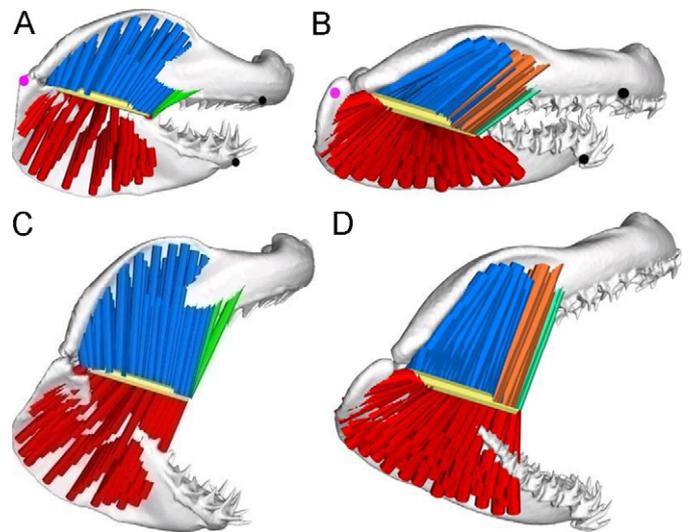


Fig. 1. Arrangement of muscle fibers in Finite Element Models (FEMs) of the jaws of great white (A, C) and sandtiger (B, D) sharks at 15° (A, B) and 55° gape angles (C, D). Each jaw adductor muscle group inserts on the mid-lateral raphe (yellow) and is represented by a series of trusses that are used to approximate muscle forces and insertion angles of muscle fibers. In both species the angle of muscle trusses becomes more orthogonal at 55° due to their insertion on the MLR, however the difference in muscle truss angle between 15° and 55° is greater in the sandtiger than in the great white. Bite points and jaw joints are indicated by black and pink dots, respectively. Truss colors correspond to the following muscle groups: blue = dorsal quadratomandibularis (QMD) and superficial division of QMD (great white and sandtiger, respectively); orange = medial division of QMD (sandtiger only); green = preorbitalis; red = ventral quadratomandibularis.

clearly define mineralized and non-mineralized layers of cartilage in heterogeneous models. Solid models of dual layered jaws were assembled in STRAND7 (v. 2.3).

2.2. Applied muscle forces

Comparisons were made under simulations designed to model bite forces and stresses imposed by the jaw musculature (intrinsic loads) during biting. Hence only jaw adductor muscles (muscles responsible for closing the jaw) were incorporated into the model (Fig. 1). In great white and sandtiger sharks the divisions of the quadratomandibularis attach to a tendinous sheet (the mid-lateral raphe, MLR; Wilga, 2005); the MLR was simulated using a divided beam (Wroe et al., 2008).

Muscle architecture was simulated using trusses (Fig. 1; Wroe et al., 2008). Each muscle group was represented by a series of truss elements (256 in total); maximum theoretical force was determined for each group on the basis of anatomical cross-sectional area (ACSA). Insertion angles of muscle fibers were obtained from dissections and were approximated by the direction of axial loads applied by trusses.

Muscle force has been shown to vary with changes in muscle fiber length (Gordon et al., 1966). Here we determined bite force using the following two muscle force–muscle length assumptions: (1) muscle force was set to the theoretical maximum (as described above) and held constant irrespective of gape angle; these bite force values are hereafter referred to as bite force CMF (constant muscle force) and (2) muscle force was determined using a muscle force–muscle length relationship; bite force results from these analyses are referred to as bite force FL (force length).

2.3. Load cases—gape angle

In order to investigate the effect of gape angle on bite force and stress, six different heterogeneous FEMs for both species were constructed in which gape angle was changed sequentially by 10° from 5° to 55°. Heterogeneous FEMs distinguished between mineralized and non-mineralized layers of cartilage in the jaws. At each gape angle, two bite points were positioned on both the upper and the lower jaws for a total of four bite points. Gape angle was measured as the angle between the upper bite point, the axis of rotation of the jaw (jaw joint), and the lower bite point (Fig. 1).

The von Mises (VM) stress is considered an indicator of failure in ductile materials and is widely used to provide an overall visual summary of FEMs under load (Rayfield, 2007; Bourke et al., 2008; Wroe, 2008; Wroe et al., 2008, in press;

Table 1
Change in bite force (N), stress (MPa), and normalized muscle force (F_{FL}) with gape angle.

