Comparative Functional Anatomy of the Oral Jaw Musculo-skeletal System in Pacific Salmons

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ABSTRACT

Food acquisition is a necessary component of survival for any organism and in order to feed effectively, a predator must meet the mechanical demands of its prey. This study's focus was to make general observations and conclusions about the evolution and adaptation of several morphological traits of pacific salmon jaws based on varied feeding behaviors. Dissections of juvenile king, adult king, and *keta* salmon were performed, during which measurements pertaining to the articular joint and adductor mandibulae were taken and recorded. The study found that king salmon have stronger adductor mandibulae, while *keta* have stronger skeletal jaw components. This trade-off is a morphological adaptation in which either force or velocity can be prioritized. Each species' jaw anatomy is specialized for their diet and feeding habits, for example stronger jaws to accommodate the crushing of tough prey or fast jaw closure for hunting fish prey. Other conclusions, like the positive correlation between head length and adductor mandibulae mass, were also drawn from the study.

INTRODUCTION

The waters of the Pacific Northwest are habitat to five species of salmon: chinook, also known as king, (*Oncorhynchus tshanytscha),* coho (*Oncorhynchus kisutch),* chum *(Oncorhynchus keta),* sockeye (*Oncorhynchus nerka),* and pink (*Oncorhynchus gorbuscha)*. These five species are difficult to distinguish from one another based on superficial anatomy, despite differences in diet (Brodeur, 2007), habitat, and other ecological factors. To coexist with one-another, these similar species must evolve ways of not competitively excluding one another. We would expect, therefore, that natural selection would modify their musculo-skeletal anatomy to be specialized for different prey items in each species. *Teleostei*, an infraclass of bony fishes that include salmon, have a common skeletal musculature that includes a movable maxilla and premaxilla, one main jaw-closing muscle, and a simple row of teeth on the oral jaw. Salmon make an excellent model system for understanding the relationship between anatomy and ecology because they are a small, easily studied group and much is known about their ecological role. Herein, my goal is to link dietary diversity in this group with musculo-skeletal anatomy and biomechanical modelling.

The varied functional anatomy of an organisms' jaw is vital for behaviors like respiration and feeding. Salmon jaws function like a lever with the articular joint, where the jaw rotates open, acting as the fulcrum of the lower jaw (Westneat 2011). This mechanism in salmon is predominantly powered by one muscle: the adductor mandibulae.

The adductor mandibulae in bony fishes first appears early in the fossil record, allowing time for the evolution, differentiation, and specialization of muscle anatomy and activity patterns (Alfaro 2001). We would therefore expect that patterns of variation in muscle anatomy should correlate with patterns of variation in habitat, behavior, size, or diet. Brodeur (2007) found that the diets of Pacific salmon species do vary significantly. King and coho have a diet high in fish prey, while *ket*a, sockeye, and pink tend to be more planktivorous, with no consistently dominant prey taxa. Juvenile king have the broadest diet content among all species with juveniles generally eating more zooplankton and larval invertebrates and adults consuming smaller fish, pelagic amphipods, or krill across all species.

I predicted that salmon species with a diet high in fish prey would have stronger jaws, more massive adductor muscles and a larger maximum gape to accommodate their feeding patterns. Consequently, I expected that species that are planktivorous or eat small prey would have a smaller jaw with smaller, lighter adductor muscles.

METHODS

Specimens

To test my predictions, I dissected the heads of 29 specimens; 27 juvenile king salmon, one adult king salmon, and one chum salmon that I will refer to by its species name, *keta*. The frozen specimens were stored in a freezer until the night before each dissection, at which time the salmon heads were removed and defrosted in a sea table.

Dissection

For each dissection, using a scalpel, I removed the skin covering and surrounding the adductor mandibulae and articular joint (Figure 1). I took the following measurements for each fish with calipers, a protractor, and a scale: the adductor mandibulae mass, the adductor mandibulae length, adductor mandibulae width , mandible length, total head length defined by the posterior most edge of the adductor muscle to the tip of the nose, length from articular joint to tip of jaw, two adductor mandibulae muscle fiber angles relative to the line of action of the muscle, the distance between articular joint and anterior most tooth, the distance between the articular joint and posterior most tooth, the distance between the adductor mandibulae origin and insertion points , the maximum gape measured as a distance in cm., and the maximum gape angle measured in degrees. I drew a detailed sketch of the head for each species type to illustrate the differences in skeletal

Figure 1- Dissection of a *keta*. The adductor muscle is visible to the left of the eye socket.

morphology and musculature (Figure 2).

