

Use the Force: scaling of jaw muscle forces in the great sculpin,

Myoxocephalus polyacanthocephalus

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ABSTRACT

Suction feeding is the most common vertebrate feeding mode. Fishes suction feed by rapidly expanding the buccal cavity, creating a subambient pressure inside the mouth that causes water (and, ideally, a prey item) to rush in. The predator's ability to close the mouth around evasive prey determines feeding success. As a fish grows, the volume it engulfs should scale with length to the third power (volume \propto length³). This becomes a burden on larger fishes, as muscle force (which drives mouth closing) should scale with length squared (force \propto muscle cross-sectional area \propto length²). Since suction volume increases faster with size than muscle force, a force deficit results as fish grow larger. Previous studies show that great sculpin counter the force deficit with increased jaw leverage and more force production at longer fish lengths. In this study, we examined muscle force and muscle strain variation across sizes in the suction-feeding great sculpin, *Myoxocephalus polyacanthocephalus*. Because muscles are subject to the limitations of the length-tension relationship, we saw maximum force (P_0) production at intermediate muscle lengths (L_0) and declining forces at longer/shorter muscle lengths. Our results show that great sculpin maintain a constant amount of muscle strain to achieve at least 50% of their maximum force (P_0) throughout ontogeny. As the great sculpin grows, it uses a wider range of this available muscle strain in feeding, stretching its muscles away from L_0 and losing force in the process. Thus in addition to an increasing muscle force deficit, larger great sculpin experience declining jaw-closing forces due to the length-tension properties of jaw-closing muscles.

INTRODUCTION

Throughout ontogeny, animals experience a wide range of environments (Bonner, 2006). Each environment places different physical demands on anatomical structures, and the morphology of these structures should adapt accordingly (Erickson *et al.*, 2013; Habegger *et al.*, 2012). Morphological traits reflect responses to different pressures between larval and adult stages. As an animal grows, the physical laws of their environment provide possibilities for their growth, but create morphological limitations (Levinton and Allen, 2005).

Variation in morphology can be accompanied by variation of muscular performance across ontogeny (Carrol and Wainwright, 2005). As an animal increases in size, the cross-sectional areas (CSA) of its muscles increase, thereby increasing available muscle force (Habegger *et al.*, 2012). Herrel (2005) observed that CSA scaled with positive allometry in relation to length, suggesting that large animals were more tailored toward force production than smaller animals. Muscular performance should relate directly to fitness because of its connection to feeding success. In fishes, feeding success is also limited by gape (Alfaro *et al.*, 2001; Gidmark *et al.*, 2013). Because active force is a function of length, prey-specific gape limits the available bite force (Cooke and Fay, 1972; Gidmark *et al.*, 2013) to a range of forces with a maximum force (P_0). To produce optimal force, muscles must stretch to the optimal length (L_0), which varies across species and sizes (Carrol and Wainwright, 2006; Dobrin, 1973; Gidmark *et al.*, 2013;). This optimal muscle fiber length (L_0) must produce enough force to close the jaw effectively but also prevent damage to the physical features of the jaw (tooth failure, jaw bone fracturing) with supramaximal force production (Hellman *et al.*, 2013).

Our study species, the great sculpin (*Myoxocephalus polyacanthocephalus*), possesses a massive mouth with potent suction power. Suction feeding is the most common feeding mode

among aquatic vertebrates (Ferry-Graham, 2003). To utilize this suction, the great sculpin approaches its prey by moving in slow bursts. Once close enough to the prey, the premaxilla is protruded rapidly; the buccal cavity expands, sucking water and prey into its mouth. To close its mouth after a suction feeding event, the great sculpin relies on the contraction of its jaw adductor muscle system, the *adductor mandibulae*. Even if a prey item is captured, the fish's ability to keep evasive prey trapped inside the mouth links jaw-closing muscles to overall feeding success.

