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Muscle activation and strain during suction feeding in the largemouth bass *Micropterus salmoides*

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Summary

Activation and strain in the sternohyoideus (SH) were measured *in vivo* in five largemouth bass *Micropterus salmoides*. The SH is thought to actuate lower jaw depression, hyoid depression and suspensorial abduction during suction feeding in teleost fish. Sonomicrometry was used to measure fascicle shortening and lower jaw kinematics, while activity was measured by electromyography (EMG). SH fascicles shortened by an average of 11% during suction feeding. In three fish SH fascicles consistently shortened during fast lower jaw depression, but in two individuals they contracted isometrically or lengthened slightly during fast lower jaw depression. The SH continued shortening after peak gape, presumably actuating hyoid depression and lateral expansion of the buccal cavity. Onset of SH relengthening and onset of lower jaw elevation were simultaneous, as were the return of the SH to resting length and gape closure. Activation followed the onset of shortening by an average of 23 ms, although the muscle was active an average of 15 ms before the onset of rapid shortening. SH fascicles reached sustained shortening velocities averaging –2.5 fascicle lengths per second, and generally increased shortening velocity after peak gape. The shortening velocities measured in this study suggest that the SH actively shortens to generate power during suction feeding. This study is the first direct measurement of *in vivo* muscle function during suction feeding, the most common mechanism of prey capture among aquatic vertebrates.

Key words: suction feeding, largemouth bass, *Micropterus salmoides*, muscle function, sonomicrometry, electromyography, muscle strain.

Introduction

Muscles generate force and strain to power animal behaviors. Muscle function may be considered as the time-course and amplitude of muscle length change (i.e. strain) and force generation in relation to skeletal kinematics and muscle activation (see, for example, Altringham and Ellerby, 1999; Biewener et al., 1998; Finni et al., 2000). Muscle function during a behavior is determined in part by the skeletal movement required by the behavior (kinematic demands), and by the muscle loads incurred during movement (mechanical demands) (Biewener, 2002; Marsh, 1999).

The use of sonomicrometry to measure muscle strain *in vivo* has vastly increased understanding of muscle function during numerous behaviors, helping to clarify how the specific kinematic and mechanical demands of a behavior affect muscle function (Biewener, 2002). Research into muscle function has predominantly focused on locomotor behaviors. Feeding behavior, although of equal evolutionary and ecological significance, has not received commensurate attention. In particular, muscle force and strain during suction feeding have not been studied despite a considerable history of research into the muscular basis of this behavior (Alexander, 1969; Lauder et al., 1986; Osse, 1969).

To successfully capture evasive prey, suction feeding musculoskeletal systems must be able to rapidly expand cranial elements against hydrodynamic pressure gradients of 5–60 kPa (Ferry-Graham et al., 2003; Lauder, 1980b; Muller et al., 1982). Understanding how muscles meet the kinematic and mechanical demands of suction feeding is a necessary first step towards understanding the functional implications of teleost musculoskeletal morphology and may shed light on the biomechanics of suction feeding, which are poorly understood (Ferry-Graham et al., 2003).

To these ends, one aspect of muscle function, the time course and amplitude of muscle fascicle strain in relation to activation and kinematics, was measured *in vivo* in the sternohyoideus of largemouth bass *Micropterus salmoides* feeding on evasive prey. The sternohyoideus originates on the pectoral girdle and posterior muscle masses to insert on the hyoid (Figs 1, 2; Edgeworth, 1935; Winterbottom, 1974). Shortening in the sternohyoideus results directly in ventral–caudal rotation of the hyoid and indirectly in lower jaw depression and lateral expansion of the suspensoria (De Visser and Barel, 1996; Fig. 1). Lower jaw depression was also measured to relate strain measurements to relevant skeletal

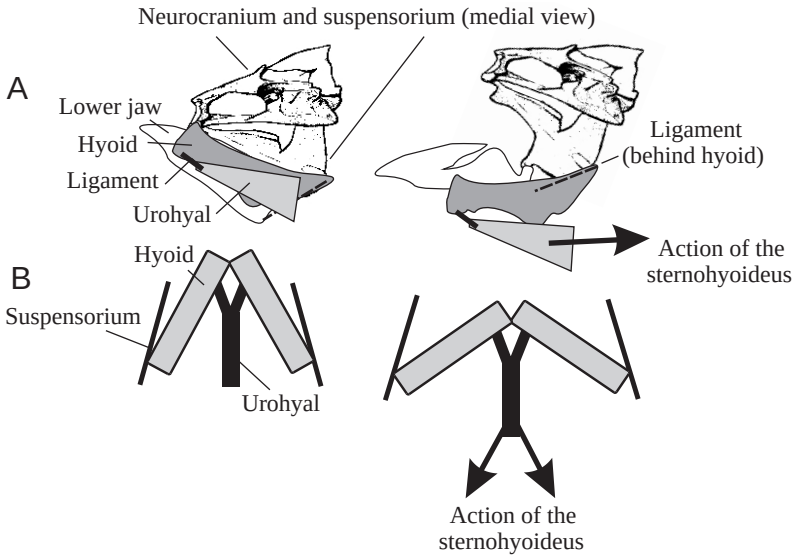

Fig. 1. Action of the sternohyoideus (SH) in medial (A) and ventral (B) views. (A) The SH originates on posterior myosepta and the pectoral girdle. Thick ligaments connect the urohyal to the hyoid structure, so that the primary action of the sternohyoideus is to rotate the hyoid about its articulation on the suspensioria, depressing the buccal floor away from the neurocranium and expanding the buccal cavity. Ventral rotation of the hyoid results in depression of the lower jaw through a linkage between the proximal ends of the hyoid and the mandible. (B) Caudal movement also widens the midventral angle of the hyoid, rotating the suspensoria laterally from the neurocranium and laterally expanding the buccal cavity.

kinematics. This study is the first direct measurement of muscle strain during suction feeding.

