

Stress, Strain, and Deformation of Chondrichthyan Hyomandibulae During Feeding

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Introduction

The powerful and aggressive feeding habits of various shark species are clear indications that individuals are capable of applying incredible force to their prey. Sharks have been known to crush hard bone and shell (Wroe et al., 2008), and are notorious for their ability to attack and crush large prey. As cartilaginous fishes lacking any hard bone, we sought to study how the jaws of these chondrichthyans are able to withstand such intense pressure while continuing to remain functional and supportive. Of the various cartilages of the jaw, we identified the hyomandibular cartilage of the hyoid arch as our primary focus. The hyoid arch is a modified gill arch that acts as a hinge between the upper and lower jaws (Maisey, 1980). This cartilage is particularly significant as it helps suspend the jaw and allows the other elements of the jaw to function properly and effectively.

Differences in pressure of the buccal cavity and pressure produced by the jaw during feeding vary in different types of chondrichthyans. Chondrichthyans feed either by suction feeding, bite feeding, or a mix of both, and jaw structure is crucial to determining which behaviors are implemented (Tomtita et al., 2011). The arrangement of the hyoid arch and the surface area of the cartilages that make up the hyoid arch can help determine what type of feeding a shark uses. For example, by calculating which cartilages have the largest surface area, the relative stiffness of the jaw can be estimated, therefore indicating the most probable type of feeding (Wilga 2008). Cartilage stiffness was tested to determine whether stronger ceratohyal cartilage was present in sharks that suction feed. The stronger the cartilages were, the more force they could withstand during the high pressures that occur during suction (Tomita et al., 2011).

The hyoid area, the area made by the opening of the hyoid arch, can provide further insight into the determination of shark feeding (Wilga, 2008). There are five main shapes and orientations of the hyoid in chondrichthyans. They include a posteriorly oriented hyoid, an anteriorly oriented hyoid, and a short, laterally oriented hyoid. Particular positioning and shape of this feature directly affects the size of the jaw opening and buccal cavity. Posteriorly oriented hyoids allow for a very large and wide bite, and are seen in bite feeders. Short, lateral hyoid positions are well suited for cutting back and forth, but do not allow for as large of a bite. This

small area creates a better setting for suction feeding and helps create stronger negative pressure inside the buccal cavity to draw in prey. Anteriorly oriented hyoids swing the jaw open much wider so the most amount of water and prey possible can flow into the buccal cavity. This is more often seen in ram and filter feeders (Wilga, 2008). Difference in hyoid orientation is an important distinguishing feature to recognize and can help connect jaw mechanics to ecological scenarios.

Mineralized cartilage, also referred to as tessellated cartilage, plays a crucial role in jaw support during the intense pressures measured in the feeding of chondrichthyans. Prismatic and globular calcifications compose of the mineralization around the jaw cartilages. They form plates surrounding the extracellular matrix (ECM), the soft, inner unmineralized cartilage. (Dean & Summers, 2006). This cartilage calcification was found to strengthen not only the skeletons of sharks considerably, but also the hyomandibular region of the jaw and the surrounding cartilages (Dean & Summers, 2006).

We chose to test each hyomandibulae for stress, strain, and deformation of four different shark species. We tested two hypotheses. The first stated that an increase in hyomandibulae cross-sectional area would yield a higher percentage of mineralized area. The second stated that hyomandibulae with a greater length and smaller cross-sectional area would be more susceptible to stress, strain and deformation than hyomandibulae with a shorter length and larger cross-sectional area. The final hypothesis stated that hyomandibulae with a higher percentage of mineralization will be stronger and therefore less susceptible to deformation under pressure. We calculated Poisson's ratio, Young's modulus, and percent mineralization of each cartilage to test these hypotheses. Poisson's ratio measured the deformation of the cartilage as it was compressed, and Young's modulus calculated the stress over strain ratio. We accepted our first hypothesis because there was an increasing trend over the cross-sectional area and percentage of cartilage mineralization. Our null hypotheses were accepted for the second two hypotheses. Stress, strain, and deformation are not affected by length or cross-sectional area and percent mineralization does not affect the ability of the hyomandibula to resist deformation.

