Scaling of In Vivo Muscle Velocity during Feeding in the Largemouth Bass, *Micropterus salmoides* (Centrarchidae)

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Accepted 8/17/2011; Electronically Published 10/3/2011

ABSTRACT

Many vertebrates undergo large increases in body size over the course of a lifetime, and these increases are often accompanied by changes in morphological and physiological parameters. For instance, in most animals, increases in size with growth are accompanied by decreases in the maximum speed of shortening (V_{max}) in locomotor muscles. Curiously, in muscles involved in suction feeding, V_{max} shows no decreases with size in vitro, despite the fact that timing of kinematic events involved in suction feeding (e.g., time to peak gape) slow with increased size. The goal of this study was to examine whether muscular speed in vivo varies with size during suction feeding in the largemouth bass (*Micropterus salmoides*). The dorsal epaxial musculature of 10 individual bass (varying from 123 to 685 g and from 18.1 to 32.0 cm standard length [SL]) was implanted with sonometric crystals to measure muscle length during feeding on elusive prey (large goldfish). No relationship was found between the mean individual or maximum speed of shortening with mean individual log-transformed SL. However, mean magnitude of shortening and maximum shortening magnitude showed nonsignificant increases with SL ($P = 0.08$ and 0.06, respectively). Average duration of shortening was found to increase with log-transformed SL. The size invariance of observed shortening velocity in the epaxial muscles during feeding may stem from size invariance of imposed loads during suction feeding. This is in contrast to what is normally seen in locomotor systems where loads on muscles often increase with body size.

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Physiological and Biochemical Zoology 84(6):618–624. 2011. 1522-2152/2011/8406-0107$15.00. DOI: 10.1086/662382

Introduction

Body size has been found to influence numerous aspects of animal morphology, physiology, and movement (e.g., Haldane 1926; McMahon 1973; Heglund et al. 1974). Increases in body size may change the physical demands imposed on animals and require compensatory changes in morphological or physiological parameters (Schmidt-Nielsen 1975; Dobson and Headrick 1995; Alexander 2005). For instance, because body mass increases faster with size than the cross-sectional area of bones and muscles, larger mammals have been found to have allometrically increased bone cross-sectional area and more upright posture than smaller mammals to reduce bone stress, bone-bending moments, and joint moments (Biewener 1989; Bertram and Biewener 1990). Physiological responses to increased body size are often more difficult to explain because the relationship between the physical requirements imposed by larger size may not affect physiological parameters as directly as they do morphological parameters (McMahon 1973). In fact, the underlying cause or causes for the ubiquitous body size–related reduction in metabolic rate have been the subject of intense controversy in the literature (Kleiber 1961; Dobson and Headrick 1995; West et al. 1999; Packard and Boardman 2009).

One physiological parameter that appears to vary with size is the maximum unloaded shortening velocity (V_{max}) of muscles. In comparisons of large and small species, it has been found that the musculature of smaller species contracts at faster speeds than that of larger species (Seow and Ford 1991; Rome 1992) and that the muscle of smaller individuals of the same species contracts faster than that of larger individuals (Altringham and Johnston 1990; Marsh 1994; James et al. 1998). A broad multispecies comparison of locomotor muscle found that V_{max} scales to the -0.12 of body mass when temperature effects are removed for swimmers and fliers (Medler 2002) but interestingly did not find an interspecific difference in V_{max} among swimmers. Slowing of intrinsic V_{max} with growth within species results from changes in the expression of myosin isoforms (James et al. 1998) and appears to result in slower movement in large animals than in smaller animals (Hill 1950; Lindstedt et al. 1985). For example, muscle strain rates during C-bends in the short-horn sculpin (*Myoxocephalus scorpius*) slow with standard length (SL), though contralateral contraction rates decrease (James and Johnston 1998).