Analysis

I used trigonometry to find the distance between the articular joint and insertion point of the adductor muscle given the known mandible length and total head length measurements. With this information, I calculated the mechanical advantage for both the posterior most and anterior most teeth of each specimen. Mechanical advantage was calculated by dividing the distance between the articular joint and adductor insertion point by the distance between the articular joint and respective tooth. In this study, the mechanical advantage serves as an indicator of relative biting force. I ran linear regressions to analyze the significance of trends for comparisons like total head length vs. adductor mass and the adductor mass vs. maximum gape angle.

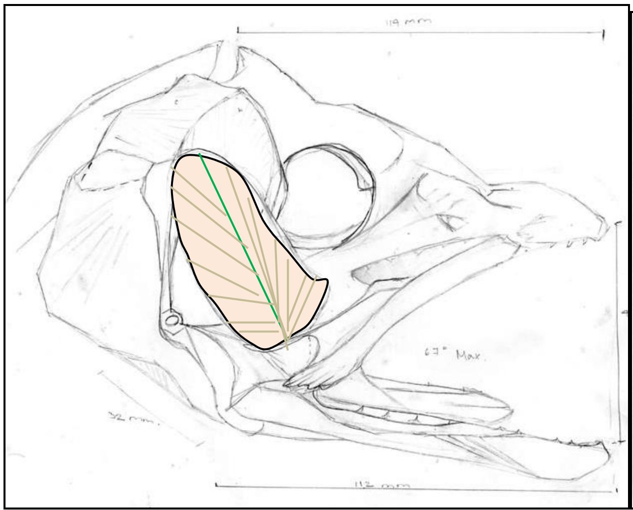

Figure 2a- Illustration of a juvenile king salmon dissection. Pink shading represents adductor muscle with the green line representing the line of action.

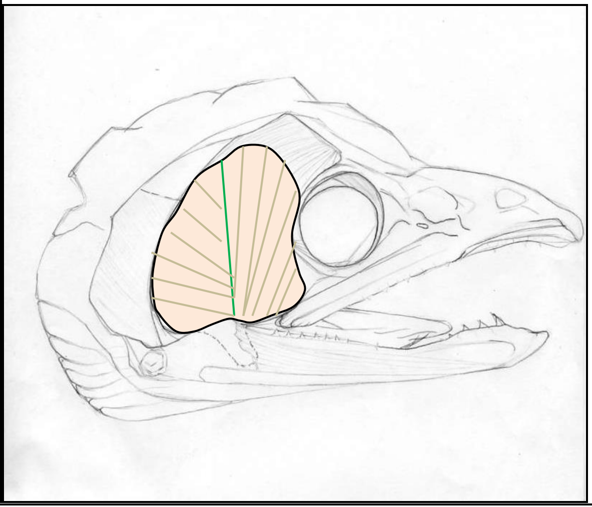

Figure 2b- Illustration of a *keta* dissection. Pink shading represents adductor muscle with the green line representing the line of action.

RESULTS

Figure 3 shows the mechanical advantage distribution between the front and back teeth in juvenile king salmon. In every sample, the back tooth, in red, has significantly more mechanical advantage; about twice as much compared to the front, meaning the back teeth have prioritized biting force rather than biting speed.