Methods

All research and tests were conducted at the University of Washington Friday Harbor Labs, and all specimens were obtained from Narragansett and Delaware Bay. Four specimens each of angel sharks (*Squatina*), bamboo sharks, (*Chiloscyllium plagiosum*), spiny dogfish (*Squalus acanthias*), and sandbar sharks (*Carcharhinus plumbeus*) were used. Jaws were dissected from each organism and cleaned so all ligaments, skin, tissue, and soft cartilages were removed and only hardened

cartilage remained. The cartilages were then separated from each other and measurements were taken of the length, width, and depth of each hyomandibula. A Material Testing System (MTS) Synergie 100 machine was set to apply a force of 50N to each element of the hyoid arch and sonomicrometry was used to measure, stress, strain, and cartilage deformation.

Before compressions began, cartilages were prepared. Each cartilage was placed vertically between two washers and set in epoxy in order to create flat, parallel surfaces on top and bottom. This allowed the hyomandibulae to stand upright and provided an even surface for the compression block. When the epoxy was set, three 2mm sonometric crystals were glued onto each cartilage. Two were placed on the ventral convex side of the cartilage close to each end, but not touching the epoxy base. The third was glued on the dorsal convex side, directly opposing one of the crystals on the ventral side. This allowed measurements of change between both length and width to be calculated as the cartilages were compressed. Cartilages were placed in elasmobranch ringers solution below the compression block and the MTS was activated, applying 50 N of force to the cartilage.

As the MTS operated, data from the sonometric crystals was sent to a program called SonoSOFT. SonoSOFT measured the change in distance between each crystal over the length of time of the test. Distance was calculated using the measurements of the sound waves sent between the crystals and the equation of speed of sound through water. Data was analyzed through SonoLAB, a program that saved the live SonoSOFT data. Onset, peak, and -0.4% onset were all measured and calculated.

Once tests were complete, we removed the cartilages from the epoxy and cut through the middle to expose a cross-sectional piece with a half-centimeter width. These pieces were placed under a Zeiss dissecting microscope, and through AxioVision Rel. 2.8, we were able to take a picture of the cross-sections and trace the areas. Both the outside area of the cartilage and the outside area of the ECM were visible and traced. AxioVision Rel. 2.8 calculated both areas, and we subtracted the ECM area from the total area to reveal the area of mineralization and percent mineralization of each cartilage. All data was compiled into a final spreadsheet and analyzed in JMP.

Results

*Note: Bamboo sharks (*Chiloscyllium plagiosum*) were the only individuals eliminated from the statistical analysis because we encountered too many errors during experimentation to produce accurate and complete results.*

Figures: Triangles indicate spiny dogfish (*Squalus acanthias*), diamonds indicate sandbar sharks (*Carcharhinus plumbeus*), and squares indicate angel sharks (*Squatina*).

Effects of Cross-Sectional Area on Cross Mineralization

We found that cartilages with a larger cross-sectional area also have an increased percent mineralization than smaller cartilages (Fig. 1). This supported our hypothesis and not only does the cartilage increase in size, but a thicker wall of mineralization is created. This trend is significant and has a P value of 0.0049 and an F ratio of 12.9062.

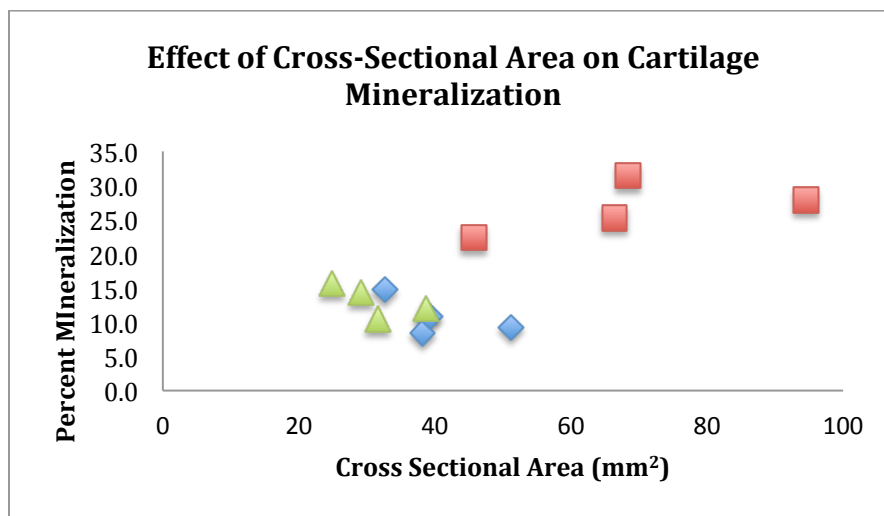


Fig. 1

Effects of Length and Cross-Sectional Area on Poisson's Ratio and Young's Modulus

We accepted our null hypothesis in this case because neither the relationship between Young's Modulus and length nor the relationship between Young's modulus and cross-sectional area showed a significant trend. The correlation between Young's modulus and length has a P value of 0.2551 and an F ratio of 1.4574 (Fig. 2). The correlation between Young's modulus and cross-sectional area has a P value of 0.4742 and an F ratio of 0.5529 (Fig. 3).