Previous studies have largely focused on locomotor muscles but have not determined whether reported decreases in V_{max} (and resultant slowing of kinematics) were a direct consequence of changes in the physical demands of moving larger body mass

or segment masses (Hill 1950) or an indirect consequence of limitations imposed by size-related reductions in mass-specific metabolism (e.g., Dobson and Headrick 1995). To address this issue, Carroll et al. (2009) investigated the scaling of suction-feeding musculature in largemouth bass (*Micropterus salmoides*) and bluegill sunfish (*Lepomis macrochirus*) and found that unlike myotomal locomotor musculature from the same fish, the V_{max} of dorsal epaxial feeding musculature did not slow with size. These data raise the possibility that scaling in some locomotor muscles might be directly related to increases in locomotor muscle loading due to increased body size (Hill 1950) and not a general effect of growing larger.

In locomotor movements, the relative muscle loading required to accelerate body and segment mass increases by definition with overall increases in size leading to slowing of in vivo muscle strain rates (Hill 1950). In contrast, loads imposed by suction feeding do not seem to depend on body size. Subambient pressures in the mouth (buccal) cavity appear to be the major source of loading during suction feeding (Van Wassenbergh et al. 2005) and do not vary with size in isometrically growing animals (Wainwright et al. 2006), such as largemouth bass (Carroll et al. 2004). The forces required during suction feeding do not change with size in isometric animals; no slowing of in vitro V_{max} has been observed (Carroll et al. 2009). Therefore, it is not obvious that in vivo strain rates would decrease with size. It should be noted that Van Wassenberg et al. (2007) found that catfish hypaxial muscles (responsible for feeding in that fish) slowed with size but only in fish greater than 60 mm; the trend was not significant over the full size range studied.

Studies of feeding kinematics—including those of largemouth bass (Richard and Wainwright 1995), other sunfishes (Centrarchidae; Wainwright and Shaw 1999), and clariid catfishes (Van Wassenbergh et al. 2005)—have found that both the velocity of movement during feeding and the duration of movements slow with increasing body size. Thus, the kinematic data do not appear to agree with the in vitro data for suction-feeding musculature (at least in largemouth bass): size shows no effect on V_{max} in feeding muscles (Carroll et al. 2009), but linear movement scales with negative allometry (Richard and Wainwright 1995). Two explanations for this discrepancy are possible: either the relationship between muscle shortening and kinematic movement changes as animals grow, so that muscle strain rates remain constant but kinematic movement slows, or the muscles of larger bass are contracting at lower relative strain rates or velocities as a proportion of maximum V/V_{max}.

The former explanation seems unlikely because largemouth bass have been found to grow isometrically with respect to the relative size and shape of feeding structures (Richard and Wainwright 1995; Carroll et al. 2004). However, the complex arrangement of the muscle fascicles that power suction feeding (see Thys 1997; Gemballa and Roder 2004) makes it difficult to rule out this explanation. The latter explanation—that relative strain rates slow with size—is also problematic. First, slowing of relative strain rates would require increases in muscle loading, but estimates of muscle stress for largemouth bass do not seem to increase with size. For instance, Carroll et al. (2004) found that estimated muscle stress during feeding does not vary across a size range of largemouth bass. Second, optimal strain rates for power production (V_{opt}) do not vary with size (Carroll et al. 2009), so reduced strain rates would reduce mass-specific power production and the amount of power available to speed water into the buccal cavity and capture prey (Carroll and Wainwright 2009).

This study sought to differentiate between these two possible explanations by measuring feeding muscle (epaxial) strain rates in vivo during suction feeding in a size range of largemouth bass. The epaxial musculature appears to contribute the majority of work and power to suction feeding of largemouth bass (Carroll and Wainwright 2006); also, their V_{max} is known to be size invariant (Carroll et al. 2009). We hypothesized that in vivo muscle strain rates would slow with increasing SL at the same rate as kinematic velocities of jaw opening (Richard and Wainwright 1995). This hypothesis would be rejected if in vivo muscle shortening velocities, such as V_{max}, do not scale with length (Carroll et al. 2009).