The sternohyoideus is known to be active during suction feeding (Grubich and Wainwright, 1997; Lauder et al., 1986; Osse, 1969), but its function cannot be determined without information on fascicle strain patterns. The sternohyoideus may shorten during contraction or may contract isometrically, either to resist action of the epaxial muscles or transmit strain from larger more posterior muscle masses (Fig. 1). Thus, a primary objective of this study was to understand how the sternohyoideus functions during feeding. Because generation of both force and velocity were thought to be important to suction feeding performance, it was predicted that the sternohyoideus would contract at velocities that permit muscular power production during some or all of its active period. In the absence of *in vitro* data on the velocity at which largemouth bass white-muscle fibers produce maximal power, it was predicted that the muscle would contract at approximately 1/3 maximum velocity or about three muscle lengths per second, assuming a maximum contraction velocity of about ten muscle lengths per second (Askew and Marsh, 1998; Hill, 1938; Rome, 1998).

Materials and methods

Animals

Five largemouth bass *Micropterus salmoides* Lacapede [28–32 cm standard length (*SL*)] were used in this study. Largemouth bass are known to specialize on large, elusive prey in the wild and to feed aggressively in captivity despite instrumentation (Etnier and Starnes, 1993; Sanford and Wainwright, 2002). Largemouth bass have also been the subject of numerous studies into the functional morphology of suction feeding (Grubich and Wainwright, 1997; Norton and Brainerd, 1993; Nyberg, 1971; Richard and Wainwright, 1995; Sanford and Wainwright, 2002; Thys, 1997). Fish were fed live goldfish (*Carassius auratus*) and squid pieces (*Loligo* sp.) prior to experimentation, with feeding discontinued 3–6 days prior to surgery. Animals were maintained at 22°C and were housed and maintained in accordance with University of California at Davis animal use and care protocols (#10211).

Surgery

Prior to surgery fish were anaesthetized by emersion in 0.3 g l^{-1} of MS-222 (tricaine methane sulfonate). Fish were then moved to a surgical tray containing 0.1 g l^{-1} of MS-222 and returned to higher concentrations only if they awoke. Surgery lasted less than 30 min and most fish did not awake during surgery.

Sonomicrometry was used to measure gape and muscle strain. In sonomicrometry, small piezo-electric crystals are used to measure distances. The crystals work by transmitting and receiving ultrasound, with the time of sound travel used to measure distance. The utility of using sonomicrometry to measure distances within muscle tissue and water has been established in numerous previous studies (Biewener, 2002; Hoffer et al., 1989; Sanford and Wainwright, 2002). The speed of sound in muscle was estimated as 1560 m s^{-1} (Mol and Breddels, 1982). This velocity underestimated kinematic measurements because the velocity of sound in water was overestimated. The timing of lower jaw depression was the parameter of interest not the absolute distance of lower jaw depression, so this overestimation did not seriously affect results.

To measure lower jaw depression, two 2 mm omnidirectional sonometric crystals (Sonometrics Corp., London, ON, Canada) were passed beneath the operculum, rostral to the first gill arch, and into the mouth. One crystal was sutured to the lower jaw just inside the mandibular symphysis, while the other was sutured to the palate lateral to the vomer (Fig. 2). Crystal wires were secured to the dorsal skin of the fish leaving enough slack for normal movement of the jaws and head.

To measure fascicle strain, two 1 mm crystals were inserted between fascicles in the lateral surface of the sternohyoideus. A 1 mm incision was made through the skin and fascia of the sternohyoideus and a 5-0 suture passed through the skin on

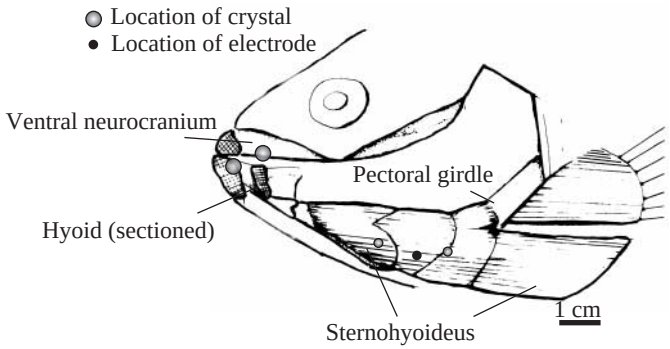

Fig. 2. Lateral view of the anatomy of the sternohyoideus *in situ*, showing the location of sonomicrometry crystals and EMG electrodes in this study. The sternohyoideus originates on the pectoral girdle and on posterior hypaxial myosepta and inserts on the urohyal bone. There are three myomeres between the pectoral girdle and the urohyal. 1 mm crystals were placed rostal and caudal to the middle myomere. An electrode was placed in the middle myomere. 2 mm crystals were placed on the symphysis of the lower jaw and on the anterior palate just lateral to the vomer. For this figure the hyoid, lower jaw and upper jaw were sectioned, and the gills and part of the suspensoria were removed to expose the sternohyoideus.

either side of the incision. Muscle fascicles were gently separated with a blunt probe and the crystal was passed between them with a plastic introducer. The suture was tightened, securing the crystal. The introducer was removed and the skin on either side of the cut was sutured tightly around the wire. Crystals secured by these methods moved freely with underlying muscle fascicles and stayed in place until the end of each experiment. Crystal distance varied from 11–17 mm between preparations. Crystals were inserted along fascicle lines so that fascicle strain would be accurately recorded. The accuracy of crystal distance was checked with calipers prior to recovery of the fish. The movement of crystals with muscle shortening was also checked prior to recovery. Crystal strain and strain rate were interpreted as fascicle strain and strain rate based on the assumptions that crystals were aligned along parallel fascicles and that changes in crystal distance reflected changes in fascicle length.

Bipolar electrodes were fashioned from 0.002 inch (0.051 mm) bi-filament stainless steel, Teflon-coated wire (California Fine-Wire, Grover Beach, CA, USA) by exposing and spreading the wire tips. The electrode wire was bent into a hook 3–5 mm before the exposed tip and the whole wire (approximately 2 m) was threaded through a 26-gauge hypodermic needle. After crystal implantation the electrodes were inserted into the sternohyoideus body *via* the hypodermic needle and kept in place by the hook in the wire. Care was taken to consistently place electrodes between and just under crystals.

Surgery took place the night before experimentation, allowing the fish to recover overnight before experimentation. Data collection took place the next morning as soon as the fish were willing to feed and continued until satiation. During data collection fish were fed live goldfish (approximately 4 cm *SL*). At the conclusion of data collection fish were re-anesthetized and instrumentation was removed. Surgical wounds were extensively cleaned with commercial povidone–iodide solution and left open to prevent infection. Fish were returned to their home tank after instrument removal and monitored for 6–8 h. All fish survived experimentation.

