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SCALING THE FEEDING MECHANISM OF THE LARGEMOUTH BASS (*MICROPTERUS SALMOIDES*): MOTOR PATTERN

PETER C. WAINWRIGHT AND BARTON A. RICHARD
Department of Biological Science, Florida State University, Tallahassee, FL 32306-3050, USA

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Summary

We present the first analysis of scaling effects on the motor pattern of a feeding vertebrate. Data are presented for the effects of body size on the pattern of activity in four head muscles during prey capture in the largemouth bass, *Micropterus salmoides*. Electromyographic (EMG) recordings were made from three expansive-phase muscles (the epaxialis, the sternohyoideus and the levator arcus palatini) and one compressive-phase muscle (the adductor mandibulae), during the capture of small fish prey. Recordings were made of 181 prey-capture events from 19 bass that ranged in size from 83 to 289 mm standard length. We measured seven variables from the myogram of each capture to quantify the temporal pattern of muscle activation, including the duration of activity in each muscle and the onset time of each muscle, relative to the onset of the sternohyoideus muscle. Regressions of the mean value of each variable for the 19 individuals on standard length revealed that only the onset time of the adductor mandibulae changed with fish body size. The increase in onset time of the adductor muscle appears to reflect the longer time taken to open the mouth fully in larger fish. Other research shows that the kinematics of the strike in this species slows significantly with increasing body size. The combined results indicate that the duration of the EMG signal is not directly correlated with the duration of force production in muscles when compared between fish of different sizes. The lack of scaling of burst duration variables suggests that the reduced speeds of prey-capture motion are explained not by changes in the envelope of muscle activity, but rather by the effects of scale on muscle contractile kinetics. These scaling effects may include changes in the relative resistance of the jaw and head structures to movement through water and changes in the intrinsic contractile properties of the muscles of the feeding apparatus.

Key words: allometry, feeding, largemouth bass, *Micropterus salmoides*, motor pattern, muscle.

Introduction

Body size affects a broad range of physiological and behavioral parameters in vertebrates (Calder, 1984; Schmidt-Nielsen, 1984), producing well-documented influences on several levels of design of the locomotor system, from whole-animal performance (Huey and Hertz, 1984; Garland, 1985) to skeletal design (McMahon, 1975, 1984; Alexander *et al*. 1979), muscle mechanics (Marsh, 1988; Altringham and Johnston, 1990) and biochemistry (Witthames and Walker, 1982; Garland, 1984). Indeed, empirical results on the scaling of locomotor performance hold a pivotal position in theoretical arguments that predict patterns of scaling in basic muscle contractile properties (Hill, 1950). However, in contrast to the central role that the vertebrate locomotor system has played in our understanding of basic physiological and biomechanical allometry of vertebrate striated muscle, little is known about the scaling of other musculoskeletal systems. Data from other systems would provide insights into the generality of paradigms derived from locomotion studies and might suggest alternative interpretations of some patterns.

In the present paper we present an analysis of scaling in the feeding mechanism of an aquatic-feeding lower vertebrate, the largemouth bass *Micropterus salmoides*. We ask whether the pattern of cranial muscle activation observed during prey capture changes with increasing body size. Elsewhere, we report on the scaling of kinematic patterns during prey capture in this species (Richard and Wainwright, 1995). Although numerous studies have addressed the scaling of feeding performance and trophic ecology of fishes (Werner, 1977; Keast, 1985; Wainwright, 1991), the physiological basis of feeding systems has not received the attention in the scaling literature that has been paid to locomotor systems (McMahon, 1975; Alexander *et al*. 1979; Marsh, 1988; Bennett *et al*. 1989; Altringham and Johnston, 1990). Our studies represent the first investigations on the scaling of prey-capture kinematics and motor patterns in lower vertebrates.

The results of our previous study of prey-capture kinematics (Richard and Wainwright, 1995) provide a context for the current analysis of scaling in muscle activation patterns in *M.*

salmoides. The salient results of the kinematic analysis were (1) that all movements of the jaws and head (including mouth opening and closing) were slower in larger fish and (2) that the morphology of the jaw muscles and the lever systems in the jaw-opening and jaw-closing mechanisms scaled isometrically. The constancy of jaw shape with slowing rates of motion led us to pose two central questions in the present analysis of the scaling of muscle activity patterns. First, given that the times to open and close the mouth increase with fish size, we ask whether there are features of the muscle activity bursts that reflect overall slower muscle contraction, such as longer bursts of muscle activity. Second, is the increase with body size in the time from the onset of mouth opening to the onset of mouth closing (time to peak mouth gape) reflected in an increase in the time between the onsets of the mouth-opening and mouth-closing muscles?

Materials and methods

Research specimens

The largemouth bass, *Micropterus salmoides* (Lacepède), is the largest member of the North American freshwater fish family Centrarchidae, reaching lengths of over 600 mm. The specimens used in this study were collected from Lake Jackson, Leon County, Florida, USA. Fish were transported from the field immediately after capture, housed separately in 30 or 100 l laboratory aquaria at room temperature (21±2 °C), and fed a mixture of golden shiners (*Notemigonus chrysoleucas*) and sailfin mollies (*Poecilia latipinna*). Nineteen individuals were studied, ranging from 83 to 289 mm standard length. This size range was chosen for two reasons. First, fish in this size range have similar feeding habits in natural populations. Largemouth bass less than 70 mm long feed mostly on invertebrate prey, but fish longer than 70 mm eat other fishes (Keast, 1985). Second, in our 100 l aquaria, fish longer than 300 mm appeared constrained and were not able to move easily and freely in pursuit of prey.