Material and Methods

Animals

Ten largemouth bass, *Micropterus salmoides* (Lacepede), ranging from 181 to 320 mm SL were collected in Putah Creek, Yolo County, California. Before experimentation, fish were housed in 100-L aquariums at 22°–24°C for a period of at least 2 wk at the University of California, Davis, in accordance with University of California, Davis, animal use and care protocols (10211). Fish were maintained on live goldfish (*Carassius auratus*), earthworms (*Lumbricus* sp.), and cut squid (*Loligo* sp.) before surgery, with feeding discontinued 3 d before experimentation. Experiments were conducted in the fish's home tank. Muscle strain data from four individuals were also reported in a previous study (Carroll and Wainwright 2006). At least three and as many as 10 trials were recorded for each individual. All feedings were deemed at the time to involve maximal effort on the basis of a subjective evaluation of the motivation level displayed by the feeding fish or were not analyzed. Fish were weighed to the nearest gram, and SL was measured to the nearest millimeter.

Surgery

Before surgery, fish were anesthetized in 0.3 g L^{-1} of tricaine methane sulfate (MS-222). Surgery lasted 20–45 min. After SL and mass measurements, fish were returned to their home tanks and artificially ventilated with a flow-head pump until recovery. During each feeding, fish were given live goldfish (2–5 cm SL) in an effort to elicit maximal feeding performance. Data were collected within 6–48 h of surgery in sessions that concluded when fish demonstrated reduced effort and began again after sufficient time for satiety to abate. At the conclusion of the experiments, fish were euthanized via overexposure to MS-222.

Table 1: Scaling exponents and intercepts (+SEM) for the parameters measured in this study when regressed on log standard length

	Slope	SEM	Intercept	SEM	r^2	P	Power
Mean strain rate (FL s^{-1})	−.01	.71	.31	.99	.00	.98	.056
Minimum strain rate (FL s^{-1})	.34	.76	−.03	1.07	.02	.66	.066
Mean strain $((l - l_0)/l_0)$	1.30	.66	−2.97	.92	.33	.08	.52
Minimum strain $((l - l_0)/l_0)$	1.68	.78	−3.32	1.09	.37	.06	.57
Mean shortening duration (s)	1.19	.41	−3.08	.57	.51	.02*	.81
Minimum shortening duration (s)	.67	.55	−2.55	.77	.15	.26	.22

Note. FL, fascicle length; l, length; l_0, resting length.
*$P < 0.05$.

Epaxial Muscle Strain

To measure epaxial muscle strain, 1-mm sonometric crystals (Sonometrics, London, Ontario) were used. Sonometric crystals use sound to measure distances within the muscle tissue or any other dense medium (Hoffer et al. 1989). The speed of sound in muscle tissue has been estimated at 1,560 m s^{-1} (Mol and Breddels 1982). To assure consistency in crystal location, the crest of the neurocranium was palpated beneath the middorsal skin of the fish, the first crystal was placed approximately 1–2 cm lateral to this crest depending on the size of the fish, and the second was placed 6–15 mm caudo-lateral to the first, along fascicle lines but in different myomeres. A more detailed description of crystal placement is given by Carroll and Wainwright (2006). To insert crystals, a 2-mm incision was made through the skin to expose underlying fascicles. Fascicles were gently separated with the tip of the blunt probe, and the crystal was inserted between them to a depth of approximately 4 mm (the length of the probe tip). Extra crystal wire was forced into the incision to ensure that the crystal could move freely as the muscle shortened. The incision was closed around the crystal wire with 5-0 silk suture. Crystal movement was confirmed at the end of surgery and was interpreted as epaxial muscle strain. Crystal position was confirmed during equipment removal except in rare cases where the crystals were pulled out before fish euthanasia.

Electromyography

Electromyography (EMG) was not essential to the goals of this study but was useful in identifying periods of activity in the muscle. Fascicle depolarization was measured with bipolar electrodes fashioned from pieces of 0.002-inch (0.051 mm) bifilar wire (California FineWire, Grover Beach, CA) loaded into a 26-gauge hypodermic needle (Loeb and Gans 1986). The tips of the wires were stripped, spread orthogonally, and bent into a hook against the shaft of the needle. The distance between stripped ends ranged from 3 to 1.5 mm. The needle was inserted into the skin 5 mm dorsal or ventral to the crystals and at the depth of the crystals.

