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Efficiency of labriform swimming in the bluegill sunfish (*Lepomis macrochirus*)

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Summary

Bluegill sunfish (*Lepomis macrochirus*) swim in the labriform mode at low speeds, generating lift and thrust by beating their pectoral fins. The maximal power output available from the two largest pectoral fin adductor and abductor muscles, constituting half of the total pectoral girdle muscle mass, was measured *in vitro* and used to estimate the muscle mechanical power output during maximal labriform swimming (P_{mech}; 0.15–0.21 W kg^{-1} body mass). Respirometry was used to estimate the total metabolic power input (P_{total}; 0.95 W kg^{-1} body mass) and the metabolic power available to the active muscle mass (P_{muscle}; P_{total} minus standard metabolic rate, 0.57 W kg^{-1} body mass) at this swimming speed. Drag measurements made on towed, dead fish were used to estimate the mechanical power required to overcome body drag (P_{drag}; 0.028 W kg^{-1} body mass). Efficiency estimates based on these data fell into the following ranges: overall swimming efficiency ($\eta_{gross}=P_{mech}/P_{total}$), 0.16–0.22; muscle efficiency ($\eta_{muscle}=P_{mech}/P_{muscle}$), 0.26–0.37; and propeller efficiency ($\eta_{prop}=P_{drag}/P_{mech}$), 0.15–0.20. Comparison with other studies suggests that labriform swimming may be more efficient than swimming powered by undulations of the body axis.

Key words: fish swimming, mechanical power, efficiency.

Introduction

Locomotion is an energetically expensive activity. Determining the efficiency and economy of locomotion is important, as these factors dictate the proportion of daily energy budgets allocated to this task. Locomotor systems may be expected to be efficient and/or economical, particularly in species that forage for patchily dispersed resources (Pettersson and Hedenström, 2000) or undertake lengthy migrations (Block et al., 2005; van Ginneken et al., 2005). Few estimates of locomotor efficiency are available. The nature of some forms of locomotion precludes this type of measurement. For example, during level, terrestrial locomotion, the net work and power per stride are zero (Cavagna et al., 1977), and energy is expended on a wide range of mechanical functions (Ellerby et al., 2005). Determining overall efficiency on the basis of power inputs and outputs is therefore not practicable for walking or running. The situation is more straightforward in swimmers and fliers where the muscles are primarily used to generate power, accelerating the fluid surrounding them to generate lift and thrust (Rayner, 1979; Biewener et al., 1992; Drucker and Lauder, 1999; Altringham and Ellerby, 1999). In systems of this type, the overall efficiency of locomotion can potentially be determined by measuring metabolic rate and the mechanical power output from the active muscle tissue.

No single study has quantified the power inputs and outputs for a given locomotor system. Metabolic rate measurements in flying birds have been compared to mechanical power estimates derived from aerodynamic models (Rayner, 1999; Ward et al., 2001) or measures of muscle force based on bone strain (Biewener et al., 1992; Hedrick et al., 2003) or measured *in vitro* (Askew and Ellerby, 2007). The mechanical power output of fish muscle has been measured *in vitro* (Altringham and Johnston, 1990; Luiker and Stevens, 1992; Luiker and Stevens, 1993; Rome et al., 1993; Coughlin, 2000; Syme and Shadwick, 2002), but these data have not been integrated with measures of the energy costs of swimming for three main reasons. First, the segmented, myotomal muscle that powers undulatory swimming has a complex architecture and properties that change along the body axis (Altringham and Ellerby, 1999). Second, the precise role of myotomal muscle remains controversial, in particular the role of the caudal musculature in power transmission as well as a power production (van Leeuwen et al., 1990; Rome et al., 1993; Altringham and Ellerby, 1999). Third, the level of motor unit recruitment changes with swimming speed (Rome et al., 1984; Jayne and Lauder, 1995), but detailed recruitment data are only available for a few species. With these uncertainties concerning muscle mechanical function and recruitment levels, muscle power outputs measured *in vitro* are difficult to relate to the actual mechanical power requirements of swimming.

In view of these problems, we measured swimming muscle power in bluegill sunfish (*Lepomis macrochirus* Rafinesque). This species swims in the labriform mode at low speeds, generating thrust by beating its pectoral fins rather than by undulating its body axis (Gibb et al., 1994). In fish of this type, the pectoral girdle muscles form a discrete, thrust-generating