Electromyography

Electromyographic (EMG) recordings of muscle activity were made from each *M. salmoides* during the capture of fish prey. Recordings were made through bipolar electrodes constructed from paired 1.0 m sections of 0.051 mm diameter poly-insulated stainless-steel wire (California Fine-Wire). The electrode ends were glued together, and the insulation was scraped away with a blade under a dissecting microscope to expose approximately 0.5 mm tips. The electrode was threaded through a 26 gauge, 0.5 inch hypodermic needle, and the tips were bent back against the shaft of the needle to form a hook, which anchored the electrode in the muscle following percutaneous insertion of the needle into the fish. Four electrodes were implanted in each fish (anesthetized using less than 0.7 g l^{-1} tricaine methanesulfonate), sutured to the fish's dorsum, and glued together into a common cable. During recordings, the electrodes were connected to the high-impedance probes of Grass P511 signal conditioners. Electrical signals were amplified 10 000 times, and a bandpass of 0.1–3 kHz was employed with the 60 Hz notch filter activated. EMGs were recorded with a simultaneous voice track on a TEAC XR-5000 FM recorder at a frequency response of up to 5 kHz. Each feeding sequence was later played back to produce a hard copy on a Graphtec Mark-11 thermal-array recorder at a speed that provided a temporal resolution of 400 mm of chart paper per second of electromyographic data.

After electrode implantation, each fish was returned to the aquarium, where it recovered from the anesthesia. Prey (golden shiners, *Notemigonus*, or sailfin mollies, *Poecilia*) were placed in the aquarium, and the bass was allowed to range freely throughout the tank to pursue and capture them. To minimize the possible effects of relative prey size on prey-capture behavior, prey diameter was adjusted to be 20–50 % of the mouth diameter of each bass. Feeding trials began as early as 2 h after electrode implantation and as late as the following day and continued until at least six prey-capture events had been recorded from the fish. A total of 181 successful prey-capture events were analyzed for the 19 *M. salmoides*. After each experiment, the bass was killed by placing it in a solution of tricaine methanesulfonate, standard length was measured to the nearest millimeter, and the positions of all electrodes were confirmed by dissection.

Recordings were made from four muscles that previous studies have shown to function prominently during prey capture in this and other percomorph species (Liem, 1979; Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988). The four muscles were the sternohyoideus (SH), the epaxialis (EP), the levator arcus palatini (LAP) and section 2 of the adductor mandibulae (AM). The SH is the major depressor of the hyoid apparatus and hence the primary suction-generating element in *M. salmoides*. The EP elevates the cranium during mouth opening. The LAP connects the neurocranium to the lateral surface of the suspensorium and abducts the latter during the expansive phase of suction feeding. The AM connects the suspensorium to the mandible and is the primary jaw-closing muscle. During implantation, care was taken to position each electrode in the same region of the left-side member of each bilaterally paired muscle. Recordings were made from the anterior region of the SH, the anterior-most mid-dorsal region of the EP, the central portion of the LAP and the anterior region of the AM. Restricting the recording area reduced the possible impact of regional variation and any bilaterally asymmetrical muscle activity.

From the chart recordings of each prey-capture event, seven variables were measured with a hand-held dial caliper that quantified the timing of muscle activity (Fig. 1). For each of the four muscles, the duration of the single activity burst that occurs during the strike was measured in milliseconds (SH-Dur, EP-Dur, LAP-Dur, AM-Dur). In addition, the onset of activity of the sternohyoideus muscle was used as a reference time from which the onset time of each of the other three muscles was measured in milliseconds (EP-Onset, LAP-Onset, AM-Onset). Onset of activity was defined as the point at which activity levels rose to three times the noise level for a period of at least 5 ms. The sternohyoideus was selected as the reference muscle because it consistently showed the highest-amplitude burst, thus providing a consistently unambiguous onset time. We measured only temporal variables, and no variables concerning the intensity of muscle activity (i.e. spike number times amplitude or integrated area under the rectified myogram), because of the potential influence of body size on the passive electrical properties of muscle tissue and the influence they could have on electromyograms. Two factors were of particular concern. First, muscle fiber diameter has been shown to increase with growth of muscles and increasing body size in some lower vertebrates (Goldspink, 1977; Sperry, 1981; Lynch, 1984). Larger muscle fibers would be expected to propagate action potentials at a higher velocity, influencing the shape of an extracellular myogram of the type used in this study (Basmajian and De Luca, 1985; Loeb and Gans, 1986). Such an effect could manifest itself as an increase in spike frequency and higher integrated areas as fiber size increases, but without precise information about the sizes of muscle fibers it would not be possible to control for this effect. Second, the size of the muscles studied was quite small in the shortest individuals, so nearby tendons and other connective tissue were more likely to interrupt the recording space of the electrodes than in larger fish, potentially affecting the recorded myograms (Loeb and Gans, 1986). Thus, had we examined integrated area variables and spike frequency variables, there would have been a substantial risk of confounding scale effects on motor pattern with scale effects on the recording properties of the electrodes. We felt that measures of the presence or absence of activity would be least sensitive to these pitfalls, and we focus on them in this study.

Quantifying the effect of body size

Our objective was to test the null hypothesis that body size has no effect on the electromyographic variables. For each fish, the frequency distribution of each variable was examined for outliers, and the mean value of each variable was calculated for each fish. These values, along with the standard length of each fish, were $\log_{10}$-transformed, and bivariate least-squares regressions were fitted for each of the seven EMG variables on standard length. Least-squares regression was used to test the null hypothesis rather than alternative regression models (i.e. reduced major axis, major axis) because (1) our principal aim was to test the effects of standard length on the EMG variables, rather than to describe the nature of the relationships between variables (Ricker, 1973), and (2) the mean values for each EMG variable were measured with considerably greater error than was fish standard length (Ricker, 1973; Sokal and Rohlf, 1985). Because variation among individuals in muscle activity variables has previously been shown to be extensive (Wainwright, 1989), a one-way analysis of variance (ANOVA) was carried out to test for differences among individual fishes in motor pattern variables that did not show a significant effect of body size.

To investigate the possibility that general scale effects might be present in the data set, but not apparent in univariate tests, we conducted a principal components analysis of the correlation matrix of the seven EMG variables for the entire data set of 181 prey-capture sequences. The factor scores of the first two principal components were then correlated with standard length.