Data Recording

Analog crystal voltages were transduced into distance measurements with a TRX-8 conversion box (Sonometrics). Pressure and EMG signals were digitized and recorded on a PC running SonoView software (Sonometrics). All data were sampled at between 550 and 1,000 Hz. In general, the highest sampling rate that permitted crystal signal quality was used. EMG signals were conditioned with a four-channel differential amplifier (A-M Systems, Everett, WA) using a gain of 10,000 and a filter bandwidth of 3,000–100 Hz. A 60-Hz notch filter was used in all recordings. Amplifier output was digitized as an analog input to the same PC and software used to record crystal signals.

Data Analysis

Raw sonometric data were converted to ASCII text files for analysis. Epaxial muscle strain and strain rate were measured with a custom MatLab (Mathworks, Boston) script. Strain was measured over the period of shortening and normalized by resting length. Strain was measured as length (l) minus resting length (l_0) divided by resting length, or $(l - l_0)/l_0$, and has units of fascicle length. Resting length was taken as the length of the muscle before muscle activity began. Strain rate was measured as strain in fascicle lengths divided by the duration of shortening. Strain rate during shortening was not constant, so the parameter reported here represents an average speed over the shortening period. These three parameters—strain, strain rate, and measurement duration—were log transformed and regressed against log-transformed SL (Table 1) but were also presented and analyzed as raw values for ease of interpretation (Figs. 1–3).

Results

The overall strain profile or the relationship between strain and muscle activity did not vary superficially among individuals. However, strain rate, strain magnitude, and timing were highly variable between individuals and preparations (Figs. 1–3).

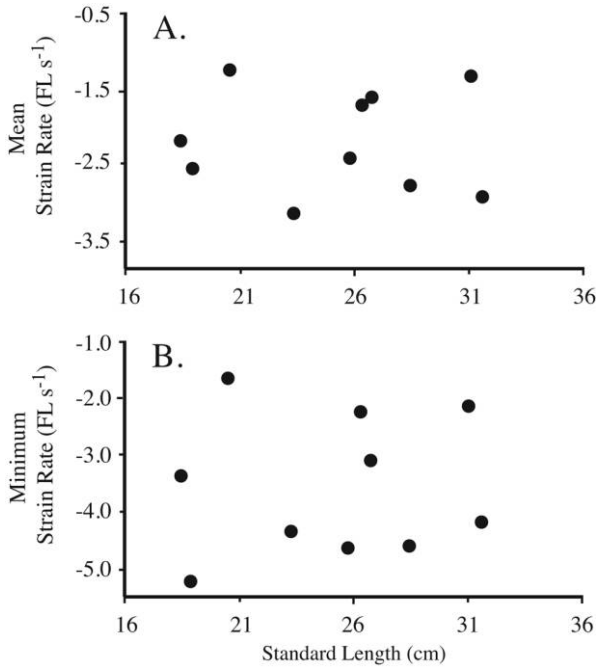

Figure 1. Relationship between raw standard length and mean individual strain rate in fascicle lengths per second (FL s^{-1}; *A*) and the minimum or fastest strain rate (*B*). Circles represent individual fish. No trend with size was observed in the range of individuals measured in this study. The relationships for log-transformed data are given in Table 1.

Strain Rate

Strain rate among individuals averaged −2.1 ± 0.23 (mean of individual means ± SEM) fascicle lengths (FLs) per second (FL s^{-1}). Note that negative strain indicates that the muscle fascicles are shortening. The average minimum individual strain rate was −3.0 ± 0.38. There was no relationship between average or minimum (fastest) individual strain rate and SL in either raw (Fig. 1) or log-transformed (Table 1) variables or between strain rate and raw or transformed body mass.

Strain

The average total strain per feeding varied from less than −4% to more than −15% among individuals (Fig. 2*A*), averaging −10% ± 2%. The greatest change in length per feeding also varied among individuals from −6% to −24% (Fig. 2*B*) and averaged −11% ± 2%. The relationship between average strain magnitude and SL was nonsignificant for both raw (Fig. 2*A*) and log-transformed (Table 1) variables. The relationship between minimum individual strain and SL was found to be significant for raw variables ($P = 0.05$); however, for the log-transformed variables, the relationship was marginally not significant ($P = 0.06$). Nevertheless, both average and minimum strain were found to be significantly correlated ($P < 0.05$) when regressed against body mass in either raw or log-transformed form.