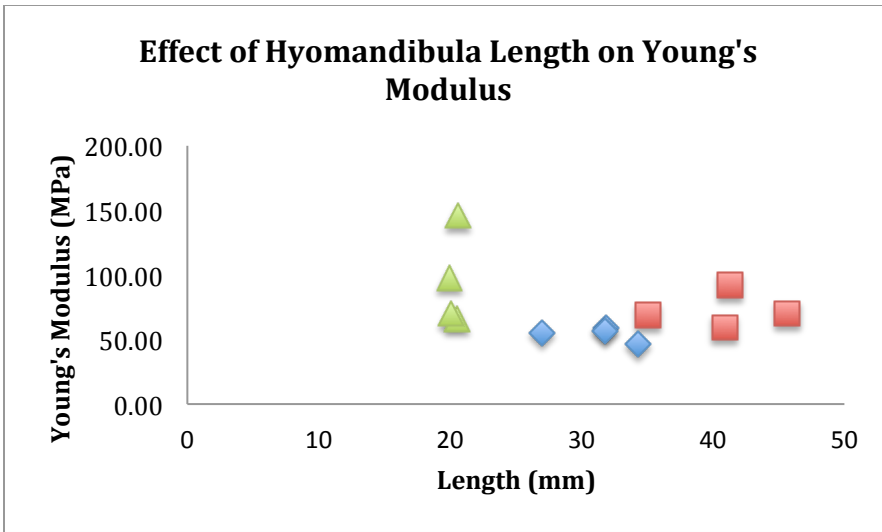


Fig. 2

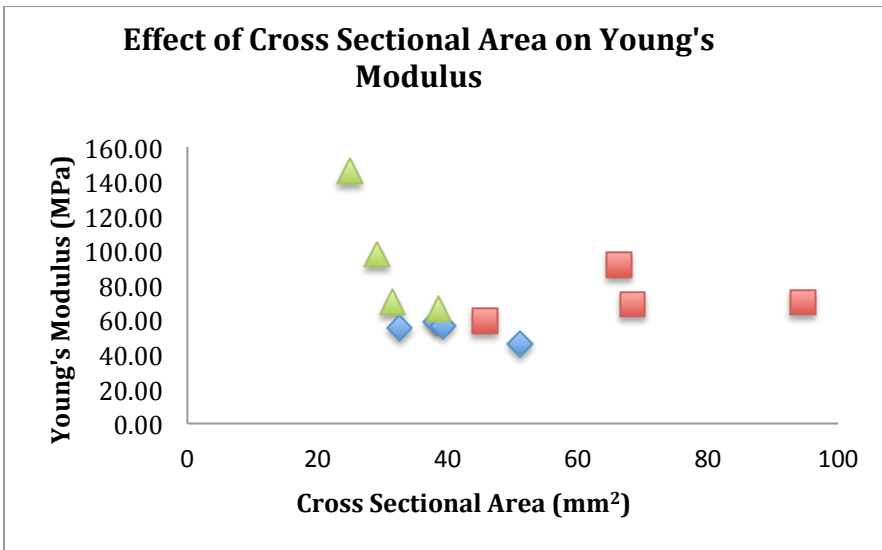


Fig. 3

We also accepted our null hypotheses in the case of Poisson's ratio and both hyomandibula length and cross-sectional area; they had no significant trend. The correlation between Poisson's ratio at peak strain and length has a P value of 0.3407 and an F ratio of 1.0008 (Fig. 4). The correlation between Poisson's ratio at peak strain and cross-sectional area has a P value of 0.5027 and an F ratio of 4.925 (Fig. 5).