As a fish grows, its feeding success is subject to a variety of physical pressures, such as area and volume. These two pressures interact in different ways with increased fish length. With any increase in length, volume scales with length³, while muscle force (proportional to muscle cross sectional area) scales with length². As fish length increases, the suction volume in the buccal cavity of the sculpin increases at a faster rate than the muscle force can keep up with (Figure 1). The muscle must overcome this force deficit at larger fish lengths to still effectively feed. A previous study (Conrades *et al.*, 2014 in progress) showed that large great sculpin increase jaw leverage to counteract the muscle force deficit. In maximizing force, larger sculpin sacrifice speed in jaw closure. Speed is critical, however, in smaller sculpin. The smaller fish's muscles experience a miniscule force deficit, if they experience it at all. At a small size, the volume-muscle force relationship is almost linear. The smaller fish's suction feeding requires it to produce a large enough volume to engulf its prey, while closing its mouth in time to prevent the prey from fleeing this smaller relative volume. To prevent prey escape, smaller sculpin rely on faster jaw closure. In depending on speed, smaller fish sacrifice strength of jaw closure. These findings indicate that force is more of a limiting factor for large great sculpins.

We hypothesize that larger fish will additionally overcome this force deficit by increasing the amount of muscle strain needed to produce at least 50% of their maximum jaw-closing force (P_0).

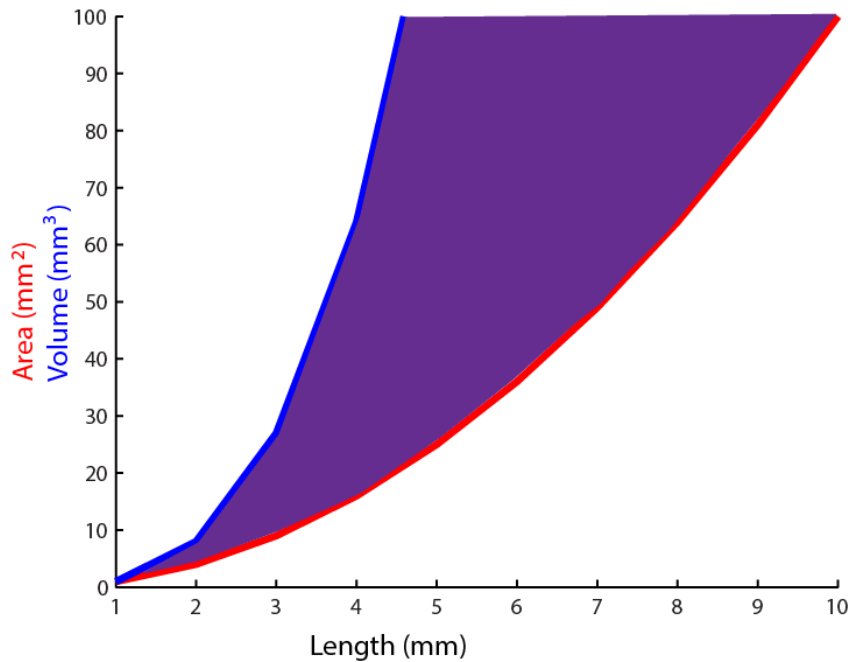


Figure 1. The scaling relationship between area and volume with length. The purple shaded region indicates the muscle force deficit that occurs as a result of volume scaling at a faster rate than muscle force.

METHODS

Specimens

The great sculpin ($N = 9$) examined in this study were obtained from the waters around San Juan Island, Washington State, USA by either trawl, seine, or captured during diving. Fish were maintained in a flow-through system at all times at 11-14 °C and sorted into size category tanks to prevent cannibalism. Animals were fed spot prawn (caught in Friday Harbor, WA) as needed. All animal housing, maintenance and experimental procedures were approved by the University of Washington's Institutional Animal Care and Use Committee.