Shortening Duration

The duration of shortening for individuals ranged from 24 to 62 ms. Mean shortening duration was significantly correlated with SL for both raw (Fig. 3*A*) and log-transformed (Table 1) variables, but minimum shortening durations did not show a significant trend with raw size (Fig. 3*B*) or log-transformed (Table 1) variables, although the negative tests should be viewed cautiously because power values for most tests were below the 0.8 standard (Table 1). Mean shortening duration was significantly correlated with body mass in both raw and transformed form, but minimum shortening duration again was not significantly correlated with body size.

Discussion

The hypothesis of slowing shortening strain rate with increased size was predicted from the observed slowing of jaw and head-rotation velocity to the 0.76 power of length (Richard and Wainwright 1995) but was not observed. Rather, both mean and minimum (fastest) individual strain rate did not scale with body size over the range of sizes investigated. This result is consistent with the size independence of V_{max} previously observed in epaxial muscle of *Micropterus salmoides* (Carroll et

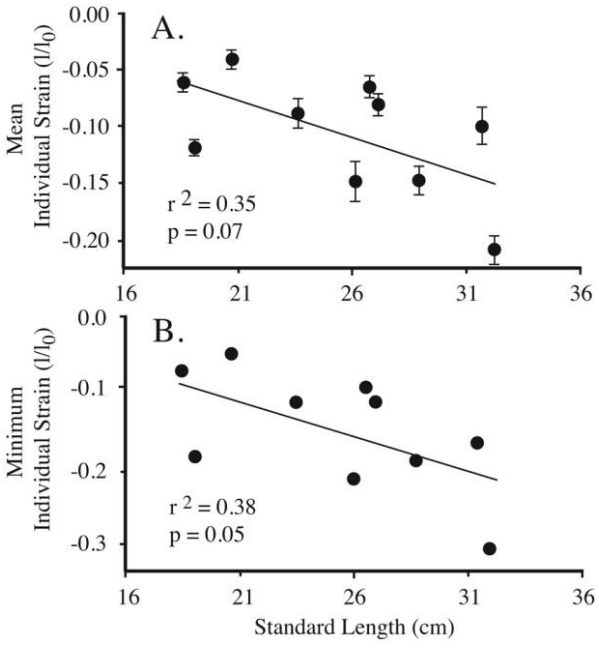

Figure 2. Relationship between raw standard length (SL) and mean individual shortening strain measured in fascicle lengths (length minus resting length over resting length: $(l - l_0)/l_0$; *A*) and the minimum shortening strain magnitude observed for each individual (*B*). Circles represent individual fish. Error bars in *A* show SEM for each individual. There was a weak ($r^2 = 0.35$) but insignificant ($P = 0.07$) trend between SL and mean strain magnitude. There was a significant increase in minimum strain magnitude with size ($P = 0.05$), with larger fish producing greater strain magnitudes. The scaling of log-transformed variables is given in Table 1. Interestingly, significant relationships ($P < 0.05$) were found between body mass and both variables.

