Tooth Morphology and Prey Handling in Durophagous Predators

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Abstract

The objective of the study was to better understand functional implications of the interaction between tooth morphology and prey handling in durophagous predators. Our goal was to identify an optimal prey orientation and tooth shape combination that requires the least amount of force to crack hard-shelled prey. Amount of force represents the energy a durophagous predator expends to crack its prey. We modeled the crushing interaction between two sets of tooth models and two *Nucella sp.* snail shell orientations. Tooth models were grouped into a set that ranges from a convex to concave occlusal surface, and set that has a central cusp with a variable radius. Snail shell orientations included an upside down position, such that the aperture was facing up; and a right-side-up position, such that the aperature was facing down. We found that it took the least total force to crush the shell in its upside down position. At this point of the shell, tight whorls have not formed to strengthen the shell as they have on the upper surface, closer to the shell's apex, where the aperature is facing down. We also found that as convexity of the tooth increased, the force needed to crack the shell decreased. Finally, we found that as the cusp radius decreased, or as the tooth becomes sharper, the force needed to break the prey item decreased. These results reveal that form and function of tooth shape determine how predators expend energy for prey handling, which affects how predator-prey relationships evolve through space and time. Some durophagous predators may have evolved sharper, more convex tooth morphology to crush hard-shelled prey in preferred orientations.

Introduction

While studies have explored how tooth morphology affects handling time and energy expenditure for marine predators that consume fleshy prey, there are few studies exploring this relationship for hard-shelled prey consumers, also known as durophagous predators. Durophagy constitutes a large trophic niche, as it includes marine invertebrates and vertebrates, and reptiles. Predator-prey dynamics of durophagous animals is important to study because as these dynamics evolve over time, ecological relationships shift over time and space.

For jawed vertebrates, teeth are the most immediate site of interaction between an organism and its food, and the amount of energy expended on food processing is closely tied to tooth morphology as well as the type of prey being processed. Massare (1987) divides teeth into three functional groups: puncturing, cutting and crushing. Within each group, there are further specializations to optimize efficiency. Cutting teeth require blade-like teeth, and animals with notched blade morphologies expend less energy cutting and handling prey than those without notched blade morphologies because notches promote cleaner cuts through tough, fleshy materials (Anderson and Barbera 2008). When teeth are used to puncture, teeth tend to be more conical and efficiency depends on strength and sharpness of the tooth, as well as prey hide thickness (Freeman and Leman 2007). In contrast to these two functional groups that process soft-fleshy materials, durophagous organisms have teeth that need to crush hard-shelled prey. Such teeth are generally low and blunt and are paired with robust jaw morphology and musculature (Hoogerhound 1987; Turnigan and Wainwright 1993).

While processing efficiency depends heavily on the material strength of prey items, as well as tooth strength and morphology, prey handling is also an important component foraging energy expenditure (Stein et al. 1984). Many marine predators selectively manipulate their prey to optimize time and energy spent on prey handling. For example, the intertidal octopus, *Octopus dierythraeus,* will try to pry open bivalve prey before expending the energy needed to drill through the shell (Steer and Semmens 2003). Additionally, Turingan and Wainwright (1993) observed that *Balistes vetula*, a durophagous Tetraodontiform fish, periodically spits out prey from the mouth to reposition or expel unwanted flesh. The results reveal that durophagous fish combine prey manipulation with specialized tooth and jaw morphology to optimize energy efficiency during prey handling. Given the time and energy that organisms invest in prey handling, morphological adaptations that reduce handling time will decrease the energy expended by the predator. This has been demonstrated by Yamada and Boulding (1998), who showed that specialist crab species show lower breaking and handling times than generalist crab species when processing snail prey.

In durophagous organisms, prey processing may include orienting prey to minimize the energy needed to break the hard shell. To better understand functional implications of the interaction between tooth morphology and prey handling in durophagous animals, we will test how well tooth models crush snail shells at different orientations. In this way, we hope to find an optimal combination of shell orientation and tooth shape that requires the least amount of force to crush.