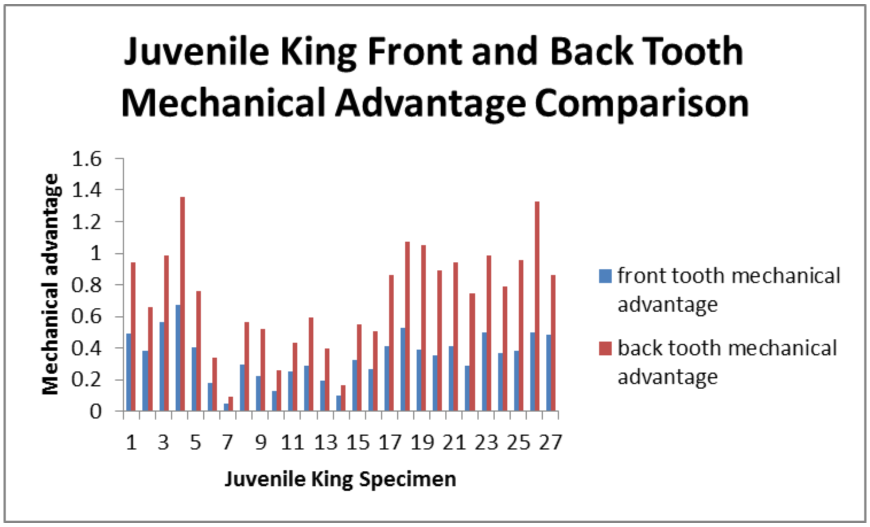

Figure 3- illustrates the difference in mechanical advantage between the front and back teeth of juvenile king salmon. Note the back tooth consistently has approximately twice the mechanical advantage of the front tooth.

The graph comparing mechanical advantage across species (Figure 4) shows that the mechanical advantage distribution between front and back teeth are extremely similar in juvenile and adult king salmon. The mechanical advantage averages for juvenile king are 0.7266 for the back tooth and 0.3493 for the front tooth and for adult king are 0.7594 and 0.3848 respectively; almost the same. In contrast, *keta* have a significantly more robust back tooth mechanical advantage with 1.391 for the back tooth and 0.514 for the front.

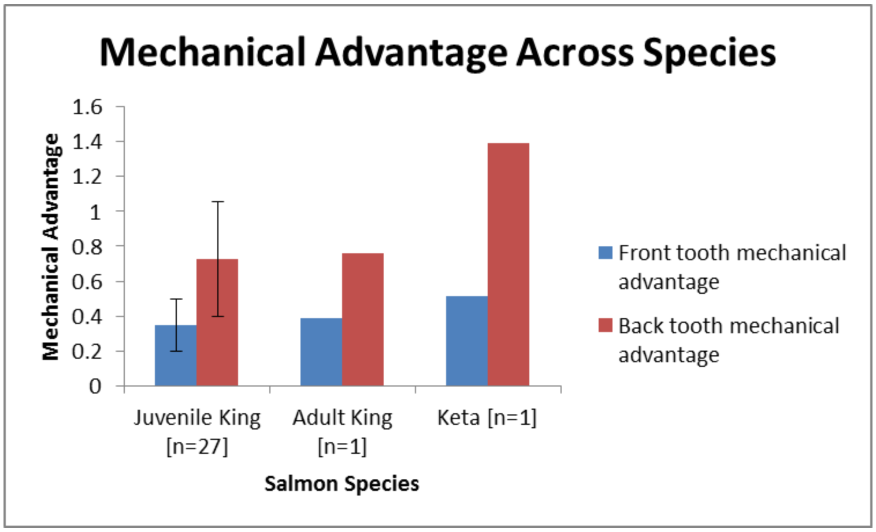

Figure 4- compares the mechanical advantage of front and back teeth between species. The *ketas* back tooth mechanical advantage falls outside of the king salmon standard deviation. The standard deviations of the juvenile king front and back tooth mechanical advantages were 0.1491 and 0.3273 respectively.

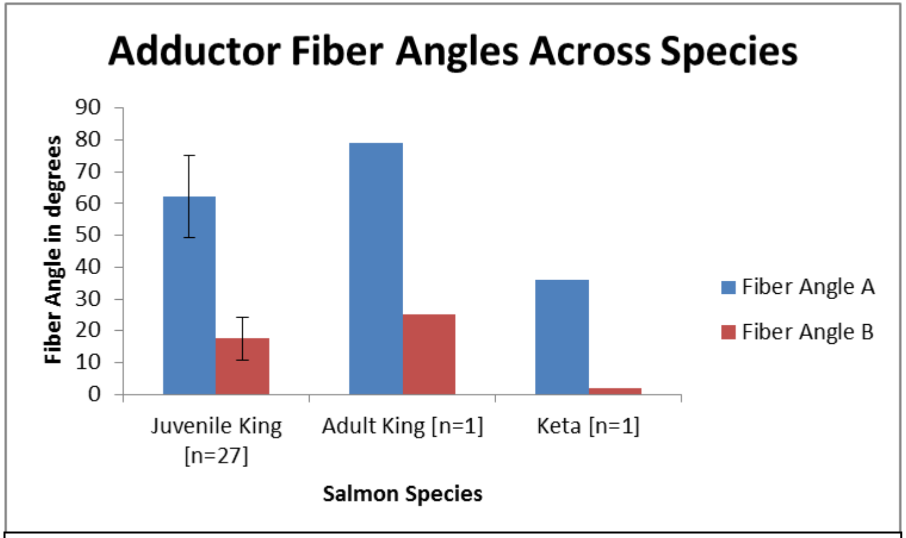

Figure 5- illustrates the fiber angles of the adductor mandibulae in the different species relative to the line of action of the muscle. The standard deviations of the juvenile king A and B muscle fiber angles are 12.89 and 6.78 respectively.