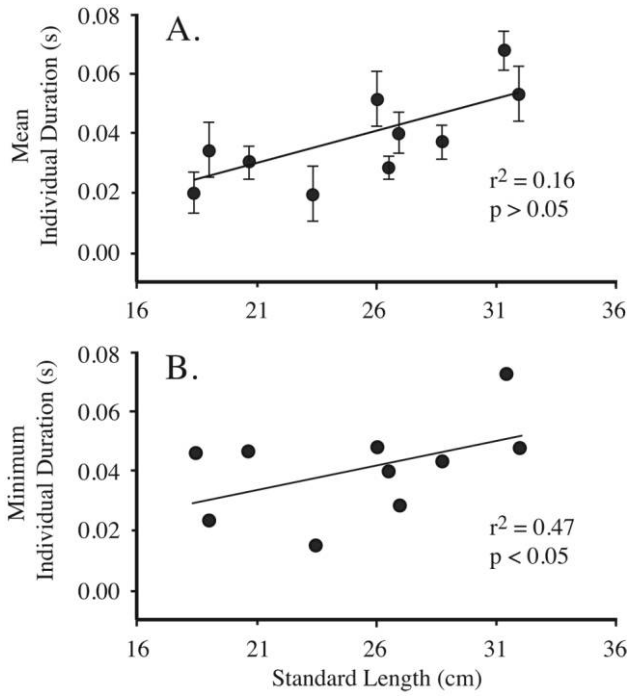

Figure 3. Relationship between raw standard length and the mean individual duration over which shortening was measured (*A*) and minimum shortening duration (*B*), both in seconds. Circles represent individual fish. Error bars in *A* show SEM for each individual. Larger fish showed longer average durations of shortening (*A*; $r^2 = 0.47$, $P < 0.05$) in a pattern consistent with longer durations of mean kinematic movements observed in other studies (e.g., Richard and Wainwright 1995). Interestingly, minimum individual shortening duration was not significant. Log-transformed relationships are given in Table 1.

al. 2009). Mean and minimum strain magnitude showed a shallow but significant increase with size (Fig. 2), as did the mean duration of shortening (Fig. 3*A*), though not minimum duration of shortening (Fig. 3*B*).

Size Invariance of Strain Rate

Neither the in vivo strain rates recorded in the anterior epaxial muscle mass during suction feeding in this study (Fig. 1; Table 1) nor the maximum unloaded strain rate reported by Carroll et al. (2009) scaled with size in largemouth bass. This result is surprising in light of the fact that suction-feeding kinematics have been shown to slow with size in this species (Richard and Wainwright 1995) and that V_{max} of fish locomotor muscle slows with size in this species (Carroll et al. 2009), in the cod *Gadus morhua* (Altringham and Johnston 1990), and in sculpin (James et al. 1998). Moreover, interspecifc comparisons of in vitro muscle function in locomotor muscle have shown reductions in V_{max} with size (Rome 1992), though not in swimming musculature (Medler 2002). Finally, in vivo strain rates during locomotor movements have also been shown to slow with size in both intraspecific (James and Johnston 1998) and interspecific comparisons (Lindstedt et al. 1985; Tobalske and Dial 2000). Thus, suction-feeding muscle appears to differ from locomotor muscle in the relationship between strain rate and body size.

It may be possible that suction-feeding muscle physiological properties and observed strain rates do not scale with size because the mechanical demands of suction feeding do not scale with size in the way that those placed on locomotor muscles do. Locomotor muscle must deal directly with the increases in inertia of body segments and the body as a whole (Hill 1950, on which the following analysis is based). According to Newton's second law, these increases in mass of body segments must require a greater force for a given acceleration. In an isometrically growing animal, however, muscle force cannot increase to meet these demands because muscle cross-sectional area scales to the second power of length while segment or body mass scales to the third power. Animals appear to deal with this constraint in part by reducing the V_{max} of muscles (Altringham and Johnston 1990; Seow and Ford 1991; Rome 1992), resulting in reduced speed of movement (Lindstedt et al. 1985) and associated dynamic loading and preserving optimal levels of stress for work and power production.

Suction feeding presents quite a different loading environment from locomotor movement. In suction feeding, the predominant loads are the result of subambient buccal pressures resulting from rapid expansion of the cranium and not the result of segment inertia (Van Wassenbergh et al. 2005). The magnitude of these forces depends on the relative size of the mouth, the relative force production capacity of muscle (i.e., cross-sectional area), and the lever system through which muscle loads are transferred to the mouth (Carroll et al. 2004). Thus, in animals that grow isometrically with respect to these parameters, such as snook (*Centropomus undecimalis*; Wainwright et al. 2006) or largemouth bass (Carroll et al. 2004), loading during suction feeding should be largely independent of changes in size.