We predict that sharp, convex teeth will require the least amount of energy crushing shelled prey while the prey is oriented such that the aperture is facing up and force loads are applied to the highest point of the shell. At this point of the shell, tight whorls have not formed to strengthen the shell as they have on the upper surface, closer to the shell's apex, where the aperature is facing down (Bourdeau 2009). We will be testing two sets of tooth models: a set that ranges from a convex to concave occlusal surface and set that has a central cusp with a variable radius. We predict that as convexity of the tooth increases, the force needed to crack the shell will decrease. This is because blunt, convex teeth aid crushing in durophagous animal jaws (Turnigan and Wainwright 1993). We also predict that as the cusp radius decreases, or as the tooth becomes sharper, the force needed to break the prey item will decrease since this will present smaller areas of contact between the tooth and the prey, increasing the stress applied to the prey for the same applied force. Therefore, we hypothesize that durophagous predators have evolved sharper, more convex tooth morphology to crush hard-shelled prey in preferred orientations.

Methods

MTS Monitoring

We modeled the crushing interaction between tooth morphology and snail shell orientations using a Materials Testing System (MTS). The MTS applies force from a moving bulk head, to which a tooth model is attached, on to the stationary prey item (Fig 1 and 2). The MTS is connected to a computer, where it graphically displays force in newtons as the tooth model applies force to the shell. For each crushing event, we recorded the amount of force required for the first crack to appear (initial force yield). The initial force yield represents the point at which an animal first penetrates its prey, where the greatest amount of force is applied before total shell deformation.

Shell Orientation

We tested two snail shell orientations: 0 (Fig 1) and 180 degrees (Fig 2). For each orientation, we simulated tooth penetration on the shell’s highest point. Arrows indicate point at which force was applied by the tooth model. For each orientation, according MTS placement is shown.

Tooth Models

We tested two series of tooth models. These two models mimicked two primary factors that influence tooth shape in durophagous animals: levels of convexity/concavity and cusp radius. Each series had five different tooth models, for a total of 10 tooth models. The two tooth series included:

Occlusal surface varied by convexity vs. concavity (Fig 3): We used this series to test how the force yields change as tooth shape changes according to convexity or concavity. This series was controlled for cusp height and cusp radius. We assigned graphic and number labels for each tooth model for later data representation. Zero indicates a flat surface. Negative numbers indicate levels of concavity. Positive numbers indicate levels of convexity.

Cusp varied by radius (Fig 4): We used this series to test how the force yields changes as the radius of the cusp on the occlusal surface changes. This series was controlled for occlusal surface concavity and convexity, and cusp height. We assigned graphic and number labels for each tooth model for later data representation.

We tested all 10 tooth models on each shell orientation. For each tooth model and shell orientation combination, we tested and recorded the initial force yields of 25 replicates.

Shell Creation

We used Z-Print© to print out 3D models of *Nucella sp.* snail shells. The shells were made out of a gypsum based powder (High performance composite powder zp 150, Z corp). After printing the shells, we cured them with Epsom Salt solution to promote hardening. Then, we baked them overnight in a vaccum oven at 80° F. After baking, we put the shells in an air tight container for 48 hours.

Data Analysis

For each orientation, we conducted one-way ANOVA tests comparing the initial load means across each of the three tooth series, to see if there were significant differences between initial loads across the five tooth models within each series. Means were compared using a Student's t-test. To test if shell orientation and tooth type were combined influences on initial load, we conducted a two-way ANOVA test which compared all shell orientations and tooth models as two independent variables against all according initial load means as the dependent variable. The level of significance for all ANOVA tests was $P<0.05$.

We used excel to graph all the initial load means for each tooth series. To calculate standard error and plot error bars for each set of means across tooth series, we conducted variance analyses for the data sets using JMP© data analysis software.

Results

Occlusal surface varied by convexity/concavity

When the shell is oriented at 0°, tooth morphology does not have a significant effect on force required for initial yield, except for severe concave shapes, which largely increase the force needed to crack the shell. It took approximately 78% more force for the first crack to appear using the most concave tooth model (Fig 5, Tooth Model -2) than the other tooth models, which had similar initial yields.

At the 180° orientation, it took approximately 22% more force for the first crack to appear using the flattest tooth model than the other tooth models. The most concave tooth model (Fig 6, Tooth Model -2) required approximately 12% more force for the first crack to appear than the most convex tooth model (Fig 6, Tooth Model 2), which required the least amount of force. Intermediate concave and convex shapes yielded similar levels of force. As morphologies become less severe and approach a flat shape, amount of force required to break the shell increases and eventually peaks when the occlusal surface is totally flat. After flat morphologies, severely concave morphologies require the most force to crack the shell, while severely convex shapes require the least force (Fig 6).