Data collection

Crystal signals were digitized with a Sonometrics TRX-8 conversion box (Sonometrics Corp.) connected to a PC running Sonoview software (Sonometrics Corp.). The PC and software were also used to collect, digitize and record amplified EMG signals. EMG signals were amplified with a differential amplifier (A-M systems, Everett, WA, USA). Using the same software to record EMG and crystal data allowed more convenient synchronization of activity, strain and kinematic signals, but required the EMG signal to be digitized at sampling rates of no more than 500 Hz. One set of data was collected at 700 Hz, but this higher sampling rate markedly increased noise in the strain signal.

Data analysis

Crystal and EMG data were converted to tab-delimited ASCII text files and opened as Microsoft Excel spreadsheets. Crystal data were first smoothed by manually removing obvious outlying points, then with a 3-point rolling average. These methods were found to produce smooth strain profiles without altering the relative timing of discrete events at the sampling frequencies used in this study. The distance between the lower jaw and the neurocranium was normalized by subtracting the minimum distance for each strike from each value and then dividing by the maximum distance for the individual. Fascicle length at each point in time was normalized by subtracting each value from length at onset and dividing by the resting length for the preparation. Because crystal distance at feeding onset varied between strikes, resting length was calculated as the mean crystal distance at onset for each strike in the preparation. The timing of kinematic events (slow onset of lower jaw depression, fast onset of lower jaw depression, peak gape and onset of lower jaw closing), strain events (onset of shortening, onset of fast shortening, peak strain and return to resting length), and activation events (onset and offset) were taken manually from kinematic, strain and activation profiles graphed in Excel. The timing of peak gape was not taken as the time of maximum gape but rather as the end of fast opening (Fig. 3). The onset of fast fascicle shortening was identified by increases to shortening velocities of –1.5 or greater fascicle lengths (*FL*) s^{-1}. Although this was an arbitrary value, it was found to be a useful way to demarcate the onset of rapid shortening. The timing of each event was subtracted from each other event to produce a matrix of latencies. Latencies were averaged for each individual and individual means were averaged (Table 1). For events thought to be simultaneous, the latencies were compared to a predicted mean of zero in single *t*-tests. Events were considered

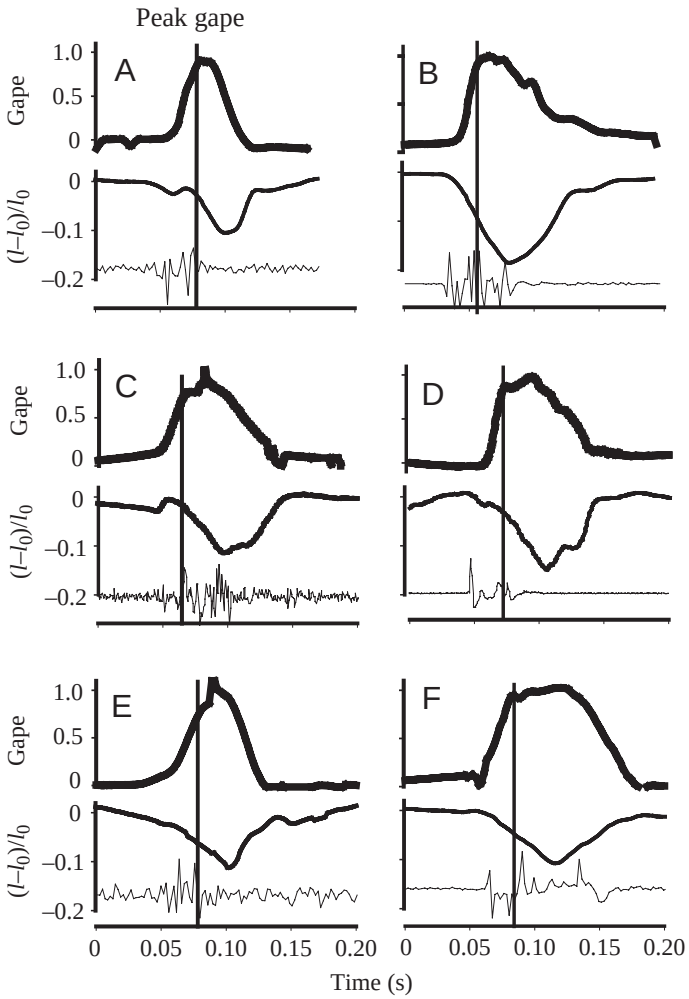

Fig. 3. (A–F) Representative profiles of the lower jaw kinematics (thick, upper trace), sternohyoideus fascicle strain (middle trace) and EMG signal (thin, lower trace) are depicted. Lower jaw displacement and fascicle strain were normalized by subtracting by the minimum crystal distance and dividing by the maximum gape distance or resting fascicle length (*FL*) for a preparation. The drop line indicates the end of fast lower jaw depression, which is defined in this study as peak gape. The timing of fascicle strain and kinematics were closely matched within each strike, but there is variability in the strain profile and in the relationship between activation and strain. (A), (C) and (D) show a 'notch' during fast lower jaw depression indicating slight lengthening. Each strike is from a different fish with the exception of (C) and (D),which are from the same fish. *l*, *FL* at each sampling time; l_0, resting *FL*; $(l–l_0)/l_0$=normalised strain. See Materials and methods for details.

simultaneous if their latency did not significantly differ from zero (P<0.05).

Instantaneous shortening velocity was calculated at each point by subtracting strain at the present time from strain at the previous point and dividing by the time between samples. Two velocities were calculated for each strike: total shortening velocity (the normalized total amplitude of shortening divided by total time to peak strain) and fast shortening velocity (the normalized change in amplitude between the onset of fast shortening and peak strain divided by the latency between these two events).

Results

Lower jaw kinematics

There was a consistent relationship among measured kinematic, strain and activation patterns (Figs 3, 4; Table 1). Lower jaw depression began with a slow phase of small amplitude, which was followed by a fast phase of large amplitude ending in peak gape (Fig. 3). The fast phase averaged 26±1 ms in duration. The lower jaw remained depressed for an average of 28±5 ms before the onset of closing and closed in an average of 44±3 ms (Table 1). The kinematics of lower jaw depression were as described in other studies of similarly sized *M. salmoides* (Richard and Wainwright, 1995; Sanford and Wainwright, 2002), indicating that instrumentation did not gravely affect performance in this study.