In the isometric largemouth bass, the loading environment experienced by feeding muscles does not appear to increase with size, and it follows that the size-related changes in unloaded muscle or in vivo (i.e., while being loaded by hydrodynamic pressure) shortening velocity should not vary with size as well. Additionally, reductions in intrinsic V_{max} would reduce the mass-specific power of suction-feeding muscle by reducing the rate at which energy is liberated from ATP. Reductions in shortening strain rate without changes in V_{max}, on the other hand, would shift the muscle away from its optimal shortening velocity for power production (V_{opt}), which is also size invariant for largemouth bass (Carroll et al. 2009), also reducing mass-specific power production (Hill 1938). Either shift would reduce suction-feeding performance and perhaps prey capture success by reducing the change in buccal volume or magnitude of subambient buccal pressure produced during feeding (for a more detailed analysis, see Carroll and Wainwright 1999), and it would therefore be maladaptive. Van Wassenberg et al. (2007) found that V_{max} (as estimated from optimal cycle frequency) decreased in clariid catfish greater than 60 mm;

however, peak muscle stress increased so that muscle power production actually increased with size. The link between skeletal loading and muscle loading may vary with size in this species. It does not in largemouth bass (Carroll et al. 2004).

The differing mechanical demands imposed on locomotor and feeding musculature appear to result in different in vitro and in vivo scaling behavior in the two types of muscle. In the former, reductions in V_{max} and perhaps in vivo shortening velocity help to reduce increases in muscle loading. In the latter, increases in muscle loading are not necessarily associated with increases in size, so no reduction in shortening velocity may be required, at least in this species.

Strain Magnitude and Shortening Duration

The above analysis does not help to explain the fact that jaw and head rotation speeds do slow down with increasing size in largemouth bass (Richard and Wainwright 1995) and in other species (Wainwright and Shaw 1999; Van Wassenbergh et al. 2005). In this study, duration of shortening does appear, on average, to increase with size (Fig. 3*A*; Table 1), and this fact is partly explained by increases in shortening strain with size for a given strain rate (Fig. 2; Table 1). Larger bass appear to increase the magnitude of epaxial muscle strain with size, requiring the longer durations of kinematic movement (e.g., time to peak gape), which increase to the 0.3 power of SL (Richard and Wainwright 1995). Increases in strain with size have also been reported in interspecific comparisons between species of different size (Tobalske and Dial 2000) and within species of variable size. In fact, a remarkably similar range of strain magnitudes (−2% to −15%) was reported for axial myotomal muscle of a similar size series (~17 to ~32 cm) of sculpin during C-starts (James and Johnston 1998). Variations in strain magnitude with size pose an interesting problem: if sarcomere length is conserved in vertebrates among species and throughout growth (Lieber 1992), then the strain range at which peak force is possible is limited by a limited range of optimal cross-bridge overlap (Burkholder and Lieber 2001). Thus, increases in strain magnitude may necessitate reduced cross-bridge overlap thin-fiber interactions that may compromise force production as animals reach larger sizes.

Increases in strain magnitude, however, cannot explain the decreases in linear velocities during cranial expansion (i.e., linear speed of cranial elevation), which scale to the 0.76 of SL in largemouth bass (Richard and Wainwright 1995). It is possible that subtle changes in the relationship between epaxial muscle strain and skeletal kinematics might result from equally subtle changes in myotome arrangement as largemouth bass grow. This possibility must be explored through detailed analyses of how the complex myomeric and myotomal arrangement of fish muscle fascicles transfers force and strain to skeletal elements (e.g., Westneat et al. 1998; Van Leeuwen 1999; Gemballa and Roder 2004). The data from this study appear to have eliminated reductions in strain rate as an explanation for reductions in linear velocity with size but cannot fully explain these phenomena.

Acknowledgments

We thank Lisa Carroll and two anonymous reviewers for their invaluable contributions to this article. Some equipment used in this study was purchased with funds from the Jastro-Shields Graduate Research Grant and a University of California Graduate Research Award. Other funding was provided by National Science Foundation grants IBN-007636, IOB-0444554, and IOS-0924489.

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