Cusp varied by radius

When the shell is oriented at 0°, different cusp radiuses require varying degrees of force to crack the shell. Tooth Models 1 & 3 required approximately 23% more force to crack the shell than Tooth Models 2 & 4, and approximately 36% more force to crack the shell than Tooth Model 5 (Fig 7). While Tooth Models 2 & 4 are statistically significant from each other, the force values are within similar ranges (40-45 newtons). Tooth Model 5 has a lower range than all other tooth models (35-38 newtons). Sharper cusps with highly accentuated points (Fig 7, Tooth Model 5) require considerably less force to crack the shell than blunter cusps (Fig 7, Tooth Model 1).

For the 180° shell orientation, initial yields decreased by a decreasing rate as cusp radius decreased, or as cusps became sharper. For example, Tooth Model 1 required 87% more force to crack the shell than Tooth Model 2, Tooth Model 2 required 85% more force than Tooth Model

3, and Tooth Model 3 required 83% more force than Tooth Model 4 (Fig 8). However, Tooth Model 4 & 5 required similar force values (Fig 8).

The combination of tooth type and orientation considerably influences initial yield values. Additionally, all mean values for the 180° orientation (Fig 7) were significantly lower than the 0° orientation (Fig 8). Furthermore, Tooth Model 5 in the 180° orientation (Fig 7) required 57% less force than Tooth Model 5 in the 0° orientation (Fig 8).

Discussion

Convex tooth morphology may be specialized in durophagous animals for select prey orientations. For the 0° orientation, Tooth Models -1 to 2 (Fig 5) had similar initial yields, which suggests that different convexity/concavity morphologies have no effect on force required to crack the shell. However, for the 180° orientation, initial yield means showed a bell-shape pattern as the convexity changed. As morphologies approached a flat shape, mean initial yield increased and eventually peaked when the occlusal surface was totally flat. Then, as convexity increased, the mean initial yield decreased until it reached its lowest value (Fig 6). The presence of a morphology pattern in the 180 orientation and the lack thereof in the 0 orientation suggests that tooth convexity in some durophagous predators may be specialized for select orientations during prey handling. Specifically, some durophagous predators may select to bite at their prey's weakest spots. In this case, the 180 orientation is comparably weaker than the 0 orientation because at 180°, the shell is upside down, where tight whorls do not form. Selecting for their prey's weaker points implies that durophagous animals and their prey may be co-evolving, which is driving the specialization of tooth morphology, as well as prey strength. If a durophagous predator selects to bite their prey at a certain orientation, then the prey may combat predation by developing stronger shell strength, which then drives durophagous tooth morphology to become more specialized for that orientation. A co-evolutionary arms race between durophagous predators and their prey has been occurring since the Late Mesozoic era, by which prey have developed anti-durophagous adaptations like burrowing behavior and remodeled shell structures (Vermeij 1977). Therefore, durophagous tooth morphology and prey handling have also evolved to optimize energy efficiency (West et al. 1991; Yamada and Boulding 1998).

Although each orientation had unique initial yield patterns, both orientations favored convex morphologies over flat and concave morphologies. In the 180 orientation, the most concave morphology had the highest initial yield, and the most convex morphology had the lowest initial yield. In the 0 orientation, the most concave morphology had a considerably higher initial yield (78% higher) than the other morphologies. This suggests that even though convex tooth morphologies may be specialized for select orientations, convex tooth shapes are optimal for breaking hard-shelled prey because as convexity increases, there is more stress applied for a larger occlusal surface area for crushing a hard surface (Bourdeau 2009). Additionally, in the 180 orientation, the flat morphology had the highest initial yield, which further suggests that while convex tooth morphologies are best suited for crushing, flat tooth morphologies may be best designed for anchoring prey (Jackson and Fritts 2003). In the 0 orientation, the mean initial yield for the flat tooth morphology does not differ from other morphologies, which further suggests that different levels of tooth convexity have not been specialized for certain orientations which may too strong to crush. In other words, if durophagous animals are choosing not to crush their prey in a certain orientation, there is little benefit of specializing flat morphologies to anchor their prey in that orientation so that they can later crush the prey using blunter, more convex teeth. This suggests that in addition to having specialized individual tooth morphologies, durophagous animals jaws may have evolved to include a variety of tooth shapes that play different roles during prey handling in order to maximize energy efficiency (West et al. 1991; Yamada and Boulding 1998).