	Gape angle						
	5°	15°	25°	35°	45°	55° HET	55° HOM
<i>Great white</i>							
Bite force (CMF)	1053	1220	1285	1320	1329	1324	1325
VM stress	1.64	1.86	1.99	2.09	2.15	2.21	2.32
Bite force (FL)	495	960	1209	1320	1281	1093	1093
F_{FL}	0.47	0.79	0.94	1.0	0.96	0.83	
<i>Sand tiger</i>							
Bite force (CMF)	328	425	476	514	534	544	1243
VM stress	1.18	1.38	1.55	1.71	1.83	1.92	2.60
Bite force (FL)	216	358	452	514	504	417	1032
F_{FL}	0.66	0.84	0.95	1.0	0.94	0.77	

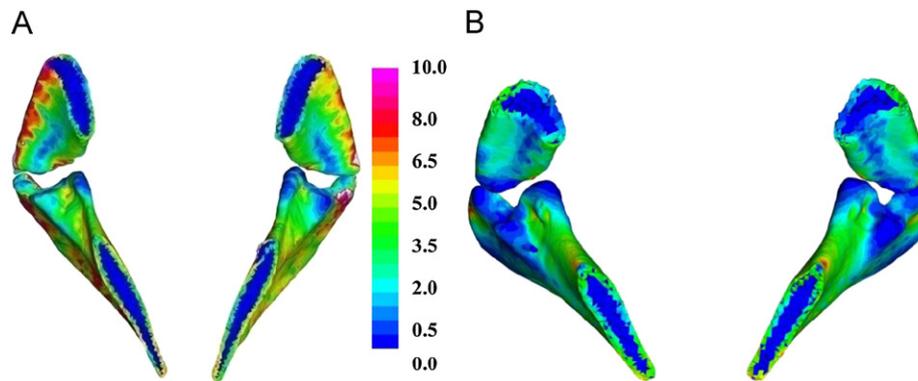


Fig. 2. Comparison of von Mises stress taken at cross-sections (in the frontal plane) in the jaws of great white (A) and sandtiger sharks (B) at a 55° gape angle. Colors shown correspond to values of von Mises stress (see legend). Note the clear distinction between the outer layer of load bearing mineralized cartilage and the inner core of non-mineralized cartilage (blue). Also note the relatively thicker layer of the mineralized outer layer of cartilage in the sandtiger (B) compared to the great white (A).

Dumont et al., 2009; Fry et al., 2009). Recent experimentally derived results support this assumption for mammalian bone (Tsafnat and Wroe, 2010). VM stress was therefore examined at cross-sections through the jaws (in the frontal plane) at comparable regions of high VM stress. Tetrahedral elements on the surface of the cross-section in both the upper and lower jaws were combined and averaged. Mechanical behavior was determined from mean VM stress of tetrahedral elements in the cross-section (Table 1) and visual examination of VM stress profiles (Fig. 2).

2.4. Load cases—jaw shape

To examine the effect of jaw shape on mechanical performance, an additional homogeneous (single material property) FEM was constructed at a gape angle of 55° for both sharks. This gape angle was chosen as it corresponded to high values for bite force (CMF) and VM stress in both species. The homogeneous sandtiger model was scaled to the same muscle force and jaw surface area as those of the great white. In models with the same muscle force, surface area, and material properties, the only parameter that influences mechanical behavior is geometry (Dumont et al., 2009). Thus a total of 7 FEMs (one homogeneous and six heterogeneous) for each shark were run under intrinsic loads. All analyses were linear static. Models run at gape angles between 5° and 45° are heterogeneous whereas results shown at 55° are from either heterogeneous (HET) or homogeneous (HOM) models (Table 1). Results for the homogeneous sandtiger model that was scaled to the same surface area and muscle force as those of the great white are shown in Table 1 in bold type. As in heterogeneous models, mean VM stress in homogeneous FEMs was calculated at cross-sections. The effect of jaw shape was based on comparisons of bite force (CMF) and stress in homogeneous models (Table 1).

3. Results

3.1. Effect of gape angle on bite force (heterogeneous FEMs)

Bite force (CMF) in both white and sandtiger sharks increased as gape angle increased (Table 1). In the sandtiger, bite force (CMF)

increased by 66% from a minimum value of 328 Newtons (N) at 5° to a maximum value of 544 N at 55°. In the great white, bite force (CMF) increased by 26% from a minimum value of 1053 N at 5° to a maximum value of 1329 N at 45° (the difference between 45° and 55° was only 0.4%). For values at or above 15°, bite forces (CMF) in the great white were within 9% of the calculated maximum (at 45°). By contrast, for the sandtiger, bite forces (CMF) at 15°, 25°, and 35° or above were within 28%, 14%, and 6%, respectively, of the calculated maximum (at 55°). Thus, the great white maintains relatively constant bite forces (CMF) across a wider range of gape angles compared to the sandtiger.