In situ Data Collection and Analysis

Methods are considered *in situ* as defined by Gidmark *et al.* (2013). Fish were anesthetized using Metomidate (Western Chemical Inc, Ferndale, WA) at a concentration of 0.01 gram per liter. Once sufficiently anesthetized (determined by inability to right itself), euthanasia was performed by cervical dislocation and exsanguination. Immediately after euthanasia, a portion of the cheek was removed including the most anterior preopercular spines, the *adductor mandibulae* system (*malaris* and *rictalis* muscles), the quadrate, upper jaw and subocular bones, and the coronoid process to which the *rictalis* attaches. The dentary was trimmed down off at the jaw joint so only the coronoid process remained to reduce the amount of force absorbed by the jaw's rotation (Figure 2). The subocular bone, levator and *malaris* muscle were removed from this section, as the *rictalis* muscle was our focus for this study. The cheek section was placed in amphibian Ringer's solution (Roberts lab) and maintained with oxygen flow via an air stone. The cheek section was anchored to a Plexiglas piece using zip ties so that the *rictalis* was oriented upright directly below the force transducer. The coronoid process was tied with Kevlar thread to a threaded rod, which attached to the force transducer. The system had an adjustable length bar, allowing for the muscle portion to be moved farther/closer to the force transducer, simulating artificial gape change. To measure muscle length change in the *rictalis* muscle, sonometric crystals (Sonometrics Corp., Ontario, Canada) were implanted along the same muscle fiber and positioned to face the neighboring crystal at a minimum of 2 mm apart. Crystals were sutured (Ethilon nylon, 18'', Ethicon Inc, Somerville, NJ, USA) in the muscle.

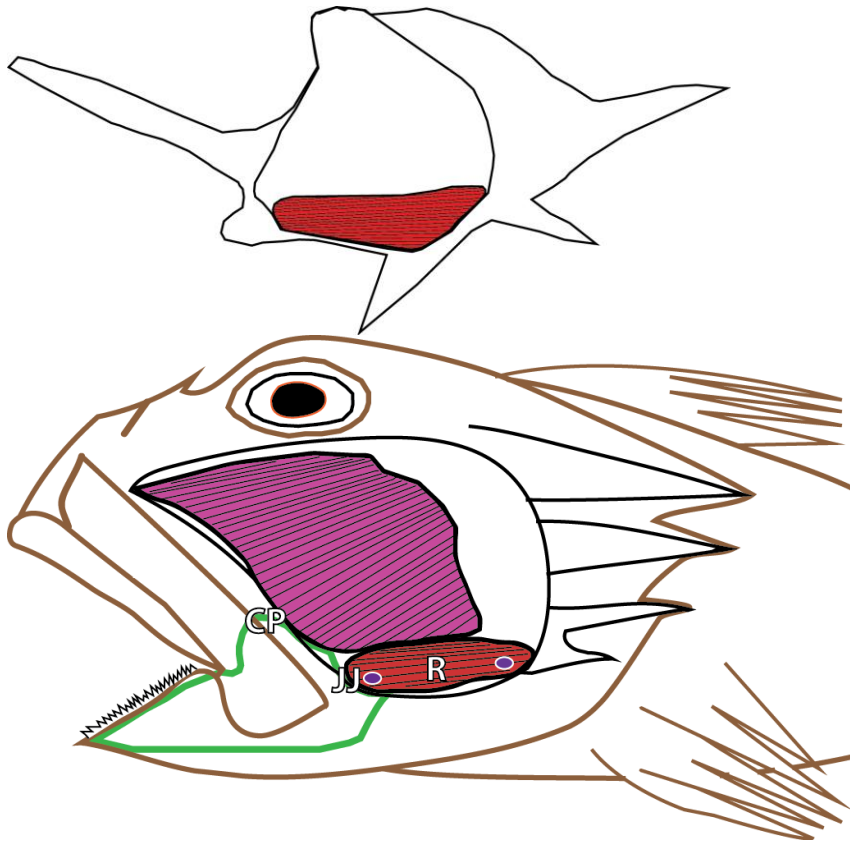


Figure 2. A) The piece removed from the fish: the rictalis in its original orientation on the quadrate bone with the coronoid process, preopercular spines and upper jaw bone attached. B) The placement of sonometric crystals in the rictalis muscle. CP = coronoid process, JJ = jaw joint, R = rictalis