Cusp morphology according to radius, or sharpness, may be specialized in durophagous animals for select prey orientations. For the 0° orientation, different cusp radiuses required varying degrees of force to crack the shell. However, for the 180° orientation, initial yields decreased by a decreasing rate as cusp radius decreased, or as cusps became sharper. The presence of a distinct morphology pattern in the 180 orientation and the lack thereof in the 0 orientation suggests that tooth convexity in some durophagous predators may be specialized for select orientations during prey handling. The 180 orientation for both tooth model series seems to indicate that some durophagous predators may select to bite at their prey's weakest spots, which presents aforementioned implications for the evolutionary relationships between durophagous predators and their prey.

Although each orientation had unique initial yield patterns for cusps varied by radius, both orientations favored sharper teeth over blunter teeth. For example, even though initial force yields varied from cusp to cusp in the 0 orientation, sharper cusps with highly accentuated points (Tooth Model 5) require considerably less force to crack the shell than blunter cusps (Tooth Model 1). This suggests that even though sharper tooth morphologies may be specialized for select orientations, sharper tooth shapes are optimal for breaking hard-shelled prey because as cusp radius decreases, there are smaller areas of contact between the tooth and the prey, increasing the stress applied to the prey for the same applied force. However, because durophagous tooth morphologies are characterized by their convex, blunt shapes (Turnigan and Wainwright 1993); tooth sharpness may be a factor that enhances the molariform tooth design of many durophagous predators. Therefore, some durophagous predators may have slightly pointed convex teeth to break through strong, hard-shelled prey items, such that the blunt occlusal surface area is not compromised for an accentuated cusp point. Because durophagous predators have robust jaws that include a combination of tooth morphologies for crushing, biting, and digesting (Jackson and Fritts 2003), some predators may use a combination of blunt, convex teeth; as well as convex teeth with accentuated points to crush their prey. This further suggests that durophagous animals jaws may be specialized to include a variety of tooth shapes that play different roles during prey handling in order to maximize energy efficiency (West et al. 1991; Yamada and Boulding 1998).

Although some durophagous predators may choose to orient their prey to maximize energy efficiency, the capability to discern weaker prey from stronger prey will vary among genera. For example, the intertidal octopus, *Octopus dierythraeus*, will try to pry open bivalve prey before expending the energy needed to drill through the shell (Steer and Semmens 2003). But, not all marine predators have the capacity to make such decisions. Redear sunfish spend more time breaking tougher shells than weaker shells of the same snail species, but do not select against tougher shells during selection. While durophagous animals might prefer certain prey, they might not be able to discern shell strength between individuals of the same prey species. Such variance is important to consider for assessing the role of coevolution in predator-prey relationships. To further investigate prey selection mechanisms in durophagous predators, individual species would need to be studied.

The interaction of tooth morphology and prey handling in durophagous predators reveal how much energy predators are expending during feeding. Feeding is intrinsic to growth and survival, and it is therefore important for an organism to adapt the morphology involved in feeding as well as prey handling behaviors to optimize the energy efficiency during feeding

(West et al. 1991; Yamada and Boulding 1998).Evolution is driven by changes in community structure and population dynamics, which are heavily influenced by the growth and survival of individual organisms (Osenberg and Mittelbach 1989). Durophagy, the consumption of hard food items, can be found in a diverse spectrum of organisms, both vertebrate and invertebrate, marine and terrestrial, all of which have specialized morphologies and behaviors that allow them to take advantage of this trophic niche. Given the range of durophagous predators, there is also a wide range of hard-shelled prey, such as molluscs, corals, and crabs. Therefore, the evolutionary ecology and diversification of durophagous animals is important to study because as predator-prey dynamics change over time, ecological relationships shift over time and space.