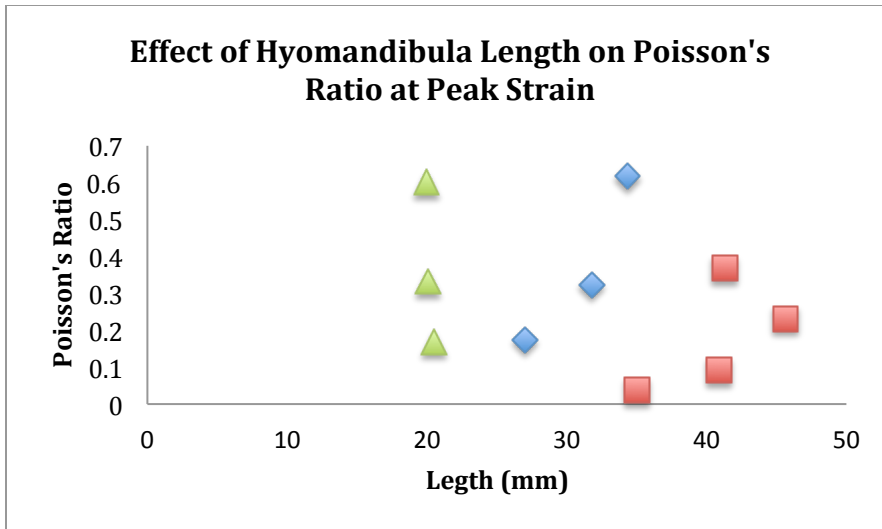


Fig. 4

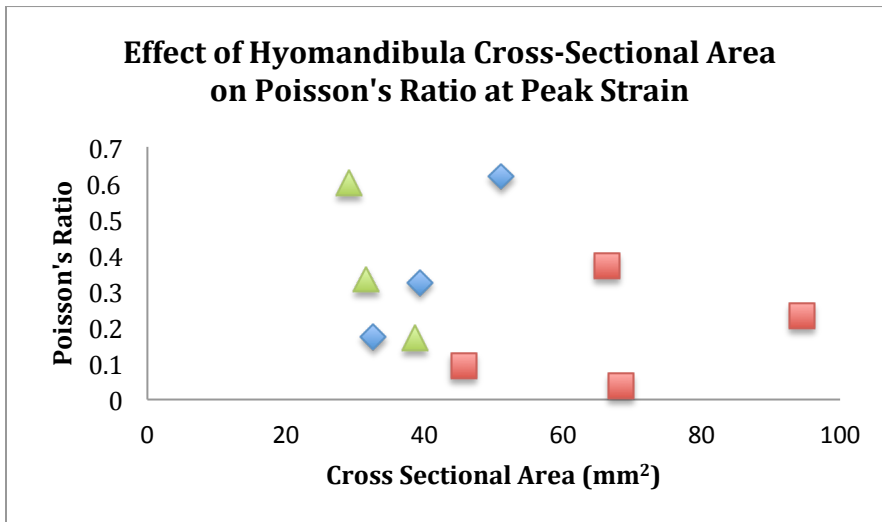


Fig. 5

Effects of Percent Mineralization on Young's Modulus and Poisson's Ratio

Our null hypothesis was also accepted for our last hypothesis because there was no strong correlation between percent mineralization and Young's modulus or Poisson's ratio. The relationship between percent mineralization and Young's Modulus has a P value of 0.6369 and an F ratio of 0.2369 (Fig. 6). The relationship between percent mineralization and Poisson's ratio at peak strain had a P value of 0.1086 and an F value of 3.2610 (Fig. 7).