As expected, bite force (FL) for both sharks was lower than values predicted using constant muscle force (Table 1). However, values for F_{FL} (see Appendix A) indicate that the influence of muscle length was more pronounced at lower gape angles in the white shark and at higher gape angles in the sandtiger. For example, at 5° the white shark maintained 47% and the sandtiger 66% of maximal bite force, whereas at 55° the white shark maintained 83% and the sandtiger 77% of maximal bite force (Table 1).

3.2. Effect of gape angle on stress (heterogeneous FEMs)

Values for mean VM stress for both species increased with increase in gape angles (Table 1). Maximum and minimum VM stress values were calculated at 5° and 55°, respectively. In the sandtiger, mean VM stress ranged from 1.18 to 1.92 MPa, with a 63% increase between 5° and 55°, whereas in the great white mean VM stress ranged from 1.64 to 2.21 MPa with a 35% increase between 5° and 55°. Excluding values at 5°, mean VM stresses in the

great white and sandtiger were within 19% and 39% of the calculated maximum (at 55°), respectively. Thus, for the great white, calculated VM stress values fell within a narrower range than for the sandtiger.

3.3. Distribution of load in the jaws

The jaws of both species are composed of an outer layer of mineralized cartilage that surrounds a non-mineralized core. Visual inspection of VM stress distributions in cross-sections from heterogeneous models shows that VM stress is concentrated in the outer layer of mineralized cartilage with negligible VM stress values in non-mineralized cartilage (Fig. 2). Measurements obtained from CT scans show that this load bearing layer of mineralized cartilage was thicker in the sandtiger specimen (3.5 mm) than in the great white specimen (2.4 mm). Further information on how these measurements were made can be found in Appendix A.

3.4. Effect of jaw shape on mechanical performance

In the homogeneous scaled sandtiger model, mean VM stress was 12% higher and bite force (CMF) was 7% lower than in the great white model, suggesting that the shape of great white's jaws allows for higher bite forces (Table 1).

4. Discussion

4.1. Functional significance of jaw muscle arrangement

Although we predicted a shallower optimum gape angle in the sandtiger, the magnitude of bite force (CMF) in both species increased as gape angle increased (Table 1). Furthermore, bite force (CMF) in the great white remained relatively constant between 15° and 55°. These trends contrast with results derived from investigations on mammalian jaw mechanics, where an optimum gape angle is evident, and bite force decreases significantly at wider gapes (Dumont and Herrel, 2003; Bourke et al., 2008). Our models, which simulate muscle architecture, indicate that these results may be partially explained by the organization of jaw adductor muscles in sharks. In both white and sandtiger sharks, the primary jaw adductor muscles are parallel fibered and are divided into dorsal and ventral divisions by a central tendinous sheet, termed the mid-lateral raphe (MLR, Wilga, 2005). This arrangement was reconstructed in our models by a series of trusses attached to a divided beam (Fig. 1; Wroe et al., 2008). As the mouth opens at a gape angle of 5–55°, the angle between the muscle trusses (fibers) and the jaw (insertion angle) in both species continually increases toward a more orthogonal configuration due to their insertion on the MLR. As maximum muscle force is distributed to the jaws at perpendicular insertion angles, we propose that one function of the MLR is to straighten and then maintain muscle fibers at near optimal insertion angles (Fig. 1).

In the great white, muscle fibers quickly straighten and remain at nearly orthogonal insertion angles, thus facilitating optimal bite forces (CMF) across a wide range of gape angles. However, in the sandtiger, insertion angles of muscle fibers at shallow gapes are more acute (Fig. 1). Bite force (CMF) in the sandtiger therefore increases at a slower rate than in the great white (Table 1) as fibers are gradually straightened by their insertion on the MLR as the mouth opens. In contrast, examination of mammalian models (Bourke et al., 2008) shows that insertion angle decreases as the mouth opens, resulting in significant reduction in bite forces at wider gapes. Thus, the muscle arrangement characteristic of shark jaw adductors allows the potential to generate high bite forces

across a much wider range of gape angles than observed in mammalian predators. This invites further investigation into the role the MLR plays in chondrichthyan feeding ecology and evolution, as well as the functional significance of similar structures in other vertebrates (e.g., the *cartilago transiliens* of reptiles). This may also explain why the sandtiger appears capable of generating high bite forces (CMF) at larger gapes, despite a preference for small prey.