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Figures

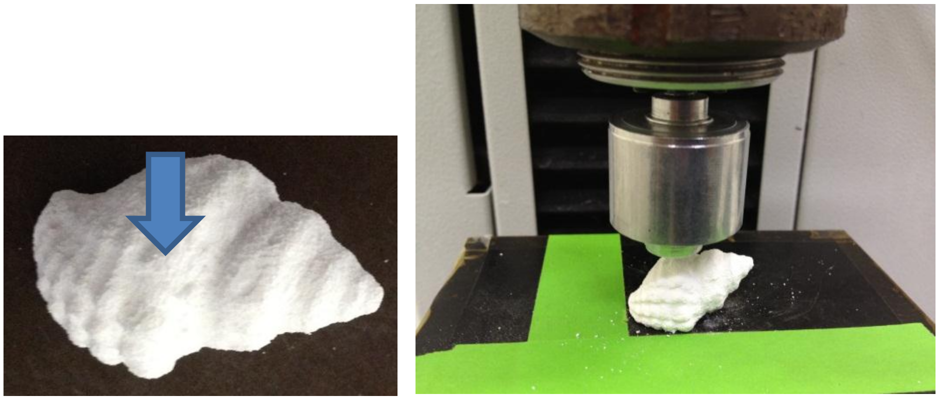

Fig 1. 0 degree orientation

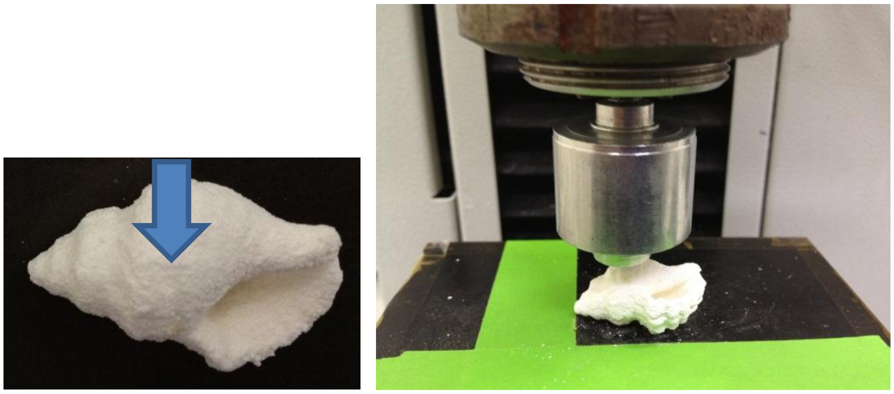

Fig 2. 180 degree orientation

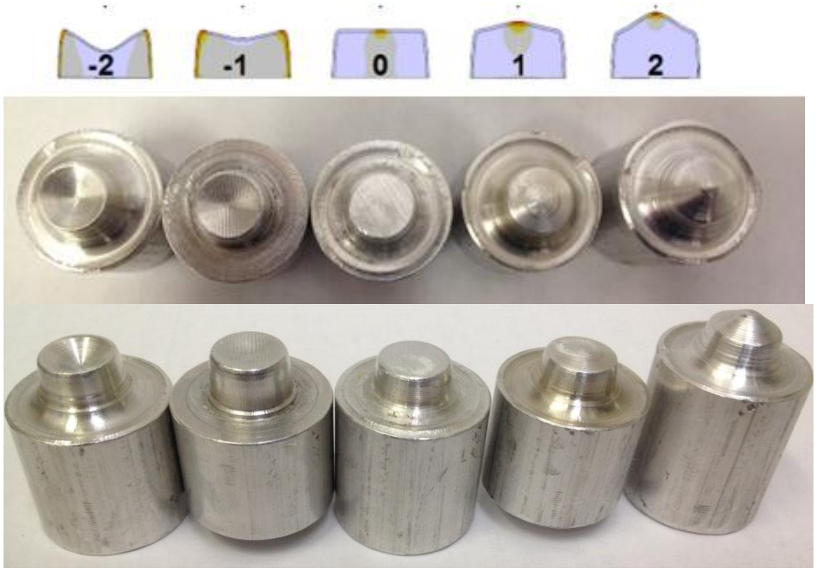

Fig 3. Tooth models varied by oclussal surface convexity/concavity

Fig 4. Tooth models varied by cusp radius

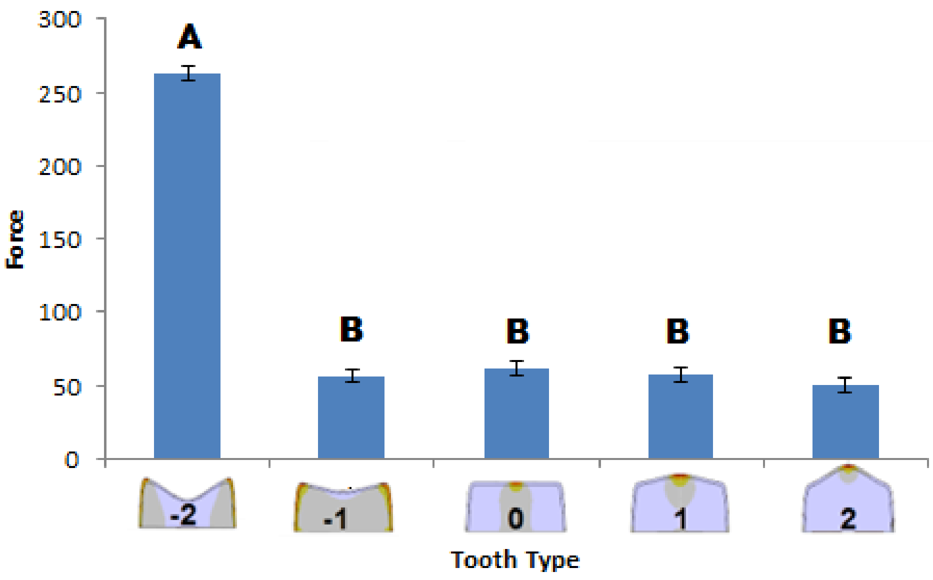

Figure 5: Force (newtons) varied by convexity and concavity of teeth for the 0° shell orientation. Means are presented with ± 4.825 standard error. Different letters indicate significant differences among means from 25 replicated force values for each tooth type. Means were compared using a Student's t-test in