Results

Electromyographic recordings of prey-capture events from all sizes of bass showed a characteristic motor pattern in which three muscles were activated nearly simultaneously and the fourth followed at a varying interval (Fig. 1). The muscle firing sequence was usually initiated by activation of the LAP, followed about 10 ms later by the near-synchronous onset of

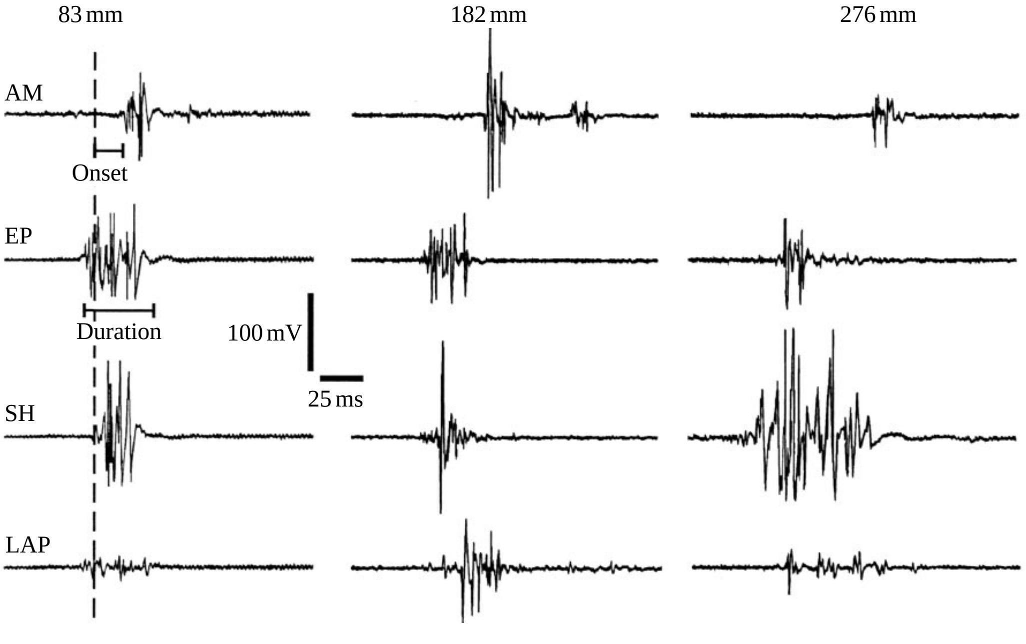

Fig. 1. Representative electromyograms recorded during prey capture in three *Micropterus salmoides* of different body sizes (given as standard lengths). Also indicated are the activity durations and onset times that were measured to quantify muscle activity pattern in this study. Note that the motor patterns are very similar, except for the onset time of the adductor mandibulae muscle, which is later in the larger fish. Abbreviations: AM, adductor mandibulae muscle; EP, epaxialis muscle; SH, sternohyoideus muscle; LAP, levator arcus palatini muscle.

Table 1. *Descriptive statistics for seven electromyographic variables*

	Adductor mandibulae duration	Epaxialis duration	Sternohyoideus duration	Levator arcus palatini duration	Adductor mandibulae onset	Epaxialis onset	Levator arcus palatini onset
Range	10.3–144.8	14.8–105.3	22.5–93.0	10.3–128.8	6.8–102.8	–25.8–17.8	–84.5–35.8
Mean	46.0	43.1	49.3	57.9	35.6	–1.5	–9.5
S.D.	24.3	15.2	15.2	25.5	18.1	8.0	21.5
One-way ANOVA test for individual effect†	8.18*	5.13*	7.86*	7.70*	NC	5.62*	9.59*

N=181 for all variables.

All values are reported in milliseconds.

*P<0.0001.

†F-ratio$_{(18,162)}$ on the individual factor reported for all variables were calculated from untransformed data.

NC, not calculated because this variable was significantly affected by body size.

the EP and SH muscles (mean EP-Onset=−1.5 ms; Table 1; Fig. 1). On average, the AM commenced activity about 36 ms after the onset of the SH muscle. The average duration of activity was similar in the four muscles, ranging from 43.1 ms for the EP to 57.9 ms for the LAP. Bass body mass scaled to standard length according to the following equation:

$$\log_{10}(\text{body mass}) = 2.98\log_{10}(\text{standard length}) - 4.68\ (r^2=0.94;\ P<0.01)\,.$$

Thus, body mass and length have the standard cubic relationship seen in an isometric relationship.

Each fish exhibited considerable variation in the seven EMG variables between feeding episodes (Fig. 2). For all fish, each variable spanned 20–50 ms between the minimum and maximum values (Fig. 2). One-way ANOVAs for individual differences were highly significant for all variables (Table 1).

Only one variable, the relative onset time of the adductor mandibulae muscle (AM-Onset), changed with fish standard length (Table 2; Fig. 3). No other EMG variable scaled with body size. The slope of the AM-Onset regression, 0.62, was significantly less than 1.0 (one-tailed t-test; $t_{(18)}$=2.53, P<0.05), indicating that this variable did not increase quite in proportion to fish length, although it did increase with body size. The maximum and minimum values of AM-Onset per individual fish also regressed significantly on standard length (Fig. 4). Maximum values (log$_{10}$-transformed) scaled to log$_{10}$(standard length) with a slope of 0.62 (S.E.M.=0.15; P=0.001) and the minimum values scaled with a slope of 0.58 (S.E.M.=0.27; P=0.045). The scaling of mean values of AM-Onset was indistinguishable from that of the regressions of minimum and maximum values of this variable.

