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In vitro estimates of power output by epaxial muscle during feeding in largemouth bass

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Abstract

Recent work has employed video and sonometric analysis combined with hydrodynamic modeling to estimate power output by the feeding musculature of largemouth bass in feeding trials. The result was an estimate of ~69 W kg^{-1} of power by the epaxial muscle during maximal feeding strikes. The present study employed *in vitro* measurements of force, work and power output by fast-twitch epaxial muscle bundles stimulated under activation conditions measured *in vivo* to evaluate the power output results of the feeding experiments. Isolated muscle bundles from the epaxial muscle, the sternohyoideus and the lateral red or slow-twitch muscle were tied into a muscle mechanics apparatus, and contractile properties during tetanic contractions and maximum shortening velocity (V_{max}) were determined. For the epaxial muscles, work and power output during feeding events was determined by employing mean stimulation conditions derived from a select set of maximal feeding trials: 17% muscle shortening at 3.6 muscle lengths/s, with activation occurring 5 ms before the onset of shortening. Epaxial and sternohyoideus muscle displayed similar contractile properties, and both were considerably faster ($V_{max} \approx 11–13$ ML s^{-1}) than red muscle ($V_{max} \approx 5$ ML s^{-1}). Epaxial muscle stimulated under *in vivo* activation conditions generated ~60 W kg^{-1} with a 17% strain and ~86 W kg^{-1} with a 12% strain. These values are close to those estimated by hydrodynamic modeling. The short lag time (5 ms) between muscle activation and muscle shortening is apparently a limiting parameter during feeding strikes, with maximum power found at an offset of 15–20 ms. Further, feeding strikes employing a faster shortening velocity generated significantly higher power output. Power production during feeding strikes appears to be limited by the need for fast onset of movement and the hydrodynamic resistance to buccal expansion.

Keywords: Epaxial muscle; Muscle mechanics; Hydrodynamic modeling; Shortening velocity; Sternohyoideus; Suction feeding; Sunfish

1. Introduction

Suction feeding is one of the most ubiquitous behaviors among vertebrates and is common to most species of teleost fish, as well as many anamniotic vertebrates, marine mammals, and aquatic reptiles (Lauder, 1980; Ferry-Graham and Lauder, 2001). Therefore, understanding how muscles function during suction feeding may yield insights into the physiology, ecology, and evolution of numerous vertebrate lineages (i.e., Ferry-Graham et al., 2002; Westneat, 2004). While it has been relatively straightforward to measure muscle activation and strain during suction feeding with either sonomicrometry or X-ray ciné along with electromyography (Carroll, 2004; Van Wassenbergh et al., 2005), muscle force has been more difficult to estimate. In this study the force produced by isolated bundles of feeding muscle was measured during imposed activation and strain cycles similar to those observed during suction feeding, as has been used routinely in studies of fish swimming muscle function (e.g., Rome et al., 1993; Coughlin, 2000; Syme and Shadwick, 2002).

These force measurements enabled estimations of cycle muscle power which could be used to validate previous *in vivo* work on suction feeding muscle function. First, estimates of muscle power during realistic activation and strain regimes (derived from literature) were compared to that measured *in vivo* to validate those results. Second, activation and strain were

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varied to elicit maximal power from these bundles. These *optimal* conditions could be compared to those found *in vivo* to understand how the mechanical and behavioral demands of suction feeding may influence suction feeding performance.

During suction feeding in fish, a predator rapidly expands its cranial skeleton to create a flow of water into the mouth which captures the prey item. To capture elusive prey this flow, and the cranial kinematics creating it, must be rapid enough to prevent the prey from escaping entrainment. These rapid kinematics in a dense fluid medium impose loads on skeletal elements (Lauder, 1980; Lauder and Lanyon, 1980) and the muscles actuating their movement (Van Wassenbergh et al., 2005). This loading is predominantly due to high sub-ambient pressures (−5 to −25 kPa for *Micropterus salmoides*) inside the oral cavity and is distinct from more well-studied accelerative or drag-based loading (e.g., Roberts and Marsh, 2003; Reilley et al., 2005). Expansion during suction feeding is due to contraction of the dorsal epaxial musculature and ventral sternohyoideus and hypaxial musculature which rotate the neurocranium away from the buccal floor and (through more complex linkages) actuate jaw opening and lateral cranial expansion. Therefore, both sternohyoideus and epaxial fibers were used in this study.