As seen in Figure 5, the king salmon have more extreme muscle fiber angles relative to the line of action of the adductor muscle than do keta. Extreme fiber angles show that king salmon adductor muscles prioritize strength more so than keta adductors. *Keta* seem to have muscle structure that emphasizes velocity at the expense of force, relative to the king specimens.

Not surprisingly, salmon adductor mandibulae mass is linked to total head length. As the head length increases, muscle mass scales with it (see Figure 6a) (linear regression, P-value=<0.001, R^2= 0.368). Noteably, however, head length and maximum gape angle are not linked at all (see Figure 6b)(linear regression, P-value=0.969, R^2=<0.001).

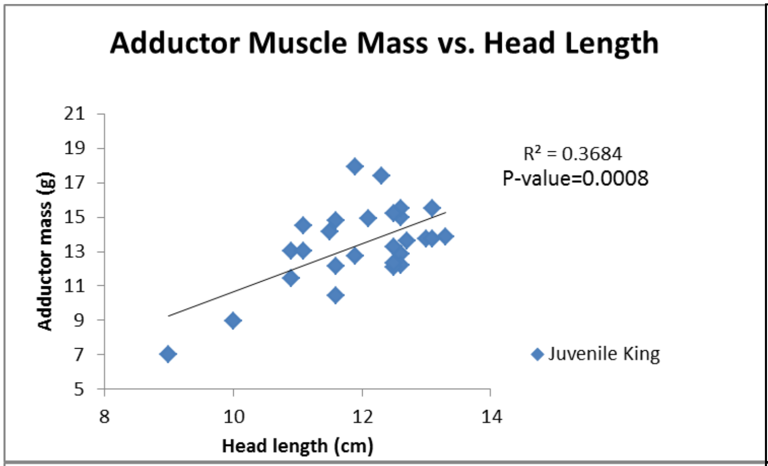

Figure 6a- shows the significant correlation between total head length and adductor mandibulae mass in juvenile king salmon.

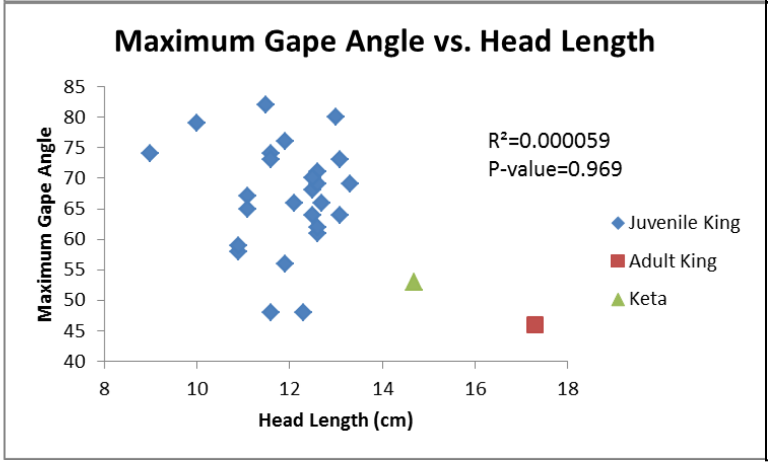

Figure 6b- shows no correlation between total head length and maximum gape angle. The P-value and R^2 value were calculated only with juvenile king data.

Most interestingly, there is a pattern linking adductor mandibulae mass and maximum gape angle. While these results are not statistically significant (linear regression, P-value=0.885, R^2=0.0008), Figure 7 shows a negative trend emerging in which individuals with a more massive adductor are not able to open their jaws as wide.