Correlations among the seven EMG variables and standard length revealed relatively little structure in the overall data set

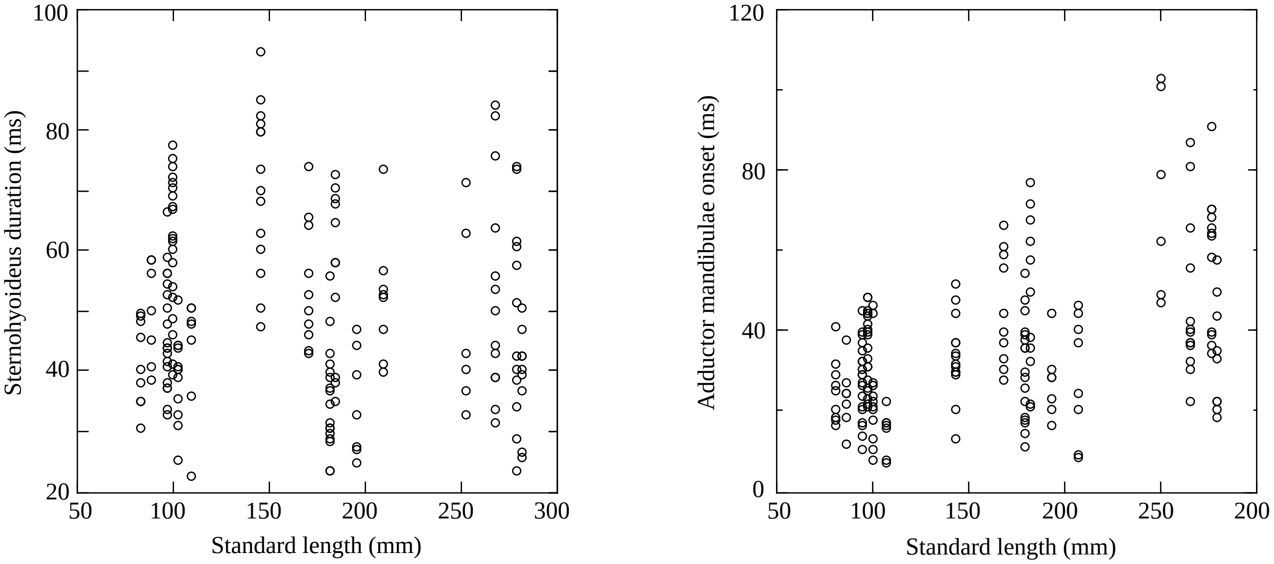

Fig. 2. Scatterplots of two motor pattern variables against fish standard length for 181 prey-capture sequences recorded from 19 *Micropterus salmoides*. Note that variation within each individual is quite high and that the relative onset time of the adductor mandibulae increases with body size, whereas the burst duration of the sternohyoideus muscle does not.

Table 2. *Allometric statistics for seven motor pattern variables against fish standard length for* Micropterus salmoides

	y-intercept	S.E.M.	Slope	S.E.M.	r^2
AM duration	–0.96	0.26	–0.19	0.12	0.13
EP duration	–1.55	0.22	0.08	0.10	0.03
SH duration	–1.24	0.28	–0.05	0.13	0.01
LAP duration	–1.39	0.47	0.04	0.21	0.01
AM onset	–2.87	0.33	0.62*	0.15	0.50
EP onset	–1.01	0.21	0.02	0.12	0.10
LAP onset	–1.21	0.31	–0.06	0.22	0.01

N=19 individuals for each variable.

All regressions based on $\log_{10}$-transformed data.

**P*=0.001; all other regressions are non-significant.

AM, adductor mandibulae; EP, epaxialis; SH, sternohyoideus; LAP, levator arcus palatini.

(Table 3). Although ten out of 27 correlations were significant, only two correlations were above 0.4, and the strongest was about 0.6. Some tendencies were apparent, however. The activity durations of all three expansive-phase muscles were positively correlated, and EP-Dur and SH-Dur were correlated with the onset time of the adductor muscle. Thus, there was a tendency for capture sequences with long bursts in one expansive-phase muscle to show long bursts in all three (SH, EP, LAP) and to show a later onset of the adductor mandibulae muscle. This pattern was not linked with body size, as standard length was uncorrelated with all EMG variables except AM-Onset (Table 3).

The principal components analysis performed on the seven EMG variables yielded two factors with eigenvalues over 1.0, which together accounted for 53.9 % of the total variance in the overall data set (Table 4). The first principal component (31.8 % of total variance) loaded most heavily on the duration and onset variables of the LAP and EP muscles. Feeding sequences that scored highly on the first principal component had relatively long LAP and EP activity bursts in association with low or negative values of LAP-Onset and EP-Onset. In observations on the means of each factor calculated for each individual, neither of the first two principal components was significantly correlated with fish standard length (Table 4; Fig. 5), indicating that the major patterns of structure in the data set were not associated with body size.

Discussion

Most features examined in this study of the prey-capture motor pattern were unaffected by increasing body size in largemouth bass. Only one of seven motor pattern variables, the relative onset time of the adductor mandibulae muscle, scaled significantly with fish size (Table 2; Fig. 3). A parallel study of the kinematics of prey capture in this species (Richard and Wainwright, 1995) indicated (1) that all movements were slower in larger fish and (2) that the morphology of the jaw muscles and lever systems of the lower jaw scale isometrically. Thus, a motor pattern of constant muscle burst duration drives a morphological system that maintains geometric similarity, producing a kinematic pattern that slows with increasing body size. These results have implications for our understanding of the scaling of *in vivo* rates of shortening of the muscles in the feeding apparatus of *M. salmoides*. Specifically, if muscle activation periods and morphological isometry are generally conserved with increasing body size, but the kinematic output becomes longer in duration, then (1) the rate of shortening of the feeding muscles per sarcomere (integrated over the whole muscle–tendon complex) must also be lower in larger fish, and (2) the difference in mechanical output of the muscles from different-sized fish cannot be accounted for by differences in burst duration.

Scaling of EMG timing variables

Why might the onset time of the adductor mandibulae muscle increase with body size, while the onset times of the other muscles do not change? A brief review of the kinematic events of the strike and the functions of the four muscles included in this study is useful before we address this issue.