a one-way ANOVA test, $F_{4,120}$ = 366.376, P=0.05. A two-way ANOVA test showed that tooth type and orientation were significant influences on force, $F_{3,1}$ = 4.619, P=0.05.

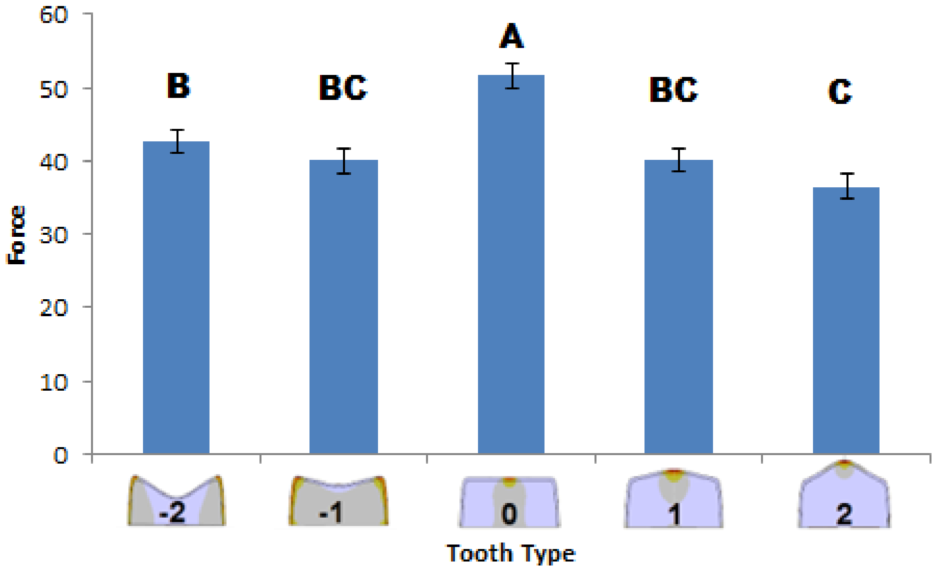

Figure 6. Force (newtons) varied by convexity and concavity of teeth for the 180°shell orientation. Means are presented with ± 1.637 standard error. Different letters indicate significant differences among means from 25 replicated force values for each tooth type. Means were compared using a Student's t-test in a one-way ANOVA test, $F_{4,120}$ = 12.124, P=0.05. A two-way ANOVA test showed that tooth type and orientation were significant influences on force, $F_{3,1}$= 4.619, P=0.05.