Copper electrodes were positioned above and below the *rictalis* muscle. Using a stimulator (Grass Institute Co., Quincy, MA), the muscle was electrically stimulated, which contracted to pull down on the coronoid process, and peak force produced was recorded each time. Length was steadily increased until forces dropped, at which time length was shortened at twice the rate of increase. Muscle stimulations were given at 7-8 V, 300 pulses/second, 0.2 millisecond duration, for 300 milliseconds. Muscle stimulations occurred every 5 minutes to prevent premature muscle fatigue. Fatal muscle fatigue was defined as a sudden, rapid decline in force. Sonolab DS3 (Sonometrics Corp., Ontario, Canada) was used to collect data from the sonomicrometer crystals during muscle stimulations. Data were collected from the sonometric transducer at a 200.30 Hz sampling rate, transmit pulse = 406.25 ns, inhibit delay = 3.08 mm.

Using the corresponding data analysis software Sonoview (Sonometrics Corp, Ontario, Canada), the trace was measured for the *riktalis*. Out of the 9 initial specimens, 6 produced usable data. Data were collected and analyzed from 51 muscle stimulations. Any points deemed aberrant (deviating from the normal range of values) were removed from the data set. To allow for comparison between fish, data were normalized by dividing each force point by the peak force (P_0) and each length point by the length corresponding to P_0 . Length was normalized in the same manner. Collected force and sonometric data were analyzed with MatLab (MathWorks, Natick, Massachusetts, USA) and linear regressions. Force produced during muscle stimulations was graphed against muscle lengths recorded from sonomicrometry to create length-tension curves (Figure 3).

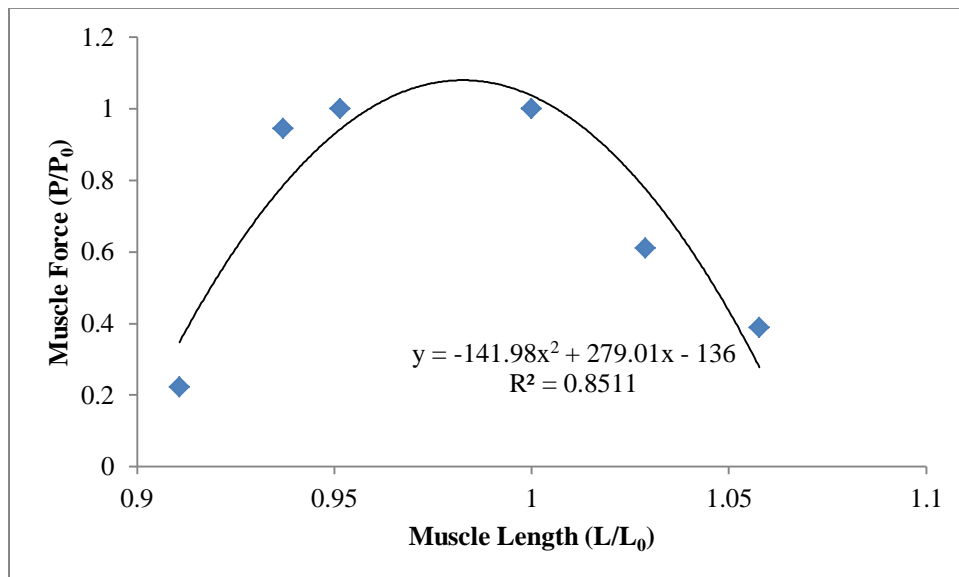


Figure 3. Example of length-tension curve from a muscle preparation of a single individual.

RESULTS

The length-tension curves showed an intrinsic property of muscle: muscles produced maximum force (P_0) at intermediate muscle lengths (L_0), and all lengths below or beyond L_0 resulted in declining forces. A second order polynomial trend line was fit to each set of data. From that

polynomial equation, x-intercepts at $y=0.5$ were calculated to see which muscle lengths produced 50% or more of P_0 . Wolframalpha.com was used to calculate the area under the 50% curve. Linear regressions were performed on data to test for a significant relationship between fish length and area under the 50% force curve, % muscle length at 50% of P_0 , and P_0 . There was a positive relationship between area under 50% force curve and P_0 (p-value for regression = 0.0035) (Figure 4). This suggests that a larger maximum force results in a wider distribution of muscle lengths that produce at least 50% of maximum force. Fish length vs. P_0 , length vs. % muscle length at 50% of P_0 , and fish length vs. area under 50% P_0 curve did not yield significant regressions.