Muscle activity

Sternohyoideus activity was observed in all feeding events, but the timing of activation varied among feeding events. For instance, in some strikes activity was nearly simultaneous with the onset of shortening (Fig. 3B), while in others sternohyoideus shortening began 40–60 ms before onset of activation (Fig. 3E). On average, observable activity began 23±6 ms after the onset of sternohyoideus strain. The sternohyoideus was always active before the fast shortening period. The latency between onset activation and onset of fast shortening was less variable within individuals than the latency between onset of activation and onset of slow shortening (*t*-test of latency S.E.M. values by individual P<0.01, N=5). Activity in the sternohyoideus usually ended simultaneously with peak strain and the onset of lower jaw closing (Fig. 4, Table 1). Sternohyoideus activity was never observed prior to the onset of muscle shortening, but was always observed before the onset of fast shortening (Fig. 4, Table 1).

Fascicle strain

Sternohyoideus fascicles shortened by an average of 11±0.7% across individuals. The onset of shortening was nearly simultaneous with the onset of slow jaw depression (Table 1), and typically continued smoothly until maximum strain was reached (Fig. 3). In two fish it was common for the sternohyoideus to discontinue shortening or lengthen after the onset of fast lower jaw depression (Fig. 3A,C,D). The sternohyoideus usually began to shorten again about the time of peak gape. The relationship between sternohyoideus shortening and peak gape varied among individuals. In three individuals there was significantly greater strain after peak gape than before peak gape (Fig. 5); in the other two individuals there was roughly equivalent strain before and after peak gape. In all strikes the sternohyoideus continued to shorten after peak gape. On average, peak strain occurred

Table 1. *Latencies (ms) between activation, strain and kinematic events of the lower jaw during suction feeding in largemouth bass*

	Gape kinematic events				Strain				EMG activation	
	Fast	Peak	Closing onset	Closed	Onset	Fast	Peak	Return	Onset	Offset
Gape										
Slow	–36±6	–62±6	–90±10	–135±12	3±4*	–42±6	–90±7	–135±13	–27±7	–94±12
Fast		–26±1	–55±5	–98±6	33±4	–6±5*	–54±2	–99±8	9±2	–58±7
Peak			–28±5	–72±7	59±4	20±6	–28±3	–73±8	35±2	–32±7
Closing onset				–44±3	87±6	49±8	–0±3*	⁻45±4	64±5	–3±3*
Closed					131±8	93±8	44±5	–1±2*	107±7	41±3
Strain										
Onset						–39±6	–87±4	–132±9	–23±6	–91±8
Fast							–49±6	–93±10	15±7	–52±9
Peak								–45±6	65±3	–3±5*
Return									108±8	41±4
EMG onset										–67±6

Values are means ± SEM for five individuals with 4–9 feedings per individual. See Fig. 3 for details.
*Latency was not significantly different from zero in single *t*-test (P<0.05).

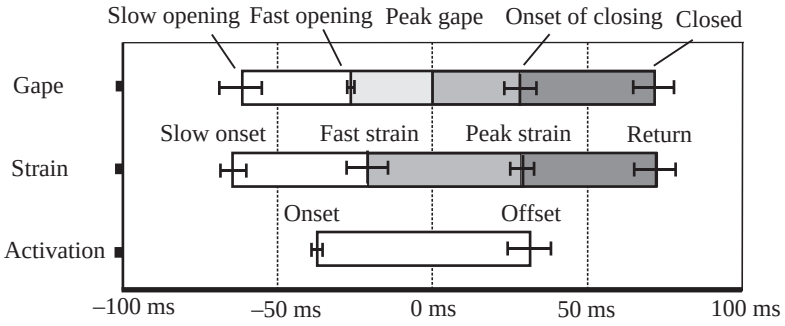

Fig. 4. Timing of kinematic, strain and activation events relative to peak gape. The timing ± S.E.M. (among individuals not within) relative to peak gape are displayed. (The same information is given in row three of Table 1.) The following events were all nearly simultaneous: (1) the onset of slow jaw opening and of fascicle strain; (2) the onset of fast jaw opening and of fast fascicle strain; (3) the onset of jaw closing, peak fascicle strain, and the offset of activity; and (4) the return of the lower jaw and of fascicle to resting length.

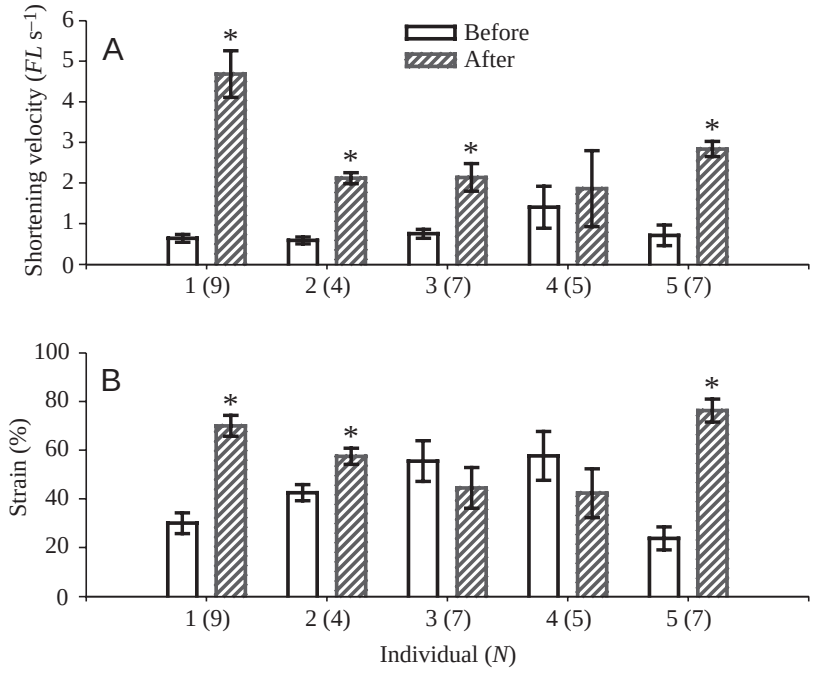

Fig. 5. Total shortening velocity (A) and strain (B) before and after peak gape in individuals, showing individual means ± S.E.M. Shortening velocity is expressed as absolute values (FL s^{-1}). An asterisk indicates a significant difference between strain or shortening velocity before and after peak gape (P<0.05). Shortening velocity always increased after peak gape, though the result was not significant in one individual. Strain is presented as percent of total strain. In three individuals the sternohyoideus generated significantly more strain after peak gape, while in the two others the levels were insignificantly different. The two individuals in whom less than 40% fascicle strain occurred before peak gape are the same two that showed isometric contraction or slight lengthening during fast jaw opening.