'motor', the properties of which can be quantified more readily than segmented myotomal muscle. It has been proposed that the labriform swimming mode may be more economical and efficient than undulatory swimming (Webb, 1975; Gordon et al., 1989; Lighthill and Blake, 1990). The thrust required to overcome body drag may be up to five times higher in an undulating body, relative to a rigid body axis, and undulatory swimmers may experience greater energy losses due to lateral recoil of the body (Lighthill, 1971; Webb, 1998). Labriform swimmers that maintain a rigid body axis may therefore be more economical and efficient than undulatory swimmers. We hypothesized that bluegill sunfish *Lepomis macrochirus*, a species that uses the labriform gait at low speeds, would be more economical and efficient than swimmers that only utilize undulatory swimming. In order to test this hypothesis, we measured the mechanical power output from the major pectoral fin adductor and abductor muscles *in vitro* using the work loop technique (Josephson, 1985) and used this as a basis for estimating mechanical power output during maximal labriform swimming. The metabolic power input into this system during maximal labriform swimming was determined using respirometry. We also estimated the propeller efficiency of the system, measuring the power required to overcome body drag in towed fish and expressing it as a proportion of the total mechanical power available from the pectoral girdle muscles. Our data are compared to available data from the literature concerning the economy and efficiency of undulatory swimming.

Materials and methods

Animals

Bluegill sunfish *Lepomis macrochirus* Rafinesque were collected from Lake Waban, MA, USA using hook and line. The fish were kept at 22°C under a 12 h:12 h light:dark cycle and fed chopped earthworms twice a week. All procedures were approved by the Institutional Animal Care and Use Committee.

Swimming flume

Swimming experiments were carried out at 22°C in a sealable, recirculating flume (Model 90; Loligo Systems, Hobro, Denmark) capable of generating flow velocities from 5 to 150 cm s^{-1}. The flume was composed of an inner chamber, 88.6 liters in volume, with a working section of 20 cm×20 cm×70 cm and an outer tank that buffered temperature changes and served as a reservoir of oxygenated water.

Kinematic analysis

Video sequences of seven fish (mass M=152.3±2.8 g, length L=19.5±0.4 cm, means ± s.e.m.), swimming at speeds ranging from 0.46 to 2.16 L s^{-1}, were recorded using a Sony HDR HC-3 camcorder at a frame rate of 120 Hz. A mirror mounted above the flume at a 45° angle allowed simultaneous recording of lateral and dorsal views of the fish. Video sequences were captured on a Macintosh iMac computer and analyzed using VideoPoint software (Lenox Softworks, Lenox, MA, USA) to determine pectoral fin beat frequencies and upstroke and downstroke durations during sequences of steady swimming (mean sequence length, 20 fin beats).

Respirometry

A self-stirring polarographic oxygen probe connected to an Accumet Excel XL40 Dissolved Oxygen Meter (Fisher Scientific, Pittsburgh, PA, USA) was inserted through a port in the lid of the sealed flume. This logged the oxygen concentration in the flume every 15 s. The rate of oxygen consumption ($\dot{M}_{O_2}$) was calculated from the rate of decline of oxygen concentration in the sealed flume. Initial oxygen concentration measurements were taken in an empty flume to determine the rate of oxygen consumption by the oxygen electrode and microorganisms in the flume. These readings were repeated after obtaining data for each fish, and the empty rate of oxygen consumption subtracted from all $\dot{M}_{O_2}$ values. Flume volume was corrected for the volume of water displaced by the fish (calculated from body mass assuming an average density equal to water). The mass specific $\dot{M}_{O_2}= R[(V_{flume}-V_{fish})/M]$ mg kg^{-1} h^{-1}, where R is the measured rate of oxygen decline in the sealed flume in mg l^{-1} h^{-1}, V_{flume} is the flume volume in liters, V_{fish} is the volume displaced by the fish, and M is the body mass of the fish in kg.

Before respirometry experiments the fish were fasted for 48 h to avoid rises in $\dot{M}_{O_2}$ associated with digestion, and were allowed to acclimate to the flume chamber overnight. Resting $\dot{M}_{O_2}$ measurements were taken over a period of 2 h in the early morning, before the usual lights-on period, during which time the fish were left in darkness undisturbed. After 2 h, the lights were switched on and the oxygen probe removed. A submersible pump was used to circulate oxygenated water through the flume chamber to elevate the internal oxygen concentration to pre-measurement levels.

Swimming $\dot{M}_{O_2}$ measurements were taken at the maximum labriform speed. To avoid disturbing the fish and ensure steady swimming, the flume was screened by a dark cloth, except for a small gap to allow observation of the fish. Data were collected for six fish (mass 156.9±12.9 g, length 19.3±0.4 cm, means ± s.e.m.), from which kinematic data had been previously obtained. Fish swam for 40 min at their maximal labriform speed, over which time the oxygen levels in the flume fell by less than 10%. Data were excluded from the analysis if the fish swam consistently within 5 cm of the wall of the working section. A linear regression line was fitted to the last 30 min of the swimming oxygen trace, allowing 10 min for the fish to reach steady state. Segments where the coefficient of determination for the linear regression was less than 0.95 were excluded from the analysis.