Muscle power output during suction feeding has recently been estimated by Carroll and Wainwright (2006) using direct measurements of intra-oral pressure and muscle strain. These results were consistent with early hydrodynamic estimates (de Jong et al., 1987). The kinematic movement and fluid loading required for suction feeding has a profound effect on muscle performance. First, because loads are developed due to movement, the muscle is not prevented from shortening prior to full activation, potentially limiting peak stress. Second, to actuate large skeletal displacement, muscle fascicles shortened by>20% strain during high performance strikes, potentially resulting in muscle sarcomeres operating off of the peak of the sarcomere-length–tension plateau. Both of these suggestions differ from previous studies of muscle systems that functions for high instantaneous power production. For instance, during jumping frog muscle is maximally activated prior to shortening and operates at low enough strains such that force production is high throughout the jump (Lutz and Rome, 1996a,b). If the *optimal* conditions found in this study differ from those found *in vivo*, it would suggest that the mechanical and behavioral requirements of suction feeding, in fact, limit suction feeding power production and, thus, performance. This potentially represents an example of suboptimal *in vivo* muscle function due to behavioral constraints. The present study was undertaken to contribute a third estimate of power output by a feeding muscle and to examine constraints on muscle performance during suction feeding events in bass.

While the musculoskeletal system may not be able to overcome certain constraints to allow maximal power productions, given a certain load, the gearing of the skeletal system may be such that loads allow muscles to shorten at or near *optimal* contraction velocities (Rome et al., 1988). Based on shortening data in the sternohyoideus, Carroll (2004) suggested that largemouth bass were geared for maximal power production. However, absent *in vitro* data on the specific relationship between power production and strain rate in this animal these statements remain conjectural. This study was undertaken with three goals: (1) to compare levels of power measured in this study under realistic strain regimes with those measured *in vivo*, (2) to compare optimal *in vitro* strain rates for power production with those measured *in vivo* two other studies (e.g., Carroll and Wainwright, 2006), and (3) to compare levels of power under *optimal* conditions with that measured *in vivo*. Prior to experiments measuring power production by epaxial muscle under *in vivo* muscle activity conditions, the contractile properties of epaxial muscle were measured. In addition, the contractile properties of the sternohyoideus muscle, another presumably fast-twitch feeding muscle, and myotomal, slow-twitch red muscle were characterized for comparison.

2. Materials and methods

2.1. Animals

Largemouth bass (*M. salmoides*) were obtained from Kurtz Fish Farm, Chester County, PA. The fish were maintained in a re-circulating aquaria at 25 °C and fed live fish. Data are reported here for nine fish (Mean±S.D.: mass, 420±135 g; TL, 29.9±5.0 cm ; SL 26.8±4.6 cm). All handling of experimental animals was reviewed by the Widener University Institutional Animal Care and Use Committee in accordance with the Guide for the Care and Use of Laboratory Animals of the National Research Council.

2.2. Physiology experiments

Epaxial, sternohyoideus and red axial muscle bundles were used to examine contractile properties. To perform mechanics experiments, the fish were killed by spinal transection and pithing. For all three muscle types, the scales were removed and strips of muscles (~1.0 mm wide) were extracted. Red muscle was extracted from the lateral myotome just above and below the lateral line at a position of 0.60 TL from the snout. Epaxial muscle was extracted from a mid-dorsal position within 2 cm of the caudal margin of the neurocranium. Sternohyoideus muscle was extracted from a mid-ventral position just in front of the pelvic girdle. Subsequent dissection was carried out in physiological saline at 4 °C with the use of stereomicroscope (Coughlin et al., 2005). Live muscle bundles were the length of one myomere (~7–9 mm in epaxial muscle bundles, ~6–7 mm for sternohyoideus bundles and ~4–5 mm red muscle) with a live muscle fibre cross-sectional area of 0.25–1.0 mm^2. Using a muscle mechanics system comprised of a servomotor (Cambridge Technology 300S) and a force transducer (Cambridge Technology 404A), the muscle bundles were tied into the system and maintained at a temperature of 25 °C for all experiments. The physiological saline was aerated gently to supply oxygen and to induce circulation. Experimental control (i.e., stimulation patterns and length change ramps) and data collection (force level and muscle length) were carried out using a National Instruments A/D board and custom LabView software routines.