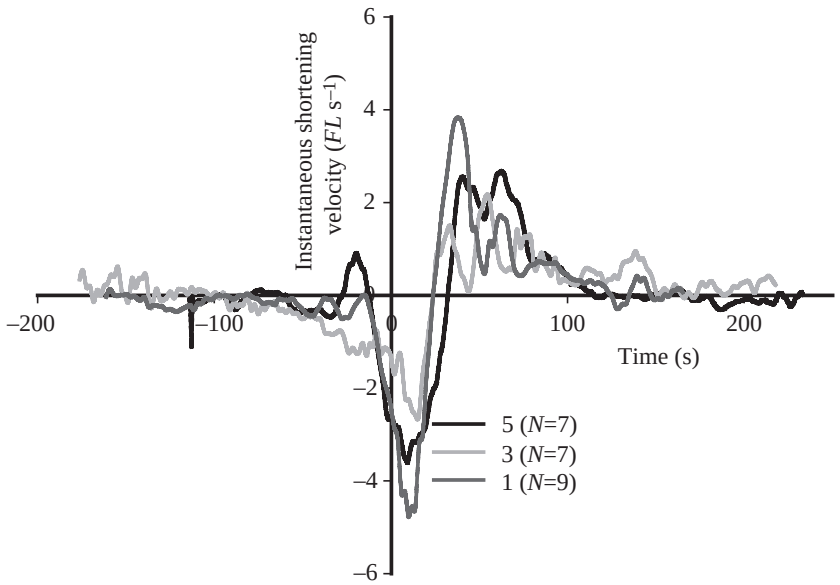

Fig. 6. Instantaneous shortening velocity relative to peak gape from three individuals are displayed. This figure shows the change in normalized length between each sampling period, averaged within individuals and smoothed. Fish 1 showed roughly isometric contraction during fast lower jaw depression, while fish 5 showed lengthening during fast lower jaw depression. These fish also displayed less than 40% fascicle strain prior to peak gape. Fish 1 showed a gradual increase in shortening velocity prior to peak gape. This pattern was also found in fish 2 and 4. Maximum instantaneous speed was variable between individuals.

28±3 ms after peak gape. The onset of lower jaw closing was simultaneous with the cessation of fascicle shortening and muscle activity (Figs 3, 4; Table 1). The return of sternohyoideus to its resting length was simultaneous with the return of the jaw to its closed position (Table 1).

Shortening velocity

Averaged velocity profiles for three individuals are shown in Fig. 6. Shortening started slowly but increased rapidly near the time of peak gape. This rapid increase in negative slope of the strain profile marked the onset of the fast shortening period. Shortening velocity during fast lower jaw depression was variable between individuals. In most individuals the sternohyoideus contracted rapidly during fast lower jaw depression, but in two individuals the sternohyoideus showed little strain or positive strain during most of rapid lower jaw depression (Figs 3, 6). In all individuals sternohyoideus shortening was faster after peak gape than before peak gape (Fig. 5). Instantaneous shortening velocities during the fast portion of shortening ranged from –2 to –5 *FL* s^{-1} (Fig. 6). Fast shortening levels were typically maintained until peak strain. Total velocity of fascicle shortening for the sternohyoideus averaged –1.3±0.12 *FL* s^{-1} across all individuals. Total fast shortening velocities averaged –2.5±0.40 *FL* s^{-1} (Fig. 7). In all strikes the majority of peak strain occurred during the fast period (Fig. 7).

Discussion

The sternohyoideus has been implicated as a suction feeding actuator because of its anatomical position, and because it typically depolarizes during suction feeding behavior (Grubich and Wainwright, 1997; Lauder et al., 1986; Osse, 1969). While the presence of activity indicates that the sternohyoideus generates force during suction feeding, no previous study has shown that the sternohyoideus actually shortens during suction feeding. Muscles may lengthen, shorten or remain of constant length when active, depending on the stress they produce and the stress under which they are placed. Only by shortening can a muscle power skeletal kinematics, but shortening, especially rapid shortening, decreases the amount of force produced by the muscle according to the force–velocity relationship observed in skeletal muscle (Hill, 1938). If the sternohyoideus maintained constant length or lengthened while active, its role might be to transmit strain from the rotation of the pectoral girdle relative to the hyoid, allowing larger, more posterior muscle masses to generate strain. If this were true its function would be analogous to the transmission of strain by posterior muscle masses in swimming fish (Altringham and Ellerby, 1999; Wardle et al., 1995). Such rotation occurs when the neurocranium is rotated dorsally by the epaxial muscles, pulling the hyoid away from the pectoral girdle, and when the pectoral girdle is rotated caudally by the hypaxial muscles (Aerts et al., 1987; Osse, 1969; Thys, 1997). The active shortening observed in the sternohyoideus indictates that it, in fact, actuates suction feeding kinematics.

The sternohyoideus consistently shortened after peak gape (Fig. 5). In three of the five individuals more strain was observed after peak gape than before. This pattern is consistent with the multiple functions of the sternohyoideus, including lower jaw depression, hyoid depression and lateral expansion of the suspensoria (Fig. 1). Suction feeding fish in general, and largemouth bass in particular, exhibit an anterior-to-posterior wave of expansion during suction feeding. Peak gape precedes hyoid depression, which precedes peak opercular expansion (Lauder, 1980a; Osse, 1969; Sanford and Wainwright, 2002). This kinematic pattern is possible because the linkage between the proximal hyoid and lower jaw allows the hyoid to continue depression after the lower jaw has reached its ventral limit (Fig. 1). Shortening after peak gape would continue ventral–caudal rotation of the hyoid, resulting in continued depression of the buccal floor and continued lateral expansion of the suspensioria.