Muscle power measurements

The maximum mechanical power output (P_{mech}) of the two largest muscles powering the pectoral fin upstroke (adductor profundus) and downstroke (abductor superficialis) was measured *in vitro* using the work loop technique (Josephson, 1985). This technique measures the mechanical power output of cyclically operating muscles under conditions that mimic those experienced by the muscle *in vivo*.

Fish were anesthetized using buffered MS222 solution at a concentration of 100 mg l^{-1} and placed in a shallow plastic container with aerated anesthetic solution circulating over their gills *via* a submersible pump. The scales were removed from the area overlying the pectoral fin musculature. An L-

shaped skin incision posterior and ventral to the pectoral muscles was made using a scalpel, and the skin covering the muscles lifted away from the underlying tissue by blunt dissection with a surgical probe. This exposed the abductor superficialis, a muscle that originates on the anterolateral cleithrum and inserts *via* tendons onto the fin rays of the pectoral fin. The muscle consists of a number of discrete muscle fascicles, each terminating on a fin ray tendon. A loop of silk suture was passed under the tendon of one fascicle and knotted securely in place. The tendon was cut distal to the knot and the silk thread used to gently elevate the distal end of the muscle fascicle while freeing it from surrounding tissue with a scalpel. The section of the cleithrum around the insertion of the fascicle was cut with bone shears and the intact fascicle removed.

Fascicles were also removed from the adductor profundus, a muscle originating on the medial coracoid and ventromedial cleithrum and, like the abductor superficialis, inserting *via* tendons onto fin rays at the base of the pectoral fin. To obtain a fascicle from this muscle, the entire pectoral girdle was removed allowing access to its medial muscles. The procedure for removing a fascicle was as described for the abductor superficialis.

After removal, the fascicle was immediately placed in a dish of chilled, oxygenated physiological saline at 5°C. The saline contained (in mmol l^{-1}) 109 NaCl, 2.7 KCl, 1.8 $CaCl_2$, 0.47 $MgCl_2$, 2.5 $NaHCO_3$, 5.3 sodium pyruvate and 10.0 Hepes, pH 7.4 at 22°C. If necessary, further muscle tissue was removed so that the diameter of the preparation did not exceed 0.5 mm. The tendon was tied to a stiff, steel hook made from an insect pin and hooked to the lever arm of the muscle lever. The bony origin was clamped to a stainless steel arm, suspending the fascicle vertically between the clamp and the lever arm of an ergometer. The muscle tissue was submerged in a water-jacketed tissue chamber containing oxygenated physiological saline. The temperature of the saline was raised from 5°C to 22°C over a period of 20 min.

Muscle power measurements were made using a muscle ergometer (300B-LR, Aurora Scientific, Ontario, Canada). This controlled muscle length and measured force while the muscle was stimulated electrically (701B, Bi-Phase Current Stimulator, Aurora Scientific). Sinusoidal length change cycles were applied to the fascicle. The frequency, amplitude, and relative timing and duration of stimulation were controlled using Dynamic Muscle Control software (Version 4.0, Solwood Enterprises Inc., Blacksburg, VA, USA). At the fin beat cycle frequency used during maximal labriform swimming (2.8 Hz), muscle strain and relative timing and duration of activation were systematically changed until the maximum power output was measured. The force and position data were captured to a PC *via* a 604A A-to-D interface (Aurora Scientific) and a PCI A-to-D card (PCI-6503, National Instruments, Austin, TX, USA). The net work done per cycle was calculated using Dynamic Muscle Analysis software (Version 3.12, Solwood Enterprises Inc., Blacksburg, VA, USA). After every three work loop measurements a set of control work loops were run to check for any decline in performance by the preparation. The decline between controls was used to correct the power outputs measured during the intervening work loops. Data collection was terminated if power output declined by 10% relative to the initial control.

After completion of the power measurements, the connective tissue and bone were removed from the fascicle, and the muscle tissue weighed. Power outputs were measured from 12 muscle fascicles in total (six from the abductor superficialis and six from the adductor profundus). These were obtained from 11 fish (mass 154.1±8.2 g, length 19.5±0.2 cm, means ± s.e.m.). In one case, a fascicle was successfully removed from both muscles in a single individual. In all other cases, a fascicle was removed from just one muscle in a given individual.

Drag measurements

Drag measurements were made using fish euthanized by anesthetic overdose (400 mg l^{-1} MS222). Data were collected for three fish (mass 155.1±9.9 g, length 19.4±0.4 cm, means ± s.e.m.). In order to reproduce fish body posture during labriform swimming, the fish were laid on a recessed foam surface. The recess ensured that the spinal column was straight. To further maintain this position during the onset of rigor a 20-gauge steel rod was inserted *via* the mouth and through the body tissues parallel and ventral to the spinal column. The fins were arranged in the posture typically maintained during labriform swimming, apart from the pectoral fins, which were positioned along the lateral body surface. Fish were only used for drag analysis if this produced a posture that did not create lateral oscillations when towed behind the force transducer.