The largemouth bass uses a combination of suction and ram feeding strategies when taking elusive prey such as small fish (Nyberg, 1971; Wainwright and Lauder, 1986; Norton and Brainerd, 1993). During the expansive phase of suction feeding, a negative pressure pulse is generated in the buccal cavity that draws the prey into the mouth. Expansion involves simultaneous opening of the mouth (sternohyoideus and epaxialis muscles), ventral expansion of the floor of the buccal cavity (sternohyoideus) and lateral expansion of the buccal cavity (levator arcus palatini). Three of the four muscles, the sternohyoideus, the epaxialis and the levator arcus palatini, function during the initial expansive phase of the strike, whereas the adductor mandibulae muscle functions during the compressive phase that immediately follows expansion (Liem, 1978; Lauder, 1985; Sanderson, 1988). The important point is that the two muscles that showed no change in onset time with increasing body size (the epaxialis and levator arcus palatini) are those that function with the reference muscle (the sternohyoideus) during the synchronous movements of the expansive phase. In contrast, the adductor mandibulae muscle functions during the buccal-compression phase that follows expansion (Lauder, 1985).

The absence of scaling in onset times of expansive-phase muscles and its presence in those of the compressive-phase muscle are consistent with observations from the kinematic analyses (Richard and Wainwright, 1995), which provided no evidence that the synchrony of expansive-phase movements changed with increasing body size, but showed that kinematic events corresponding to the onset of activity in the adductor mandibulae muscle became more delayed with increasing body size. The time between the onset of activity in the sternohyoideus and the onset of activity in the adductor mandibulae may correspond to the time between the onset of mandibular depression and the onset of mandibular elevation.

This kinematic variable (‘time to peak gape’) scaled to fish standard length with an exponent of 0.31 (s.e.m.=0.07; Richard and Wainwright, 1995), not significantly different from the scaling of the adductor mandibulae onset time (Student’s *t*-test; $t_{(27)}$=1.15, P>0.2). Previous observations with this and other fish species have suggested that the timing of mouth closure during prey capture is linked to the timing of activity in the antagonistic adductor mandibulae muscle (Liem, 1978; Wainwright and Lauder, 1986). We suggest that the increased time before the onset of activity in the adductor mandibulae muscle in larger individuals is necessitated by the longer time taken to open the mouth fully.

An alternative view would hold that the scaling of kinematic patterns (the slowing of movements with increasing body size) is determined by the timing of mouth closing through the timing of activity in the adductor mandibulae muscle, but patterns of kinematic slowing exist that cannot be accounted for in this way. The important point here is that all the movements of the jaws, hyoid and head are slower in larger fish, including those that occur before the onset of activity in the adductor mandibulae muscle. Although the fish may ultimately control the beginning of jaw closing with the timing of the adductor muscle, it does not begin to close the jaw until it is fully opened (Richard and Wainwright, 1995), and the