In all individuals the sternohyoideus increased shortening velocity after peak gape (Fig. 5). This pattern suggests that

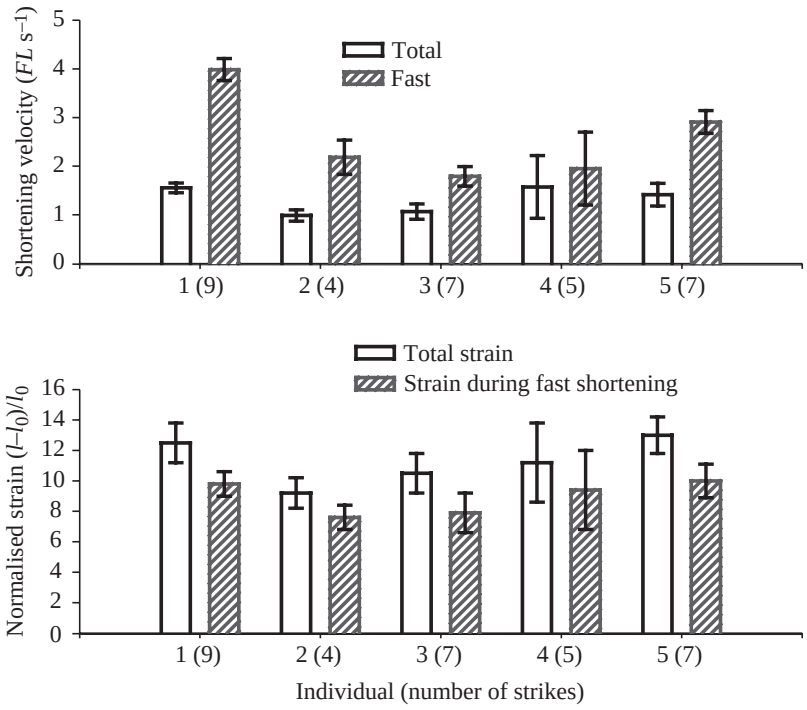

Fig. 7. Velocity and strain by individual. Total shortening velocity is the total strain distance divided by the time between strain onset and peak strain. Fast shortening velocity is the total strain between onset of fast shortening and peak strain divided by the time between the onset of fast shortening and peak strain. Strain and shortening velocity are expressed as negatives to facilitate viewing. Mean total shortening velocity (including slow shortening) was –1.3 *FL* s^{-1}. Mean fast shortening velocity across individuals was –2.5 *FL* s^{-1}, suggesting that the sternohyoideus functions to produce mechanical power. The majority of strain occurred in the fast portion of the strain cycle in all individuals. l, minimum *FL*, l_0, resting *FL*.

sternohyoideus loading may be reduced after peak gape. Loads may be reduced because the lower jaw is no longer rotating, and because other cranial structures are not accelerating as rapidly as prior to peak gape, reducing hydrodynamic load (Sanford and Wainwright, 2002). The major source of loading during suction feeding appears to be negative internal buccal pressure (Alexander, 1969), the magnitude of which is greatly decreased after peak gape (Sanford and Wainwright, 2002). These factors would all contribute to decreased loading and increased shortening velocity after peak gape.

Individual variation in sternohyoideus function

In two of the five studied individuals the sternohyoideus lengthened slightly or contracted isometrically during fast lower jaw depression. One explanation for this observation is that the sternohyoideus was stretched by rotation of the hyoid away from the pectoral girdle as described above. By contracting eccentrically the sternohyoideus might be able to generate greater force than it would be able to during shortening (Hill, 1938; Lindstedt et al., 2002). Why this pattern was consistently observed in some individuals and not others is not apparent from this study, but it may have been the result of subtle differences in muscle activation between individuals. Individual variation is common in studies of both suction feeding and muscle function (e.g. Gillis and Biewener, 2000; Grubich and Wainwright, 1997). Furthermore, jaw opening in teleosts is actuated by multiple complex and redundant musculoskeletal systems (Adriaens et al., 2001; Lauder, 1980a; Westneat, 1990), so there is potential for variation in how these systems are used between individuals.

Activation and strain

In many reported vertebrate behaviors muscle activation precedes shortening by 20–80 ms (e.g. Franklin and Johnston 1997; Gillis and Biewener, 2000; Olson and Marsh, 1998; Lutz and Rome, 1994). In this study measurable activation was not detected until an average of 23 ms *after* the onset of the slow fascicle shortening (Table 1, Fig. 4). The sternohyoideus may be returning to resting length after being passively stretched by an antagonistic muscle or be slackening by action of a synergistic muscle. Elevation of the lower jaw by the adductor mandibulae would stretch the sternohyoideus, but these muscles are not detectably active prior to expansion in largemouth bass (Wainwright and Richard, 1995).

Passive shortening in the sternohyoideus might also have been caused by depression of the lower jaw through the opercular linkage (Lauder, 1980a). A small muscle, the levator operculi, links the operculum to the neurocranium and is thought to depress the lower jaw through a linkage involving the opercular series. This muscle is typically active prior to the sternohyoideus (Grubich and Wainwright, 1997; Lauder et al., 1986; Osse, 1969) and is thought to actuate the slow phase of lower jaw depression (Aerts et al., 1987; Osse, 1969). In doing so it may allow the sternohyoideus to shorten. The onset of shortening and the onset of activation were variable within individuals, but the sternohyoideus was never active prior to shortening. However, several strikes showed nearly simultaneous onset of shortening, jaw depression and activation (Fig. 3). In these strikes the levator operculi may have been activated at the same time as the sternohyoideus.