4.2. Feeding mechanisms in sandtiger and great white sharks

Previous investigation of jaw mechanics in the white shark suggested that gape angle influenced bite force estimations (Wroe et al., 2008). When we include a muscle force–muscle length relationship, the results show that for larger gape angles the great white bites relatively harder than the sandtiger and for smaller gape angles the sandtiger bites relatively harder than the great white. However, even at large gape angles, F_{FL} indicates that the sandtiger retains a high percentage of bite force (CMF). Our data also show that, compared with VM stress at lower gapes, the jaws of sandtiger sharks are less capable of resisting the higher stress associated with increased bite forces at wide gapes (Table 1). We consider the most parsimonious explanation of these results to be that the sandtiger uses high bite force at wider gapes in order to generate high velocity when closing its jaws, prior to the teeth impacting small prey at lower gape angles. This is consistent with high-speed video footage of sandtiger sharks biting food items in captivity (Fig. 3). In combination with the slender, nail-like teeth of the sandtiger, this mechanism appears well adapted to impale soft bodied prey and facilitate the capture of fast and agile fish. Given the diet of the sandtiger, its jaws are unlikely to encounter prey at higher gape angles and hence there is no requirement for its jaws to resist higher loadings at larger gapes.

Our data suggest that the jaws of great whites maintain relatively consistent bite force (CMF) despite considerable changes in gape angle (Table 1). This trend is also supported by the F_{FL} , as between 15° and 55° white sharks maintain between 79% and 96% of bite force (CMF) regardless of change in muscle truss length (Table 1). As adult great whites target prey that range in size from small fish to large marine mammals (Tricas and McCosker, 1984; Cliff et al., 1989), this data accords with feeding behavior in this species. In contrast to sandtigers, adult great whites also gouge and cut through dense tissue such as blubber, bone, and sea turtle carapaces (Long, 1996). Transmission of high bite forces to the saw-like dentition of the great white would assist in rapidly dispatching large prey.

At 2.5 m length, our great white specimen is at a transitional stage in its ontogeny when it is starting to shift from a primarily piscivorous diet to one that ultimately contains a high proportion of large marine mammals (Tricas and McCosker, 1984; Cliff et al., 1989). While analysis of homogeneous models indicates that the shape of the great white's jaws is slightly better adapted to resist

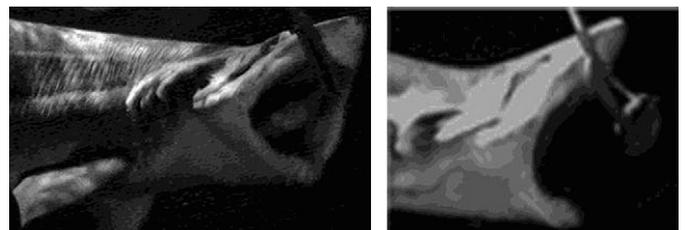


Fig. 3. Still images from kinematic sequences of the sandtiger shark (*Carcharias taurus*) filmed using a high-speed camera. The images show the sandtiger approaching a small fish at a wide gape angle prior to rapid closure of the jaws. (Images courtesy from D. Lowry, M. Matott and D. Huber, unpublished).

intrinsic loads, results from heterogeneous models show that higher values of VM stress are associated with increased gape angles in our specimen (Table 1). Furthermore, the thickness of the load bearing layer of mineralized cartilage in the sandtiger was considerably higher than in the great white. However, unlike most shark species, additional layers of mineralized cartilage (up to five in sharks 5 m in TL) are deposited in the jaws of the great white during growth; this is not evident in other skeletal elements (Dingerkus et al., 1991). Thus, although the jaws and muscle architecture of sub-adult great white sharks possess features not present in the sandtiger that are consistent with adaptations to biting off large portions of tissue, our findings suggest that the distribution of material properties in the great white's jaws renders them vulnerable to damage until additional mineralized cartilage forms. This interpretation is consistent with the observation that great whites ~1.5–3 m in TL fed preferentially on softer flesh, rather than tougher, yet higher energy-yielding, fatty tissues when scavenging whale carcasses (Dicken, 2008).

The success of adult great white attacks on pinnipeds is high if the seal is immobilized in less than 1 min, as longer intervals post-capture allow seals to struggle free and escape (Martin et al., 2005). The great white's inability to effectively hunt large marine mammals at this transitional stage in its ontogeny (< 3 m TL) has been ascribed to a lack of suitable dentition (Tricas and McCosker, 1984). At approximately 3 m TL, the narrow teeth of younger individuals begin to broaden at the base, becoming more triangular and serrated for gouging and cutting flesh (Tricas and McCosker, 1984). However, we posit that until the great white's jaws are further reinforced by additional mineralization of the load bearing outer layer of cartilage (which would reduce stress), the jaws are mechanically disadvantaged when capturing large prey.

Conflict of interest statement

The authors declare no conflict of interest.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jbiomech.2010.09.028.

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