Force measurements were made using a Grass FT03 force-displacement transducer (Grass Instruments, West Warwick, RI, USA). The voltage output was amplified by a ETH-200 transducer amplifier (Grass Instruments) and captured to a PC *via* an A-to-D card. The transducer was mounted vertically above the flume with a 9.5 cm extension made from a stiff 1 mm diameter stainless-steel rod projecting into the water. The unloaded force transducer output was recorded at a flume speed of 0.24 m s^{-1}, equivalent to the mean maximal labriform swimming speed. The fish were then attached to the distal end of the rod by a 2 cm length of fishing line and the force output of the transducer recorded at the same speed. The drag force on the fish was determined by subtracting the drag force acting on the transducer extension and thread from the total drag force.

Statistical analyses

All statistical analyses were carried out using SPSS (Version 14.0, SPSS, Chicago, USA). The mechanical properties and stimulus parameters for maximizing power output of the adductor profundus and abductor superficialis were compared using unpaired *t*-tests. A general linear model (GLM) including a fish identifier was used to compare pectoral fin upstroke and downstroke durations at the maximum labriform swimming speed.

Results

Pectoral fin kinematics

Pectoral fin beat frequency increased across the range of labriform swimming speeds. The fin beat frequency at the maximum speed the fish could sustain using their pectoral fins alone was 2.83±0.07 Hz, mean ± s.e.m., N=7, Fig. 1). This cycle

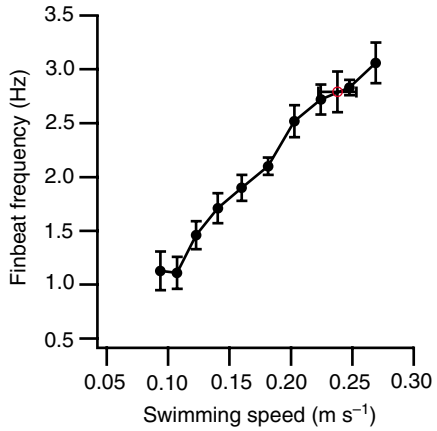

Fig. 1. Pectoral fin beat frequency in relation to swimming speed (closed circles). Red circle, mean fin beat frequency and speed achieved during labriform swimming. *N*=7, mean ± s.e.m.

frequency was used to determine the maximum power available from the abductor superficialis and adductor profundus muscle using the work loop technique. We detected no significant difference between the upstroke and downstroke durations (GLM, F=1.71, P=0.155). In contrast, Drucker and Lauder (Drucker and Lauder, 1999) detected a slight asymmetry in the relative pectoral fin upstroke and downstroke durations at the gait transition (approximately 0.43:0.37 upstroke:downstroke). On the basis of our measurements a sinusoidal strain wave with equal lengthening and shortening durations was used to approximate *in vivo* strain trajectories during *in vitro* muscle power measurements.

Muscle mechanical properties

No significant difference was detected between the maximum power output of the abductor superficialis and adductor profundus (t-test, d.f.=10, P=0.07). The muscle power data were therefore pooled to calculate a mean overall power output from the muscles. The maximum power output of these muscles with a sinusoidal strain trajectory at a cycle frequency of 2.8 Hz was 16.5±2.4 W kg^{-1} (mean ± s.e.m., *N*=12, 6 abductor superficialis and 6 adductor profundus, Fig. 2). Isometric properties of the two muscles and the strain and stimulus parameters used to obtain maximum power output at 2.8 Hz strain cycle frequency are shown in Table 1. Maximum isometric stress is similar to that previously measured in the pectoral musculature of a related species, the pumpkinseed sunfish *Lepomis gibbosus* (Luiker and Stevens, 1992; Luiker and Stevens, 1993).

There are two potential sources of error in our approach for determining the mechanical power required for maximal labriform swimming in this species. First, that the muscles may not be producing their maximum power output *in vivo* and that our measurements of maximum power *in vitro* are not representative of performance during maximal labriform swimming, and second, that we have not accounted for the power available from the total pectoral girdle muscle mass.

There are a number of lines of evidence suggesting that peak power output is reached during maximal labriform swimming. First, the pectoral fin beat frequency used just prior to the gait transition maximizes pectoral muscle mechanical power output in this species (Kendall et al., in press). Second, the momentum transferred to the wake by the beating pectoral fins is maximized at the gait transition in this species, and shows no capacity for increased power transfer to the wake above the transition speed (Drucker and Lauder, 1999). Third, the intensity of EMGs in the abductor superficialis muscle does not change across the gait transition, showing that there is no capacity for additional recruitment of motor units and increased force production in this muscle (E.A.J., unpublished data). It is therefore likely that the pectoral girdle muscles are operating at, or near, their maximum power output at the gait transition, and our *in vitro* measurements are a reasonable measure of *in vivo* performance during maximal labriform swimming. In this regard the bluegill pectoralis muscles may be similar to muscles in other systems that demand high mechanical powers, where the relationship between strain trajectory and activation recorded *in vivo* has been shown *in vitro* to correspond to that which is optimal for maximizing power output (Askew and Marsh, 2001; Girgenrath and Marsh, 1999).