Muscle function for power production

The shortening velocities measured in this study suggest that the sternohyoideus functions to generate mechanical power during suction feeding. In all individuals, the sternohyiodeus actively shortened during part or all of its active period, generating mechanical power. Shortening velocity averaged –2.5 *FL* s^{-1} during fast shortening. Although it cannot be concluded from *in vivo* data alone, this velocity may maximize

mass-specific production of muscle velocity. Peak muscular power production occurs at approximately 1/3 maximal velocity (Askew and Marsh, 1998; Hill, 1938). Maximal velocities for suction feeding muscles are not known in fish, but maximum velocities for fish white axial muscle at 22° approximate 7–10 $FL\ s^{-1}$ (Aerts et al., 1987; Beddow and Johnston, 1995). Furthermore, the shortening velocities measured in this study were similar to those of other ectothermic vertebrates performing power-limited behaviors at similar temperatures (Ellerby and Altringham, 2001; Lutz and Rome, 1994; Nelson and Jayne, 2001; Olson and Marsh, 1998). Without *in vitro* data, however, it cannot be concluded that the sternohyoidues contracts at velocities that permit maximal mass-specific power production.

Maximizing muscular power production may be an important component of successful suction feeding on evasive prey (Aerts et al., 1987; Alexander, 1969). To be successful a suction-feeding predator must accelerate a sufficient volume of water to entrain prey before the prey has a chance to escape. The energetic cost of doing so equals the pressure resisting expansion multiplied by the total change in buccal volume (see, for example, Marsh et al., 1992). With variable pressure, the total work (W_{tot}) equals the pressure resisting expansion as a function of volume V integrated from starting volume (V_0) to final volume (V_{final}). The total pressure resisting cranial expansion (P_{tot}) is the sum of sub-ambient pressure inside the mouth (P_{out}) and the supra-ambient pressure outside expanding cranial elements (P_{in}):

$$W_{tot} = \int_{V_0}^{V_{final}} P_{tot}(V)\mathrm{d}t, \quad (1)$$

where

$$P_{tot} = P_{out} - P_{in}, \quad (2)$$

The power required for cranial expansion is equal to the total mechanical work done on the water divided by the total time t of volume expansion:

$$\frac{W_{tot}}{t_{final} - t_0} = \text{Total power}. \quad (3)$$

The power required for suction feeding would therefore increase linearly with decreasing duration of cranial expansion (t_{final}–t_0) even if the incurred hydrodynamic resistance were independent of strike duration. In fact, hydrodynamic loading probably increases with increasing speed of volume expansion. Although the hydrodynamics of suction feeding are extremely complex and poorly understood, the pressure measured inside the expanding buccal cavity probably results from the inertia of water entering the mouth (Muller et al., 1982); it can therefore be expected that the more rapidly the volume expansion takes place the more intense the negative pressures that resist expansion. There is empirical evidence to support this assumption: Sanford and Wainwright (2002) found that internal pressure in largemouth bass increased with increasing acceleration of cranial expansion.

Similarly, positive pressures outside expanding cranial elements may increase with increasing suction feeding speed. This pressure is due to the inertia of water (added or virtual mass) displaced by the expanding cranial elements and would be expected to increase linearly with increasing cranial acceleration (Batchelor, 1967; Daniel, 1984; Vogel, 1994). In a detailed theoretical analysis of shrimp tail flips, which occur on time scales similar to suction feeding, Daniel and Meyhofer (1989) found that predicted muscle force increased exponentially with decreasing duration of the tail flip. Furthermore, differential pressures measured on the tail of swimming cod *Gadus morhua* were shown to increase with increasing tail rotational acceleration (Webber et al., 2001).

If the above analysis is correct, increased suction feeding performance, in an individual fish, is limited by muscular power. Therefore, fish that use suction feeding to capture evasive prey ought to possess musculoskeletal morphologies that permit fascicles to shorten at velocities that maximize their intrinsic power capabilities. In other words, fish that feed on evasive prey ought to be ‘geared’ for power generation. This study supports this theoretical prediction: sternohyoideus fascicles contract at velocities consistent with the production of mechanical power. Whether the shortening velocities measured in this study approximate the optimal shortening velocity for power production must be determined by *in vitro* measurements of muscle fiber performance, as has been done in other systems (Lutz and Rome, 1994; Marsh et al., 1992; Peplowski and Marsh, 1997; Rome et al., 1993; Wakeling and Johnston, 1998).

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References

Adriaens, D., Aerts, P. and Verraes, W. (2001). Ontogenetic shift in mouth opening mechanisms in a catfish (Clariidae, Siluriformes): A response to increasing functional demands. *J. Morphol.* **247**, 197-216.

Aerts, P., Osse, J. W. M. and Verraes, W. (1987). Model of jaw depression during feeding in (*Astatotilapia elegans*: Teleostei Cichlidae): mechanisms for energy storage and triggering. *J. Morphol.* **194**, 85-109.

Alexander, R. M. (1969). Mechanics of the feeding action of a cyprinid fish. *J. Zool. (Lond.)* **159**, 1-15.

Altringham, J. D. and Ellerby, D. J. (1999). Fish swimming: patterns in muscle function. *J. Exp. Biol.* **202**, 3397-3403.

Askew, G. N. and Marsh, R. L. (1998). Optimal shortening velocity (V/V_{max}) of skeletal muscle during cyclical contractions: Length–force effects and velocity-dependent activation and deactivation. *J. Exp. Biol.* **201**, 1527-1540.

Batchelor, G. K. (1967). *An Introduction to Fluid Dynamics*. Cambridge, England: Cambridge University Press.

Beddow, T. A. and Johnston, I. A. (1995). Plasticity of muscle contractile properties following temperature acclimation in the marine fish *Myoxocephalus scorpius*. *J. Exp. Biol.* **198**, 193-201.