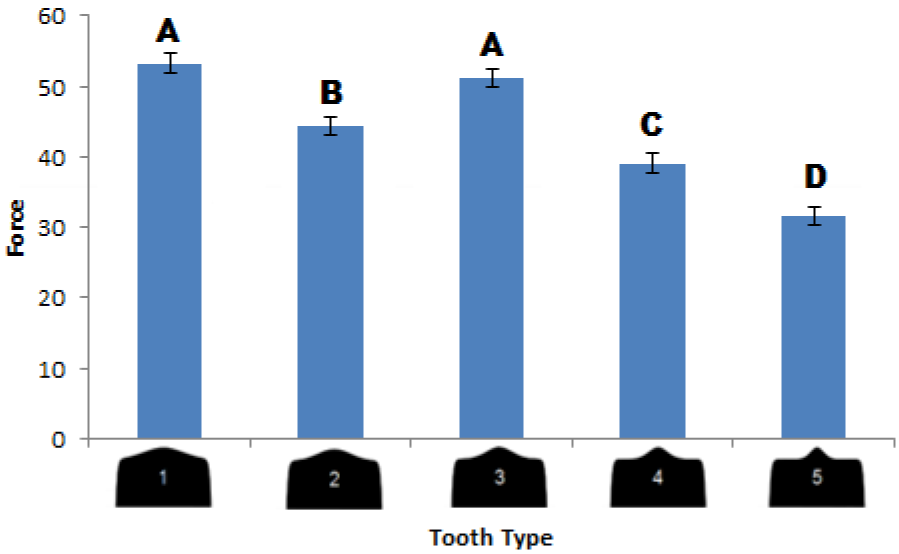

Figure 7. Force (newtons) varied by tooth radius for the 0°shell orientation. Means are presented with ± 1.304 standard error. Different letters indicate significant differences among means from 25 replicated force values for each tooth type. Means were compared using a Student's t-test in a one-way ANOVA test, $F_{4,120}$ = 46.079, P=0.05. A two-way ANOVA test showed that tooth type and orientation were significant influences on force, $F_{4,1}$ = 78.000, P=0.05.

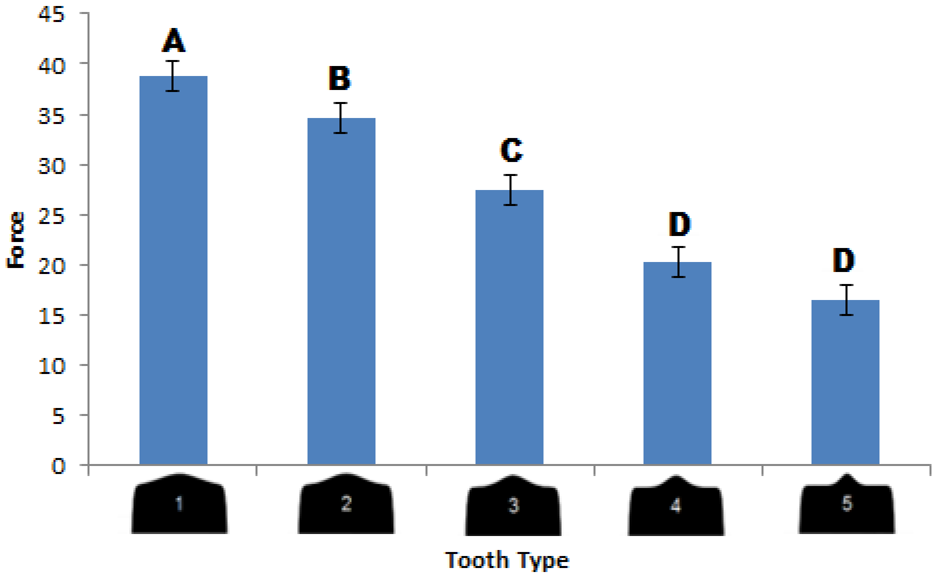

Figure 8. Force (newtons) varied by tooth radius for the 180°shell orientation. Means are presented with ± 1.493 standard error. Different letters indicate significant differences among means from 25 replicated force values for each tooth type. Means were compared using a Student's t-test in a one-way ANOVA test, F (4, 120) = 39.567, P=0.05. A two-way ANOVA test showed that tooth type and orientation were significant influences on force, $F_{4,1}$ = 78.000, P=0.05.

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