The pectoral girdle muscles were 1.28±0.08% (mean ± s.e.m., *N*=5, Table 2) of the total body mass of the fish. During maximal labriform swimming in this species, thrust is generated during both adduction and abduction (Drucker and Lauder, 1999; Drucker and Lauder, 2000). Muscle activity and kinematic data from other perciform species suggest that the abductors superficialis and profundus are the major sources of mechanical power during fin abduction (Drucker and Jensen, 1997; Westneat and Walker, 1997; Lauder et al., 2006). The anatomical arrangement of, and the relationship between, activity and fin movement for these muscles suggests that they are active while shortening, and therefore doing positive work on the fin and surrounding water to generate lift and thrust. The

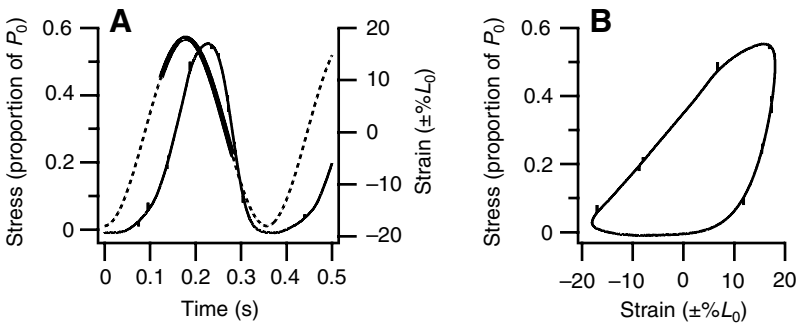

Fig. 2. Mechanical performance of a bluegill sunfish abductor superficialis muscle fascicle *in vivo*. (A) Fascicle stress production during an applied sinusoidal length change. The broken trace shows fascicle length, and the unbroken line fascicle stress. The bold line shows the timing of the applied stimulus. (B) Work loop obtained from the data in A by plotting fascicle stress against fascicle length. The area enclosed by the loop indicates the net work done by the fascicle. Stresses are shown relative to maximal isometric tetanic stress, P_0, and strains relative to L_0, the length at which maximum isometric tetanic stress was measured.

Table 1. *Mechanical properties of the adductor superficialis and abductor profundus muscles of bluegill sunfish*

Mechanical property	Muscle		*P* (*t*-test)
	Abductor superficialis	Adductor profundus	
Twitch rise time (ms)	42.8±6.5 (6)	56.3±7.2	0.19
Time from peak twitch force to 90% relaxation (ms)	121.5±21.4	138.3±27.8	0.64
Twitch:tetanus ratio	0.39±0.01	0.40±0.03	0.76
Maximum isometric tetanic stress (kN m^{-2})	179±6	183±7	0.35
Optimum sinusoidal strain ± proportion of L_0.	0.18±0.01	0.18±0.02	0.58
Optimum stimulus duty cycle (proportion of cycle duration)	0.43±0.01	0.41±0.01	0.22
Optimum stimulus onset phase (proportion of cycle before maximum length)	0.11±0.01	0.11±0.01	0.63

Values are means ± s.e.m., *N*=6. *P*-values are from an unpaired *t*-test comparing the mean values for each muscle, d.f.=10.
L_0, muscle length at which maximum isometric, tetanic stress was produced.

role of the arrector ventralis is less clear. This muscle inserts on the fin ray and could potentially power abduction. However, its activity largely coincides with the reversal between adduction and abduction (Drucker and Jensen, 1997; Westneat and Walker, 1997). It may therefore play a role in decelerating the fin at the end of adduction, as well as powering abduction.

Activity in the adductor profundus coincides with fin adduction, and like the large abductors, its anatomical arrangement and relationship between activity and fin movement suggests activity during shortening, and therefore the production of positive work (Drucker and Jensen, 1997; Westneat and Walker, 1997). The anatomy and activity patterns of the arrector dorsalis also suggest a role in power production during adduction (Westneat and Walker, 1997). The contribution of the abductor superficialis to power production during abduction is less certain. The posterior, superficial portion of the muscle inserts on the posterior fin rays and its fascicles run perpendicular to the fascicles of the abductor profundus. This part of the muscle is likely to be involved in controlling the orientation of the fin, rather than powering abduction. The ventral portion of the abductor superficialis inserts on the anterior fin rays and has fascicles lying parallel to those of the abductor profundus. This part of the muscle could do positive work when active during abduction, but is also active during late adduction and pauses between fin beats (Drucker and Jensen, 1997).