Biewener, A. A. (2002). Future directions for the analysis of musculoskeletal design and locomotor performance. *J. Morphol.* **252**, 38-51.
Biewener, A. A., Konieczynski, D. D. and Baudinette, R. V. (1998). *In vivo* muscle force-length behavior during steady-speed hopping in tammar wallabies. *J. Exp. Biol.* **201**, 1681-1694.
Daniel, T. L. (1984). Unsteady aspects of aquatic locomotion. *Am. Zool.* **24**, 121-134.
Daniel, T. L. and Meyhofer, E. (1989). Size limits in escape locomotion of carridean shrimp. *J. Exp. Biol.* **143**, 245-266.
De Visser, J. and Barel, C. D. N. (1996). Architectonic constraints on the hyoid's optimal starting position for suction feeding of fish. *J. Morphol.* **228**, 1-18.
Edgeworth, F. H. (1935). *The Cranial Muscles of Vertebrates.* London, UK: Cambridge University Press.
Ellerby, D. J. and Altringham, J. D. (2001). Spatial variation in fast muscle function of the rainbow trout, *Oncorhynchus mykiss*, during fast-starts and sprinting. *J. Exp. Biol.* **204**, 2239-2250.
Etnier, D. A. and Starnes, W. C. (1993). *The Fishes of Tennessee*. Knoxville: University of Tennessee Press.
Ferry-Graham Lara, A., Wainwright, P. C. and Lauder George, V. (2003). Quantification of flow during suction feeding in bluegill sunfish. *Zoology* **106**, 159-168.
Finni, T., Komi Paavo, V. and Lepola, V. (2000). *In vivo* human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. *Eur. J. Appl. Physiol.* **83**, 416-426.
Franklin, C. E. and Johnston, I. A. (1997). Muscle power output during escape responses in an Antarctic fish. *J. Exp. Biol.* **200**, 703-712.
Gillis, G. B. and Biewener, A. A. (2000). Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). *J. Exp. Biol.* **203**, 3547-3563.
Grubich, J. R. and Wainwright, P. C. (1997). Motor basis of suction feeding performance in largemouth bass, *Micropterus salmoides*. *J. Exp. Zool.* **277**, 1-13.
Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. Lond. B* **126**, 136-195.
Hoffer, J. A., Caputi, A. A. and Griffiths, R. I. (1989). Roles of muscle activity and load on the relationship between muscle spindle length and whole muscle length in the freely walking cat. *Prog. Brain Res.* **80**, 75-85.
Lauder, G. V. (1980a). Evolution of the feeding mechanism in primitive actinopterygian fishes: a functional anatomical analysis of *Polypterus*, *Lepisosteus*, and *Amia*. *J. Morphol.* **163**, 283-317.
Lauder, G. V. (1980b). The suction feeding mechanism in sunfishes (*Lepomis*) and experimental analysis. *J. Exp. Biol.* **88**, 49-72.
Lauder, G. V., Wainwright, P. C. and Findeis, E. (1986). Physiological mechanisms of aquatic prey capture in sunfishes: Functional determinants of buccal pressure changes. *Comp. Biochem. Physiol.* **84A**, 729-734.
Lindstedt, S., L., Reich, T. E., Keim, P. and LaStayo, P. C. (2002). Do muscles function as adaptable locomotor springs? *J. Exp. Biol.* **205**, 2211-2216.
Lutz, G. J. and Rome, L. C. (1994). Built for jumping: The design of the frog muscular system. *Science* **263**, 370-372.
Marsh, R. L. (1999). How muscles deal with real-world loads: the influence of length trajectory on muscle performance. *J. Exp. Biol.* **202**, 3377-3385.
Marsh, R. L., Olson, J. M. and Guzik, S. K. (1992). Mechanical performance of scallop adductor muscle during swimming. *Nature* **357**, 411-413.
Mol, C. R. and Breddels, P. A. (1982). Ultrasound velocity in muscle. *J. Acoust. Soc. Am.* **71**, 455-461.
Muller, M., Osse, J. W. M. and Verhagen, J. H. G. (1982). A quantitative hydrodynamical model of suction feeding in fish. *J. Theor. Biol.* **95**, 49-79.
Nelson, F. E. and Jayne, B. C. (2001). The effects of speed on the *in vivo* activity and length of a limb muscle during the locomotion of the iguanian lizard, *Dipsosaurus dorsalis*. *J. Exp. Biol.* **204**, 3507-3522.
Norton, S. F. and Brainerd, E. L. (1993). Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11-29.
Nyberg, D. W. (1971). Prey capture in the largemouth bass. *Am. Mid. Nat.* **86**, 128-144.
Olson, J. M. and Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles of the bullfrog *Rana catesbeiana* during jumping. *J. Exp. Biol.* **201**, 2763-2777.
Osse, J. W. M. (1969). Functional morphology of the head of the perch (*Perca fluviatis* L.): an electromyographic study. *Neth. J. Zool.* **19**, 289-392.
Peplowski, M. M. and Marsh, R. L. (1997). Work and power output in the hindlimb muscles of cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.* **200**, 2861-2870.
Richard, B. A. and Wainwright, P. C. (1995). Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): Kinematics of prey capture. *J. Exp. Biol.* **198**, 419-433.
Rome, L. C. (1998). Some advances in integrative muscle physiology. *Comp. Biochem. Physiol.* **120B**, 51-72.
Rome, L. C., Swank, D. and Corda, D. (1993). How fish power swimming. *Science* **261**, 340-343.
Sanford, C. P. J. and Wainwright, P. C. (2002). Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. *J. Exp. Biol.* **205**, 3445-3457.
Thys, T. (1997). Spatial variation in epaxial muscle activity during prey strike in largemouth bass (*Micropterus salmoides*). *J. Exp. Biol.* **200**, 3021-3031.
Vogel, S. (1994). *Life in Moving Fluids: The Physical Biology of Flow*, 2nd edition. Princeton, NJ: Princeton University Press. xiii+467p.
Wakeling, J. M. and Johnston, I. A. (1998). Muscle power output limits fast-start performance in fish. *J. Exp. Biol.* **201**, 1505-1526.
Wainwright, P. C. and Richard, B. A. (1995). Scaling the feeding mechanism of the largemouth bass (*Micropterus salmoides*): Motor pattern. *J. Exp. Biol.* **198**, 1161-1171.
Wardle, C. S., Videler, J. J. and Altringham, J. D. (1995). Tuning in to fish swimming waves: Body form, swimming mode and muscle function. *J. Exp. Biol.* **198**, 1629-1636.
Webber, D. M., Boutilier, R. G., Kerr, S. R. and Smale, M. J. (2001). Caudal differential pressure as a predictor of swimming speed of cod (*Gadus morhua*). *J. Exp. Biol.* **204**, 3561-3570.
Westneat, M. W. (1990). Feeding mechanics of teleost fishes (Labridae: Perciformes): A test of four-bar linkage models. *J. Morphol.* **205**, 269-296.
Winterbottom, R. (1974). A descriptive synonymy of the striated muscles of the Teleostei. *Proc. Acad. Nat. Sci. Phil.* **125**, 225-317.