Muscle strain to produce at least 50% of P_0 was calculated by subtracting the minimum 50% muscle length from the maximum 50% muscle length (example from Fish 2: $1.01414 - .95693 = .05721$). When comparing muscle strain above 50% P_0 to fish length, there was a non-significant positive correlation (p-value: 0.56) (Figure 5).

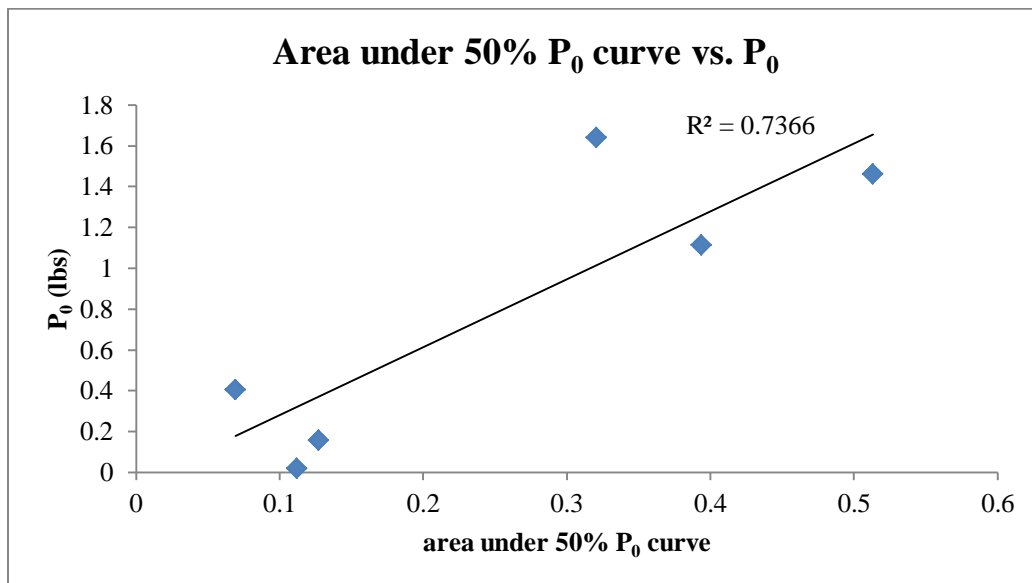


Figure 4. Maximum force (P_0) compared to area of the length-tension curves at 50% of P_0 . As P_0 increases, the area below 50% of P_0 also increases