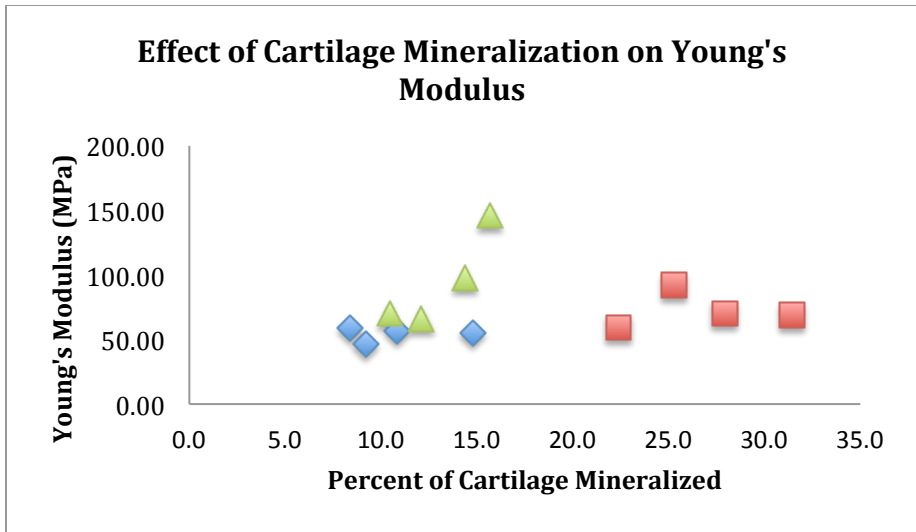


Fig. 6

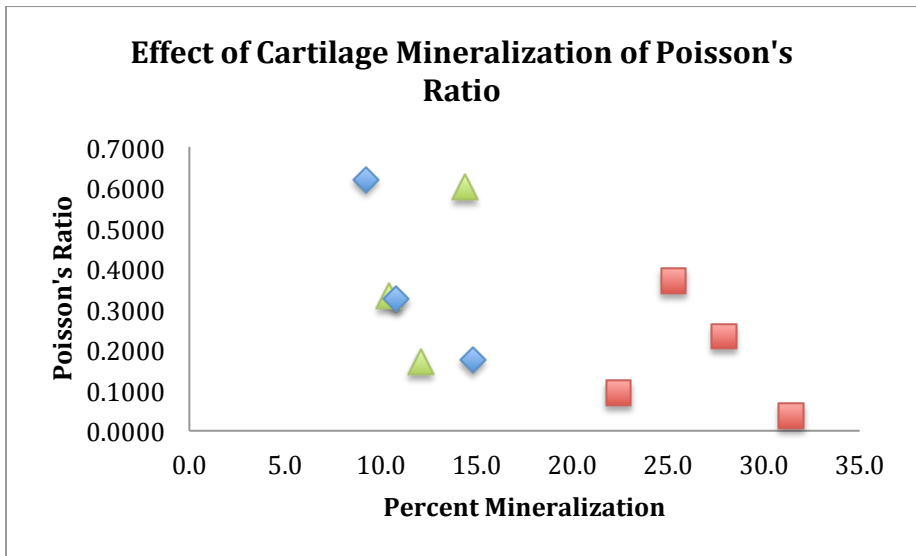


Fig. 7

Discussion

Many of our results did not support our original hypotheses. It was most interesting that there was a significant increasing trend regarding the cross-sectional area and percent mineralization, yet there was no effect of percent mineralization on reducing stress, strain or deformation. We expected a larger area of mineralization would decrease both Poisson's ratio and Young's modulus, since there would be a larger amount of harder calcified cartilage surrounding the ECM core. Because mineralized cartilage substantially supports the vertebral cartilages of chondrichthyans (Dean & Summers, 2006), it seems unusual that a thicker layer of tesserae it would not increase stiffness in the cartilages of the jaw and hyoid area.

Larger cartilages might need thicker mineralization than smaller cartilages just because they are needed to move other large cartilages of the jaw. It is also possible that simply the presence of mineralization can strengthen the cartilages enough, and that the percentage of mineralization does not have as great of an effect. Another explanation could be the possibility of different types of mineralization being more successful at resisting strong forces than the physical amount of mineralization present.

Concerning the size of the hyomandibulae, we anticipated that longer and thinner cartilages would be more susceptible to stress, strain, and deformation, than shorter and stubbier cartilages. Because short structures with wide bases are generally more steady and sturdy than tall structures with narrow bases, we predicted that this concept would translate to hyomandibula cartilages. However, cross-sectional area and length had no significant effect on Poisson's ratio or Young's modulus. This indicates that there is no advantage or disadvantage of differently shaped or oriented hyomandubulae regarding stiffness and resistance to deformation.

Our results pose many questions about the jaw mechanics and composition of cartilages in chondrichthyans. Future studies on the types of mineral components that make up the tessellated cartilage could indicate whether or not certain minerals make stronger calcified cartilage than others. Ecological implications could include the energetic cost of producing larger hyomandibulae and thicker layers of mineralization, and why these factors differ when there seems to be little to no benefit. This study could also branch out into analyzing more shark species, the differences between shark and ray hyoids and jaws, and testing other elements of chondrichthyan jaws including the upper and lower jaws.

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