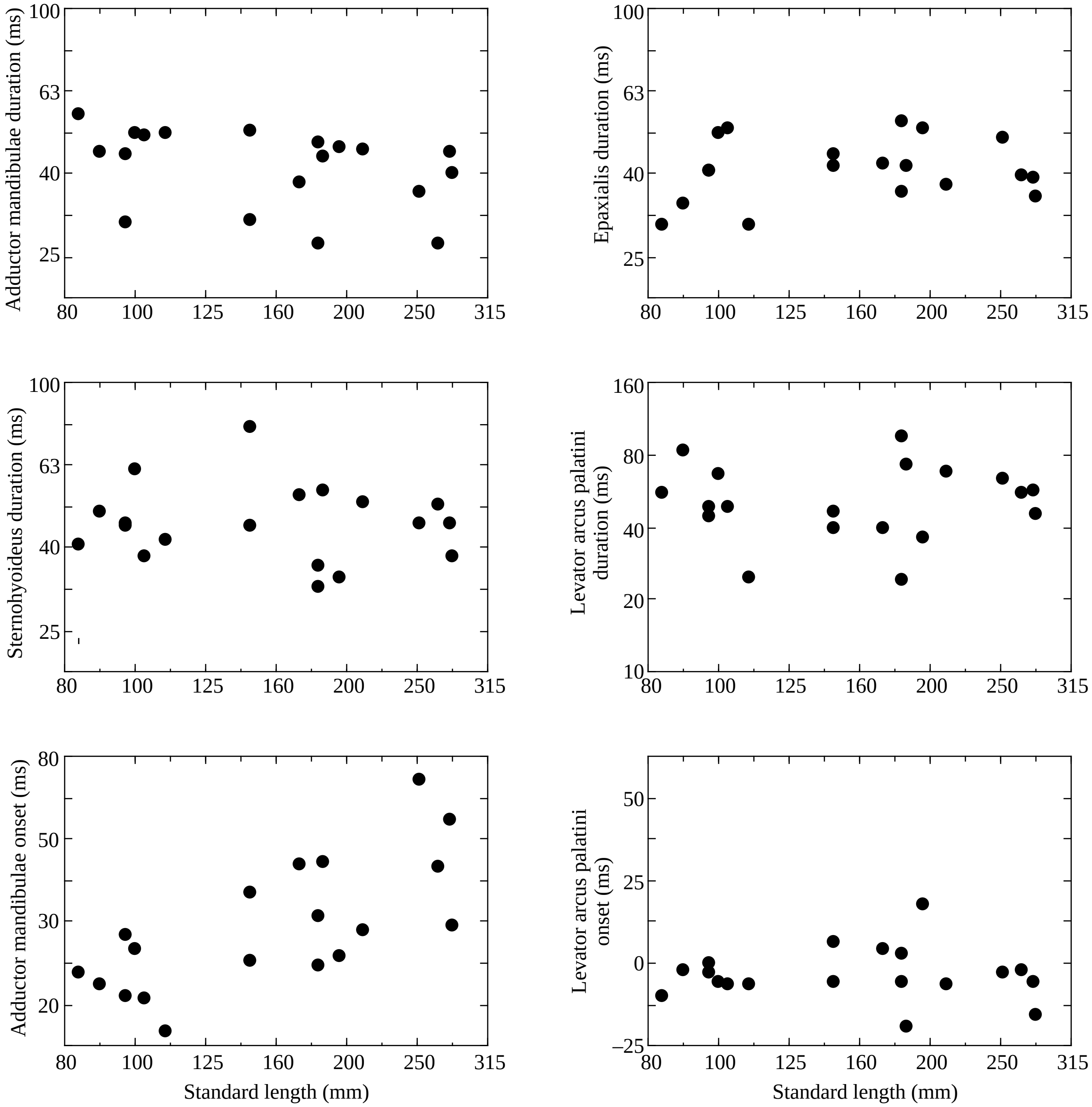

Fig. 3. Scatterplots of the mean values for six motor pattern variables against fish standard length for 19 individual *Micropterus salmoides*. All plots are on $\log_{10}$–$\log_{10}$ axes. Only one variable, the relative onset time of the adductor mandibulae muscle, was significantly affected by body size (see Table 2).

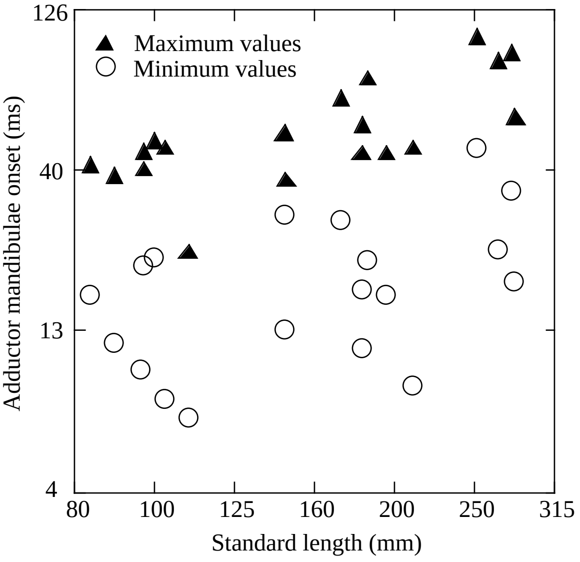

Fig. 4. $\log_{10}$–$\log_{10}$ scatterplot of the maximum and minimum adductor mandibulae onset times against fish standard length for 19 *Micropterus salmoides*. Both minimum and maximum values scale with standard length with slopes that are indistinguishable from the scaling of mean relative onset time (see text).

process of jaw opening is longer in larger fish. The increased duration of the jaw depression process cannot be explained by changes in the lever geometry of the jaw. We suggest that the increased time before the onset of activity in the adductor muscle is best viewed as a consequence of the fact that the time taken to open the mouth is longer in larger fish.

Scaling of EMG burst duration

Muscle burst durations did not change with body size, although virtually all kinematic timing variables for the mouth-opening and mouth-closing periods were longer in larger individuals (Richard and Wainwright, 1995). Our morphological measurements revealed no departures from isometry in the morphology of the adductor mandibulae and sternohyoideus muscles or in the lever system of the lower jaw (Richard and Wainwright, 1995). This combination of results (no change in burst duration, morphological isometry and an increase in kinematic durations with body size) indicates that the mechanical output of the feeding muscles does not scale by simple geometric increases in the overall rate of muscle shortening (rate of sarcomere shortening times the length of the muscle). The slower movements in larger fish imply that the rate of muscle shortening per sarcomere decreases with increasing body size (Richard and Wainwright, 1995). Two central questions are raised by these results and are discussed below. (1) Why does the rate of sarcomere shortening decrease with increasing body size? (2) Why was the increase in kinematic duration not reflected in longer bursts of muscle activity?

Factors that could account for apparent decreases in the per-sarcomere rate of muscle shortening during prey capture include non-isometric growth of muscles and changes in the lever system of the jaws. If the number of sarcomeres acting in series does not increase in proportion to body length, then the calculations of per-sarcomere rates of muscle shortening would have to account for this departure from isometry. Furthermore, if the lengths of the lever arms in the jaw-opening and jaw-closing system do not scale isometrically, then an isometrically scaling mechanical input (e.g. the overall shortening velocity of the jaw adductor muscle) will produce allometric kinematic patterns. The morphological scaling of the bass feeding apparatus appears to be relatively simple, as isometry is retained in all components that we have measured (Richard and Wainwright, 1995). The morphologies (mass, length and thickness) of the adductor mandibulae and sternohyoideus muscles scale isometrically, as do the lever system and mass of the mandible. For muscle bursts of constant duration to drive an isometrically scaling morphology and produce a kinematic pattern that slows with increased body size, the per-sarcomere rate of muscle shortening must decrease with increased body size. In the absence of direct *in*

Table 3. *Spearman pairwise correlation matrix for seven electromyographic variables measured from recordings of 181 prey capture events from 19* Micropterus salmoides

	AM duration	EP duration	Sternohyoideus duration	Levator arcus palatini duration	Adductor mandibulae onset	Epaxialis onset	Levator arcus palatini onset	Standard length
AM duration								
EP duration	–0.04							
SH duration	0.15	0.29*						
LAP duration	–0.09	0.27*	0.24*					
AM onset	–0.01	0.32*	0.31*	0.16				
EP onset	–0.16	–0.39*	0.17	–0.20	–0.01			
LAP onset	0.26*	–0.20	0.16	–0.59*	–0.13	0.53*		
Standard length	–0.14	0.04	–0.07	0.04	0.47*	–0.19	–0.15	

*Bonferroni corrected, $P<0.05$.

AM, adductor mandibulae; EP, epaxialis; SH, sternohyoideus; LAP, levator arcus palatini.