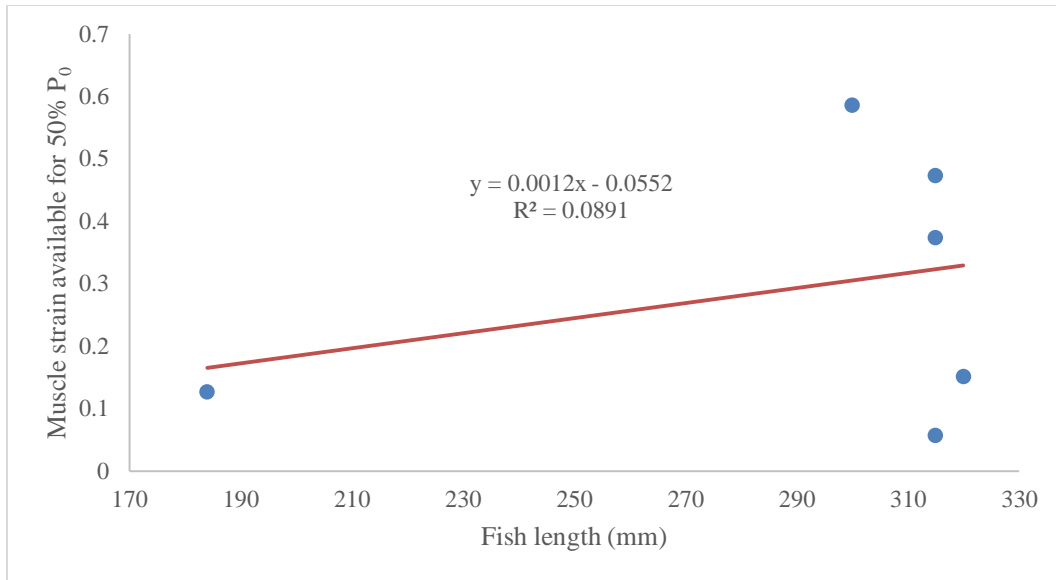


Figure 5. Muscle strain available to achieve at least 50% P₀ compared to fish length. Since no correlation was found, it can be said that available muscle strain to achieve at least 50% P₀ remains constant across sizes.

DISCUSSION

Since muscle strain did not significantly increase with increased fish length, this suggests that the percent muscle length change performed to still maintain at least 50% of peak force does not change with size. In a previous study (Conrades et al., 2014 in progress) rictalis muscle strain data collected from live fish during feeding showed a positive correlation (p-value: 0.005) with fish length (Figure 6), suggesting that larger fish are using more of this available muscle strain to achieve at least 50% P₀. With increased muscle stretching, a fish deviates more and more from

L_0 and thus experiences increased loss in forces.

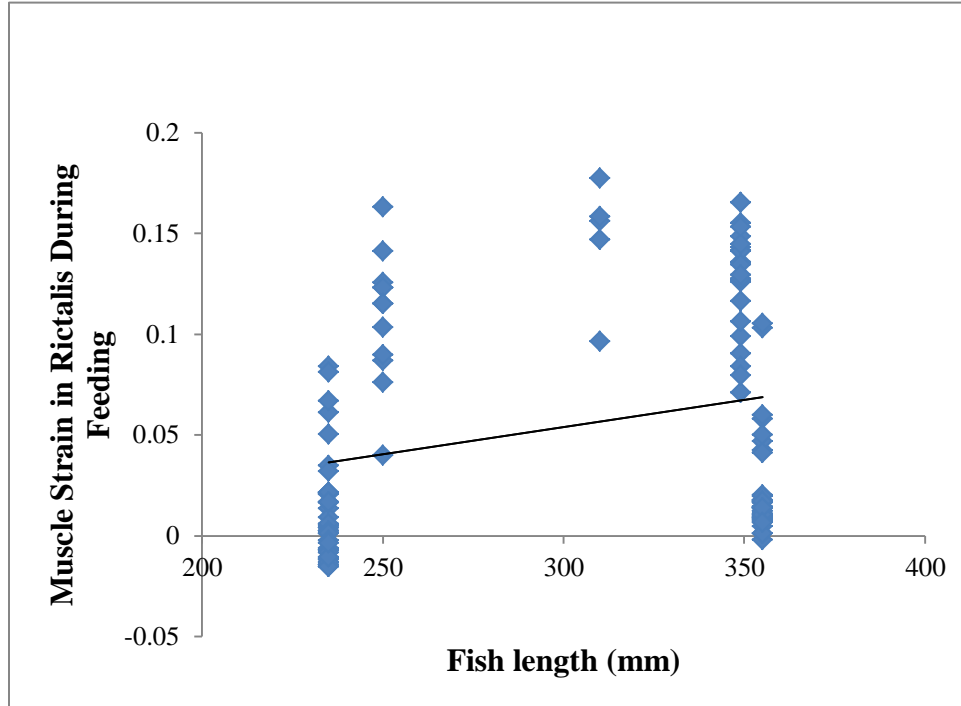


Figure 6. Muscle strain in the rictalis during feeding compared to fish length. With increased fish length, more muscle strain of the rictalis muscle is used in feeding.

CONCLUSION

The jaw closure muscle force data from this study demonstrates that in addition to an increased muscle force deficit as a fish increases in length, larger fish are using a wider range of the available muscle strain to reach at least 50% of maximum force. This causes larger fish to experience declining forces as a result of length-tension limitations. For great sculpin, being bigger isn't always better. This study is another example of the physical pressures limiting great sculpin throughout ontogeny and how those pressures are reflected in their musculoskeletal morphology.

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