Table 2. *Masses of the major bluegill sunfish pectoral girdle muscles*

Muscle	Mass (g)	Mass as % of body mass
Lateral		
Abductor superficialis*	**0.444±0.026**	**0.32±0.02**
Abductor profundus*	0.250±0.022	0.19±0.03
Arrector ventralis	0.200±0.025	0.15±0.02
Medial		
Adductor superficialis, posterior dorsal	0.176±0.02	0.13±0.02
Adductor superficialis, ventral	0.140±0.039	0.07±0.01
Adductor profundus*	**0.464±0.073**	**0.34±0.01**
Arrector dorsalis*	0.064±0.013	0.05±0.01
Adductor radialis	0.070±0.017	0.05±0.01
Total muscle mass	1.816±0.160	1.28±0.08
Total body mass	141.4±12.6	

Values are means ± s.e.m. (*N*=5). Muscle power measurements were made for the two muscles shown in bold type.

*Muscles whose likely primary role is the production of positive power during fin abduction and adduction (Drucker and Jensen, 1997; Westneat and Walker, 1997; Lauder et al., 2006).

In view of these uncertainties regarding muscle function, a range of estimates for the mechanical power, P_{mech}, supplied by the pectoral girdle muscles during maximal labriform swimming will be used to calculate efficiency. If the entire pectoral girdle musculature (Table 2) supplied the maximum measured power output, the available mechanical power output would be 0.21 W kg^{-1} body mass. Given the available data concerning muscle recruitment (Drucker and Jensen, 1997; Westneat and Walker, 1997) this is unlikely to occur, but it will allow us to set an upper limit to our efficiency estimates. Based on the anatomy of the muscles and recruitment data from other labriform swimmers (Drucker and Jensen, 1997; Westneat and Walker, 1997) the mass of muscle likely supplying power in this species is 0.92±0.04% (mean ± s.e.m., *N*=5) of the total body mass of the fish. This is the total mass of the adductors superficialis and profundus, the abductor profundus and arrector ventralis. The two muscles for which we have power output measurements constitute 75% of the total mass of this group. If the mass-specific power output of the smaller muscles is assumed to be equal to that of the abductor superficialis and adductor profundus, then this mass of power producing muscle could supply 0.15 W kg^{-1} body mass. This P_{mech} range 0.15–0.21 W kg^{-1} body mass will be used in subsequent efficiency calculations.

Metabolic rate

Fig. 3 shows representative flume oxygen content traces at rest and during labriform swimming. Standard metabolic rate (SMR) was 98.2±15.5 mg O_2 kg^{-1} h^{-1} (mean ± s.e.m., *N*=6). Swimming $\dot{M}_{O_2}$ at the maximum labriform speed was 250.4±21 mg O_2 kg^{-1} h^{-1} (mean ± s.e.m., *N*=6). Oxygen consumption was converted to energy units using an oxycaloric value of 13.54 J mg^{-1} (Brett and Groves, 1979). The total metabolic power input during maximal labriform swimming, P_{total}, was 0.95 W kg^{-1} body mass. The net metabolic requirements of swimming were estimated by subtracting

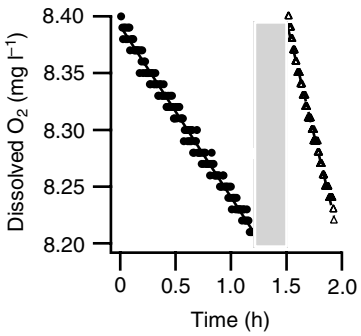

Fig. 3. Changes in dissolved oxygen content within the flume created by a 150 g bluegill sunfish at rest (closed circles), and swimming at 1.2 fish lengths s^{-1} (open triangles). The grey bar represents a period when measurements were suspended to allow flushing of the flume chamber with oxygen-saturated water.

resting $\dot{M}_{O_2}$ from total swimming $\dot{M}_{O_2}$. This subtracts out the energy requirements of maintenance processes not directly associated with swimming and provides an estimate of the energy expenditure of the active pectoral girdle muscles. The mean net power input for maximal labriform swimming, P_{muscle}, was 0.57 W kg^{-1} body mass.

Body drag

The drag force measured at the maximum labriform swimming speed (0.24 m s^{-1}) was 18.3±1.6 mN (mean ± s.e.m., N=4). The mean power required to overcome body drag (P_{drag}) for the fish used in the drag measurements was 0.028 W kg^{-1} body mass.