Table 4. *Component loadings and statistics from a principal component analysis on the EMG data set from 181 prey capture sequences recorded from 19* Micropterus salmoides

	Principal component 1	Principal component 2
LAP onset	–0.79	0.37
LAP duration	0.72	0.06
EP onset	–0.64	0.36
EP duration	0.63	0.39
SH duration	0.16	0.80
AM onset	0.39	0.58
AM duration	–0.32	0.38
Correlation with standard length*	0.19	0.10
Eigenvalue	2.23	1.55
Percentage of total variance explained	31.8	22.13

Table entries for the seven EMG variables are the correlation of each variable with the first two principal components.

*Based on mean factor scores per individual, the critical value of r at $P<0.05_{(18)}=0.53$.

LAP, levator arcus palatini; EP, epaxialis; SH, sternohyoideus; AM, adductor mandibulae.

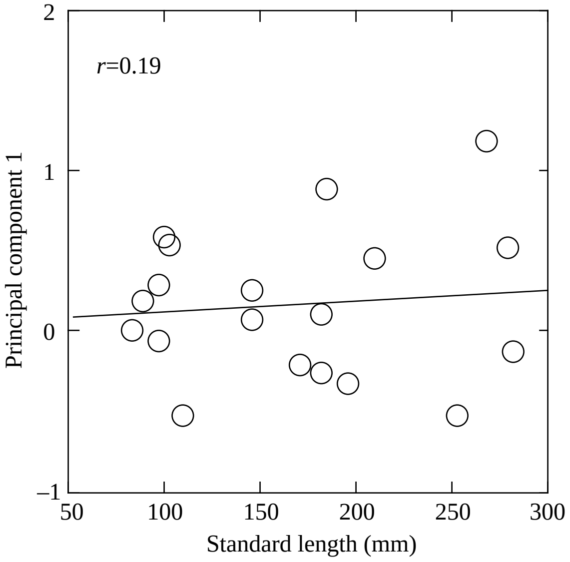

Fig. 5. Scatterplot of mean principal component 1 scores per individual fish against fish standard length for data based on 181 prey-capture sequences from 19 *Micropterus salmoides*. The correlation between mean scores on the first principal component and fish standard length, indicated in the upper left portion of the figure, is not significant.

vivo measurements of the per-sarcomere rate of muscle shortening, this conclusion assumes that the number of sarcomeres in series increases in proportion to muscle length and that the mechanical properties of the tendons scale in proportion to body size.

Why would the per-sarcomere rate of muscle shortening decrease with increasing body size? One possibility is that the decrease in per-sarcomere shortening speed is associated with a general decrease in the rates of muscular contraction that is associated with increasing body size. The skeletal muscles of lower vertebrates typically reach peak forces during isometric contractions more slowly in larger individuals (Marsh, 1988; Bennett *et al*. 1989; Altringham and Johnston, 1990; Archer *et al*. 1990), and limited data suggest that estimates of maximum unloaded shortening velocity scale less than isometrically (Marsh, 1988). In this view, a large bass that powers the expansion of the buccal cavity during a strike with muscle bursts of the same duration as a smaller fish may take longer to open its mouth simply because the mechanical contraction will be slower. In this model, the duration of kinematic events would scale in the same fashion as the time course of muscle contractile properties (e.g. time to maximum isometric tension).

A second perspective was introduced by Hill (1950), who predicted that animals will optimize power output and efficiency of muscles when different-sized individuals perform similar behaviors. In this model, per-sarcomere rates of muscle contraction would be slower in larger fish because the mass of feeding structures increases more rapidly than the force-producing capacity of the feeding muscles. As a result, the muscles of larger fish would be accelerating relatively larger masses, causing the muscles to move down the force–velocity curve to a position of lower rates of per-sarcomere contraction. This model predicts that the duration of kinematic events will be directly proportional to the length of the animal if muscle and skeletal morphology scale isometrically. Skeleton and muscle morphology did scale isometrically in our study; however, the scaling exponents of kinematic duration variables were considerably closer to the scaling exponents of contractile variables such as isometric time to peak twitch tension. Thus, for the variable ‘time to maximum gape distance’, the scaling exponent was 0.31, whereas Hill’s model predicts a slope of 1.0. Empirical values of scaling exponents for muscle contractile properties, such as time to peak twitch tension, for lower vertebrate muscle fall in the range 0.2–0.5.

A third view is offered by McMahon (1984), who derives predictions for the scaling of the rate of sarcomere contraction based on his theory of elastic similarity. This model predicts that the duration of kinematic events should scale to length measurements of body size with an exponent of 0.375. This is very close to the observed values in the kinematic analysis, which mostly fell between 0.3 and 0.4. However, elastic similarity assumes that the scaling of body-part diameters to lengths has an exponent of 1.5, whereas our morphological measurements indicated that all linear variables scale to lengths with an exponent of about 1.0. Thus, the assumptions underlying McMahon’s predictions appear to be violated by this system.

These perspectives provide possible explanations for the scaling pattern of movements during feeding by *M. salmoides*, but why were the increases in kinematic durations not reflected by increases in EMG burst durations? Some insight into this phenomenon may be provided by previous research on the scaling of muscle contractile kinetics in lower vertebrates. As indicated above, a common result in studies of isolated whole-muscle and single-fiber preparations has been that the rate of contraction (e.g. estimated maximal shortening velocity, time to peak isometric tension, time to relaxation) is slower in muscles from larger animals (Marsh, 1988; Bennett *et al*. 1989; Altringham and Johnson, 1990; Archer *et al*. 1990). If one stimulates the muscles from both a small and a large individual with tetanic trains of the same duration, the muscle from the larger individual can be expected to reach peak force more slowly and to require a longer time for relaxation. Hence, when muscles are taken from animals of different sizes, the duration of the electrical events associated with contraction may not have a constant relationship with the time course of the mechanical output of the muscle.