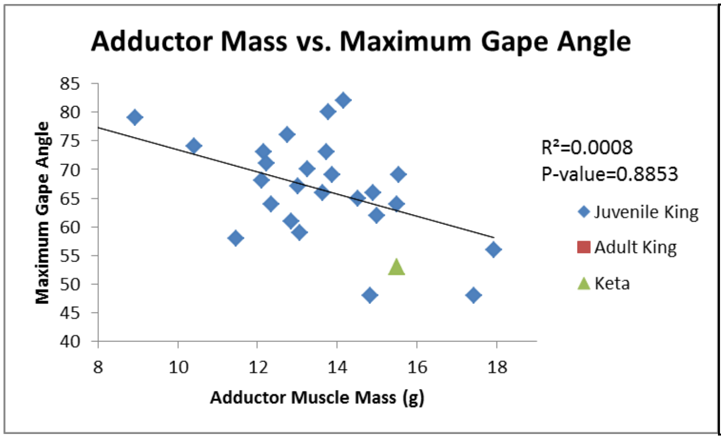

Figure 7- shows a negative pattern linking heavier adductor muscles with a smaller maximum gape angle, although this trend is not statistically significant.

DISCUSSION

These data lead to the conclusion that the morphology of the adductor mandibulae and jaw system in king salmon are significantly different from that system in *keta*. In all species, the back tooth had a much higher mechanical advantage than the front tooth, which means more force is distributed to the back of the mouth for crushing, much the way our molars function. The front teeth, with a lower mechanical advantage, are specialized for agile biting rather than force based upon their position farther away from the articular joint.

The *keta* has a significantly higher back tooth mechanical advantage compared to the king species during both juvenile and adult stages. This means that the skeletal frame of *keta* prioritizes jaw force over jaw dexterity. *Keta* have a broad diet of insects, invertebrates, copepods, mollusks, tunicates, and fish (NOAA 2014), so the greater skeletal force enables *keta* to have a wider range of feeding abilities to accommodate for their prey diveristy. Eating mollusks or tunicates with a tough exterior or shell would require more strength to consume than would small, fleshy fish prey. Since adult king salmon eat primarily other fish, it is reasonable that they would evolve to have a more agile, quick jaw structure to capture fast moving but softer prey in the water column. This conclusion is supported by the mechanical advantage data in Figure 4.

Adductor mandibulae fiber angles were also measured and used as an indicator of muscular force production, rather than skeletal force transmission. Wide fiber angles compared to the line of action of the muscle, the stright line between the origin and insertion points, allow for more efficient contraction and thus more force. Contrastingly, king have significantly stronger adductor muscles than do keta. King salmon adductor muscles have a narrower shape compared to the more round *keta* adductor, as shown in Figure 2a, but the muscle fiber angles extend from the line of action in greater degree incraments. Keta adductor fiber angles are more parallel to the line of action, providing less force, as shown in Figure 5.

There is likely a fitness advantage to prioritizing either skeletal or muscular force depending upon niche. Not specializing in either would result in a predator with inefficient, weak jaws. Strength in both categories would not be well suited for general salmon feeding behavior, as the individual would be less energetically efficient and have difficulty capturing non-sessile prey items. The king and *keta* have adaptive morphological traits via natural selection to suit their ecological roles.

Figure 6a illustrates the statistically significant correlation between the salmon head length and adductor muscle mass. Longer fish have proportionately more massive adductor muscles. We can also conclude, based on data from Figure 6b that there is no relationship between the length of a salmon and the salmon's maximum gape angle: the angle measured from the jaws widest possible open position. This means that size of the fish does not play a role in the maximum gape angle of the jaws. Larger fish cannot necessarily open their jaws wider than smaller fish.

Figure 7 illustrates a technically insignificant but intriguing trend; more massive adductor muscles appear to be linked with a smaller maximum gape angle. The maximum gape angle does not scale with adductor size, as does head length, but instead appears to be correlated in the opposite way. A wide maximum gape could be an adaptive morphological trait of naturally small fish to compete with the larger predators within their species. The small fish are able to open their jaws the same distance between upper and lower jaw tips, as measured in centimeters, but have perhaps adapted to achieve this disproportional feat by having a wide maximum gape angle as measured in degrees.

Several findings from these data were conclusive, however during the data collection process, there was room for error. Possible sources of error include innacurate calibration of measuring equipment, human errors in measuring or recording, possible errors in trigonometric calculations, or interference from nonrepresentative sampling bias with an n=1 in some categories.The results of this study have lead to further questions for investigation. To continue the study, I would suggest repeating the procedure with a greater sample size for the adult king and *keta* categories, along with adding more pacific salmon species, such as pink and sockeye for a comprehensive morphological perspective.

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