Discussion

Our primary aims were to estimate the efficiency of labriform swimming in bluegill sunfish and to determine whether this gait was more efficient than undulatory swimming. Overall efficiency ($\eta_{gross}=P_{mech}/P_{total}$) for bluegill swimming at their maximum labriform speed fell in the range 0.16–0.22 for the lower and upper estimates of P_{mech}, respectively. As the present study is the first integrated attempt to measure both the power outputs and inputs in any fish species, few data are available for comparison. There are data available from separate studies of yellowfin tuna (*Thunnus albacares*) and Pacific bonito (*Sarda chiliensis*) swimming metabolism (Dewar and Graham, 1994; Sepulveda et al., 2003) and *in vitro* muscle power output (Altringham and Block, 1997), where both types of data were obtained at the same temperature, allowing overall efficiency to be estimated for these species. Swimming at a tail beat frequency of 3 Hz, bonito $\dot{M}_{O_2}$ was equivalent to a power input of 3.6 W kg^{-1} body mass at 18°C (Sepulveda et al., 2003). The muscle mass-specific power output of bonito slow muscle at this cycle frequency and temperature was approximately 8.8 W kg^{-1} (Altringham and Block, 1997); no data are available for muscle power at 18°C, but power–frequency curves constructed at 15°C and 20°C coincide at a 3 Hz cycle frequency. Slow muscle makes up 4.51% of the bonito body mass (Graham et al., 1983), so the body mass-specific mechanical power output potentially available to the 1.191 kg bonito in the energetics study was approximately 0.40 W kg^{-1}. Based on these data, the overall efficiency of a bonito is therefore 0.11. A similar calculation for yellowfin tuna [power input of 4.11 W kg^{-1} body mass at 4 Hz tailbeat frequency (Dewar and Graham, 1994); muscle mass specific power output 7.5 W kg^{-1} at 4 Hz (Altringham and Block, 1997); slow muscle mass 6.51% of body mass (Graham et al., 1983); body mass-specific power output 0.49 W kg^{-1} in a 2.17 kg fish at 25°C] yields an overall efficiency of 0.12.

These efficiency estimates are lower than those obtained for labriform swimming in bluegill (0.16–0.22). Based on the available data it appears that labriform swimming in bluegill may be more efficient overall than undulatory swimming in the bonito and yellowfin tuna. There are, however, a number of reasons why these estimates of undulatory swimming efficiency should be viewed with caution. First, the mass specific power output data are from single muscle preparations, so they may not be representative of muscle performance in the fish from which metabolic data were obtained. Second, the muscle power measurements are point measures of performance. Muscle properties are likely to vary with axial location (Altringham and Ellerby, 1999), and these point measures may not be indicative of the properties of the whole muscle mass. Third, the strains applied to the muscle preparations were not based on *in vivo* strains as they preceded direct *in vivo* measurements by sonomicrometry (Ellerby et al., 2000; Katz et al., 2001), and the measured powers may only approximate *in vivo* performance. Finally, the muscle power data were obtained from supra-maximally stimulated muscle. The mechanical power data are therefore most meaningfully compared to maximal metabolic rate data where the aerobic capacity of the animal, and presumably its capacity to generate power from its aerobic muscles, have been reached. It is not clear that the metabolic rate data are maximal; therefore comparing maximal muscle powers to sub-maximal metabolism may have overestimated efficiency. In view of these uncertainties, further data concerning muscle performance and metabolism in both labriform and undulatory swimmers are required before this difference in overall efficiencies can be confirmed. Muscle performance and metabolic cost data are required from integrated studies of undulatory swimming. Additionally, direct muscle strain data for the pectoral girdle muscles of labriform swimmers are required to precisely determine the mechanical functions of all the muscles inserting on the pectoral fins.

While data concerning swimming efficiency are scarce, several studies have quantified changes in swimming costs and economy within individual species that transition from labriform or ballistiform swimming at low speeds to undulatory swimming at high speeds (Brett and Sutherland, 1965; Parsons and Sylvester, 1992; Korsmeyer et al., 2002). These do not show a consistent pattern concerning the relative economy of these gaits measured as cost of transport (COT, the energy required to travel a unit distance). In the pumpkinseed sunfish *Lepomis gibbosus* (Brett and Sutherland, 1965) and triggerfish *Rhinecanthus aculeatus* (Korsmeyer et al., 2002) there was no clear change in COT on the transition from paired-fin based, to undulatory swimming. An increase in the slope of the metabolic rate *vs* speed relationship in triggerfish was detected (Korsmeyer et al., 2002), indicating an increase in incremental cost on switching to undulatory swimming, but the overall COT range measured for each gait was similar. In contrast, the

transition from labriform to undulatory swimming in the white crappie *Pomoxis annularis* (Parsons and Sylvester, 1992) resulted in a clear decrease in COT. Unfortunately, without data concerning muscle power output, the relative efficiency of different gaits within these species cannot be determined.