Comparisons with locomotion

We are unaware of data on the scaling of motor patterns associated with other behaviors, but it is interesting to compare the results of this study with the relationship between muscle burst duration and kinematic cycle duration in locomotor behaviors. One correlate of increased locomotor speed in vertebrates is an increase in the rate of limb cycling, in the case of tetrapods, and an increase in the rate of body undulations in swimming taxa and snakes. Furthermore, the time course of the kinematic cycle is known to correlate strongly with the duration of muscle activity bursts (Grillner and Kashin, 1976; Jayne, 1988; Jayne *et al*. 1990). For example, burst duration of a leg muscle in the lizard *Varanus exanthematicus* decreases as the duration of each stride decreases with increased running speed (Jayne *et al*. 1990).

If the activity patterns of cranial muscles in the largemouth bass followed a similar pattern, we might expect that increases in the time to depress the mandible and the hyoid apparatus and to elevate the cranium would be associated with increases in the burst duration of the muscles that cause the movements. Instead, burst duration variables are unchanged with increasing body size, in spite of increases in the duration of prey-capture motions. Two independent factors could be contributing to this difference between locomotor data and our results on prey capture. First, as discussed above, the increased duration of kinematic events in larger fish may be related to a scale-dependent effect on the rate of muscle shortening during feeding behaviors. That is, some effect of increasing size might cause a decrease in the per-sarcomere rate of muscle shortening. A second possibility is that the explosive prey-capture behavior of fishes differs fundamentally from the constant, oscillating nature of steady locomotion. That is, the apparent decoupling of burst duration and kinematic duration might be a general feature of explosive behaviors such as aquatic prey capture in *M. salmoides*.

A caveat

The *caveat* must be offered that the experimental conditions in our two studies were not identical. During the kinematic analysis (Richard and Wainwright, 1995), prey were offered in forceps and capture sequences were only analyzed if mouth opening was maximal. In the present study, prey swam freely in the aquarium and fish were permitted to move about the aquarium in pursuit. All successful capture attempts were analyzed, and many did not involve a fully opened mouth. If the tendency to open the mouth fully changed with body size, and we have no evidence that it did, such a pattern could potentially influence the observed scaling of motor patterns. We assume in our analyses and interpretations that such a bias did not exist. At least one line of evidence directly supports this assumption. EMG variables showed the same level of variation in individuals regardless of body size, as indicated in Fig. 2, where the duration of the sternohyoideus muscle is shown for all 181 prey-capture events. Fig. 4 shows the scaling of maximum and minimum values of adductor mandibulae onset time. ANCOVAs indicated that the scaling patterns of minimum, mean and maximum values of adductor mandibulae onset time did not differ. All three variables scaled to fish length with an exponent of about 0.6. Thus, there is no evidence that body size biased the range of values observed in these variables, suggesting that a similar range of behavioral responses was elicited in fishes of all sizes.

Implications for comparative studies

A current trend in comparative research on the feeding mechanisms of vertebrates is the use of increasingly quantitative intertaxonomic comparisons of functional attributes, such as morphological features, kinematic patterns and muscle activity patterns (Shaffer and Lauder, 1985; Sanderson, 1988; Wainwright, 1989; Reilly and Lauder, 1992). Typically, analyses of variance are used to compare the mean values of variables among taxa to test a null hypothesis of no difference among species. Significant differences among species are generally interpreted as representing evolutionary change in the feeding mechanism (Sanderson, 1988; Wainwright *et al.* 1991; Reilly and Lauder, 1992), and in many cases these differences are thought to be related to differences in feeding performance or patterns of prey use by fish in natural populations (Liem, 1980; Lauder, 1983; Westneat, 1994).

One factor that has the potential to confound quantitative comparisons among species, but which has received relatively little attention, is body size. The results of this study imply that body size may have surprisingly few effects on the prey-capture motor pattern, although additional comparative data will be needed to establish the generality of this result. Although body size may not have the widespread influence on prey-capture motor pattern that it appears to have on morphology and kinematics (Richard and Wainwright, 1995), some types of variable may be expected to be particularly sensitive to scale. The present study suggests that relative timing variables for muscles that function during different stages of the strike are the most likely to change with body size.

We could remove body size as a potentially confounding variable by choosing specimens of a common size, as has been done in previous interspecific studies (Shaffer and Lauder, 1985; Wainwright and Lauder, 1986; Sanderson, 1988). In cases where a range of body sizes is available, an analysis of covariance design would permit a more complete comparative picture. Standard length was used in the present study as a proxy for body size, but it may be more precise to think of the scaling effects we observed as having their roots in the increasing size of the head and its parts. Hence, a more subtle source of scaling effects could be the differences between species in the size of the structures under consideration. Different species may have the same body mass or the same body length, but head and jaw shape may differ widely. For example, the Centrarchidae, of which *M. salmoides* is a member, vary widely in head shape, body shape and typical body size. If one were to compare feeding motor patterns of *M. salmoides*, a large-mouthed, elongate species, with those of *Lepomis macrochirus* (the bluegill sunfish), a deep bodied, small-mouthed form, the appropriate covariate to use in correcting for scale effects might be some measure of jaw dimensions rather than body size. Until comparative data become available on the specific sources of scaling effects in feeding behaviors, it will not be possible to make a more specific recommendation on how to adjust for size in interspecific studies.

Comparative data on the scaling of motor patterns in feeding and other behaviors are currently lacking. Two points that emerge from our analyses could be considered in future investigations. (1) The relative timing of activity of muscles that function during different stages of a behavior may exhibit the clearest scale effects. (2) The duration of activity in many muscles may not scale isometrically during explosive behaviors such as suction feeding in fishes. Such a pattern contrasts with steady oscillating movements, such as locomotion, in which there is a strong relationship between the period of the behavior and muscle burst duration. Activity duration variables in explosive behaviors may not scale isometrically in spite of significant scaling relationships for the kinematic events that correspond to the action of the muscles.

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