The only other locomotor system for which estimates of power outputs and inputs are available is avian flight. This system is similar to labriform swimming in that the majority of the active muscle mass is concerned with generating power to accelerate a fluid. Estimates of avian whole organism efficiency based on aerodynamic estimates of mechanical power range from 0.12 to 0.2 (Rayner, 1999), comparable to the estimates of whole organism efficiency we have obtained for bluegill. It may be that this overall efficiency range is common to locomotor systems in which the acceleration of a fluid is the main function of the locomotory muscles.

Muscle efficiency estimates ($\eta_{muscle}=P_{mech}/P_{muscle}$) for bluegill swimming at their maximum labriform speed fell into the range of 0.37 to 0.26, based on the upper and lower estimates of available mechanical power, respectively. The latter figure is probably more realistic as the entire pectoral girdle muscle mass is unlikely to be supplying mechanical power. This approach is analogous to that used to determine efficiency during human cycle ergometer exercise, where resting metabolic costs are subtracted from total metabolism to estimate energy expenditure by the active muscles. For this activity, muscle efficiency estimates range from 0.18 to 0.23 (Gaesser and Brooks, 1975; Luthanan et al., 1987). Our estimates also fall within the range obtained for vertebrate muscle *in vitro* (reviewed by Smith et al., 2005). The efficiency of skeletal muscle crossbridges in transducing chemical to mechanical energy is 0.36–0.38 (Reggiani et al., 1997; He et al., 1999). This represents an upper limit for possible whole muscle efficiency. Given this constraint, and the similar efficiency values measured in other muscles, our efficiency estimate for bluegill pectoralis girdle muscles seems reasonable, supporting our approach as a means of estimating *in vivo* mechanical power in this system.

A portion of the total mechanical power (P_{drag}) is used to generate thrust to overcome body drag. P_{drag} is the product of the drag force acting on the fish's body and swimming velocity. Based on our measured value for P_{drag} (0.028 W kg^{-1}), and the range of mechanical power output estimates, propeller efficiency (P_{drag}/P_{mech}) fell in the range 0.15–0.20. This propeller efficiency range is lower than that previously calculated for this species using flow visualization as a means of measuring mechanical power transferred to the wake (0.39) (Drucker and Lauder, 1999). This may in part be due to differences in the methods used to measure body drag between the two studies. Initial attempts to measure drag in anesthetized fish in a similar way to Drucker and Lauder (Drucker and Lauder, 1999) were abandoned due to 'flagging' of the body and fins. In the absence of muscle tone, oscillations of the body axis and fins increased the drag acting on fish. By measuring drag on dead fish that had gone into rigor these effects were reduced. This may account for our measured drag powers being a lower proportion of total mechanical power. An additional factor is that propeller efficiency in bluegill may change with swimming speed. Our estimates were obtained at 1.2 L s^{-1} relative to 0.5 L s^{-1} in the previous study (Drucker and Lauder, 1999). Power not accounted for as P_{thrust} is used to impart lateral momentum to the water for stabilization (Drucker and Lauder, 1999), overcome drag on the pectoral fins themselves, and overcome energy losses in the linkages between the muscles and fin rays.

The potential efficiency and economy of swimming fish is a major factor in the use of biological designs to inspire swimming robotic vehicles (Fish, 2006; Triantafyllou et al., 2000). Given the interest in developing biomimetic autonomous underwater vehicles (AUVs), it is important to place our performance data in context with that of existing AUVs and other fish species. For AUVs, economy may be more important than efficiency *per se*. In battery-powered vehicles minimizing the rate of energy expenditure extends operational duration and range. COT is therefore an important basis for comparison. In the present study, bluegill had a COT of 3.9 J kg^{-1} m^{-1} during maximal labriform swimming. This is similar to the COT of robot Madeleine, a flapping foil powered, biologically inspired, robot [4.0 J kg^{-1} m^{-1} (Long et al., 2006)]. Fish that swim by undulating their body axes have a wide range of COT values, from 0.4 to 5 J kg^{-1} (Webb, 1971; Brett, 1973; Dewar and Graham, 1994; Reidy et al., 2000; van Ginneken et al., 2005; Claireaux et al., 2006). Propeller-driven systems appear to be more economical than most swimming fish. The COT of a typical propeller-driven AUV is approximately 0.4 J kg^{-1} m^{-1} (Allen et al., 1997). Fish and robots powered by flapping fins appear to fall at the upper end of the COT range exhibited by swimmers. So while labriform swimmers may be efficient in terms of the ratio of power input:power output during swimming, they may not be as economical as undulatory swimmers in turning that power output into forward velocity. At present, the main advantage in pursuing a biomimetic approach to AUV design may be improved maneuverability relative to propeller driven designs (Bandyopadhyay et al., 1997), rather than improved efficiency or economy.

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