Mechanical and energetic factors underlying gait transitions in bluegill sunfish (*Lepomis macrochirus*)

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Summary

As their swimming speed increased, bluegill sunfish (*Lepomis macrochirus*) switched from pectoral-fin-powered labriform swimming to undulations of the body axis. This gait transition occurred at a mean swimming speed of 0.24 ± 0.01 m s^{-1} and a pectoral fin beat frequency of 2.79 ± 0.11 Hz (mean ± s.e.m., $N=6$). The power output available from the main upstroke (adductor profundus) and downstroke (abductor superficialis) muscles, measured using the work-loop technique was maximal at the gait transition point. The cost of transport, measured by respirometry, increased as the fish switched from labriform to undulatory swimming. Our data show that bluegill changed gait as swimming speed increased to recruit additional muscle mass, rather than to maximize economy, as is the case for many terrestrial animals.

Key words: swimming, power, metabolic rate, cost of transport.

Introduction

Speed-related changes in the basic patterns of movement are a feature of locomotion in many animals. These gait changes are typically associated with mechanical and/or energetic factors. For example, during terrestrial locomotion, gaits may be chosen to minimize locomotor costs at a given speed or to limit mechanical stresses (Alexander, 1989). The underlying reasons for gait changes in swimming animals are less well understood, although it is likely that similar factors are important.

Bluegill sunfish (*Lepomis macrochirus*) swim in the labriform mode at low speeds, generating lift and thrust by beating their pectoral fins (Gibb et al., 1994; Drucker and Lauder, 2000; Lauder et al., 2007; Jones et al., 2007). As swimming speed increases, they change gait from labriform swimming to combined use of their pectoral fins and undulations of the body axis. Pectoral fin movements are powered and controlled by a number of pectoral girdle muscles. Undulations of the body axis are powered by the segmented myotomal musculature. It is unclear whether mechanical or energetic factors drive this gait transition. The switch in swimming style may be driven by a need to recruit additional muscle mass as speed increases, or, at higher speeds, undulatory swimming may be more economical than the labriform gait.

The energetic costs of swimming have been determined in a number of similar species that change gait from a median paired fin (MPF) gait at low speeds to an undulatory gait at higher speeds (Brett and Sutherland, 1965; Parsons and Sylvester, 1992; Korsmeyer et al., 2002). For any given species, however, the factors driving gait changes can only be fully understood if both the metabolic power inputs and the available muscle power have been quantified across the gait transition. By taking an integrated approach to studying the gait change in bluegill sunfish, we have examined both the energetic and mechanical factors underlying a fish gait change for the first time.

Using respirometry to measure swimming costs, and *in vitro* measurements of muscle power output, we have determined the energetic consequences of changing gait and the limits to mechanical power output by the pectoral girdle muscles that power labriform swimming. This has enabled us to test two hypotheses concerning the factors underlying the bluegill gait change. First, that, as swimming speed increases, the power available from the pectoral girdle muscles can no longer meet the increasing power requirements of swimming, necessitating the recruitment of the myotomal musculature. In order to test this hypothesis we measured the mechanical power available from the two largest pectoral girdle muscles that power the pectoral fin upstroke and downstroke across a range of pectoral fin beat frequencies spanning the gait transition. The absence of an increase in the available pectoral mechanical power across the gait transition would support the hypothesis that power constraints drive the gait change. Second, we hypothesized that at the upper end of the labriform speed range, this swimming mode becomes uneconomical relative to undulatory swimming, and that a change in swimming style maximizes swimming economy. In order to test this, we used respirometry to measure the metabolic costs of swimming across the gait transition. A decrease in the cost of transport on switching to undulatory swimming would show that energetic factors drive the gait change.

Materials and methods

Experimental 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 earthworms twice a week. All procedures were approved by the Institutional Animal Care and Use Committee.

Swimming flume

Swimming experiments were carried out 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 comprised an inner chamber 88.6 liters in volume with a working section of $20\times20\times70$ cm and an outer tank that buffered temperature changes and served as a reservoir of oxygenated water. Water temperature was maintained at 22°C for all experiments.

Kinematic analysis

Video sequences of seven fish [mass 134.7±13.4 g; length (L) 19.5±0.4 cm; mean ± s.e.m.] were recorded using a Sony HDR HC-3 camcorder at a frame rate of 120 Hz swimming at speeds ranging from 0.10 to 0.27 m s^{-1}. 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 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 were subsequently subtracted from all fish $\dot{M}_{O_2}$ 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). 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. Standard metabolic rate (SMR) measurements were taken over 2 h in the early morning, before the usual lights-on period, during which time the fish were left undisturbed in darkness. During these periods the fish typically remained motionless, resting on the bottom of the working section. 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 made at a range of speeds spanning the labriform–undulatory transition. To avoid disturbing the fish and ensure steady swimming, the flume was screened by a dark cloth with a small gap to allow observation of the fish. Data were collected for nine fish (M=127.9±4.2 g, L=19.3±0.4 cm). Fish swam for up to 40 min at each 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 at each speed. Segments where the coefficient of determination was less than 0.95 were excluded from the analysis. Measurements were taken at three to four speeds each day with flushing to replenish oxygen levels between each speed. The fish were then left to recover overnight before further measurements were taken.

Muscle power measurements

Fish were anesthetized using buffered MS-222 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. These two muscles were selected as they are the single largest adductor and abductor muscles, constituting about half of the total pectoral girdle muscle mass in this species (Jones et al., 2007). Other muscles, such as the abductor profundus, adductor superficialis and arrectors are also likely to contribute to power production (Drucker and Jensen, 1997; Westneat and Walker, 1997; Lauder et al., 2007).

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 (see below). The muscle tissue was submerged in a water-jacketed tissue chamber containing oxygenated physiological saline. The temperature of the saline was raised from 5 to 22°C over a period of 20 min.

Muscle power measurements were made using the work-loop technique (Josephson, 1985). Experiments were carried out 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). The aim of these experiments was to determine the maximum power available from the pectoral girdle muscles during labriform swimming. Sinusoidal length change cycles approximating the *in vivo* muscle strain 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). Sinusoidal strain trajectories were applied to the fascicles at a range of cycle frequencies spanning the *in vivo* fin beat frequency range. For each frequency, strain amplitude and the relative timing and duration of activation were systematically changed until the maximum power output was measured. The force and position data were captured on a PC *via* a 604A analog-to-digital interface (Aurora Scientific) and a PCI analog-to-digital 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.). 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%. 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 (six from the abductor superficialis and six from the adductor profundus) from 12 fish (M=134.1±9.1 g, L=19.4±0.2 cm), one fascicle being removed from each fish.

Statistical analysis

A general linear model (GLM) in the statistics package SPSS (version 14.0; SPSS Inc., Chicago, IL, USA) was used to test for changes in muscle power output with strain cycle frequency. A fish identifier was included as a random factor in the model to quantify inter-individual variability. A GLM was also used to test for speed- and gait-related changes in swimming power output and cost of transport. A fish identifier was also included as a random factor in this model. If the GLM detected significant changes in a variable in relation to cycle frequency or swimming speed, Tukey's HSD *post-hoc* test was used to make pair-wise comparisons between mean values.

Results
Swimming kinematics

Pectoral fin beat frequency increased with swimming speed (Fig. 1). The upper limit for labriform swimming was a mean swimming speed of 0.24±0.01 m s^{-1}, at which the pectoral fin
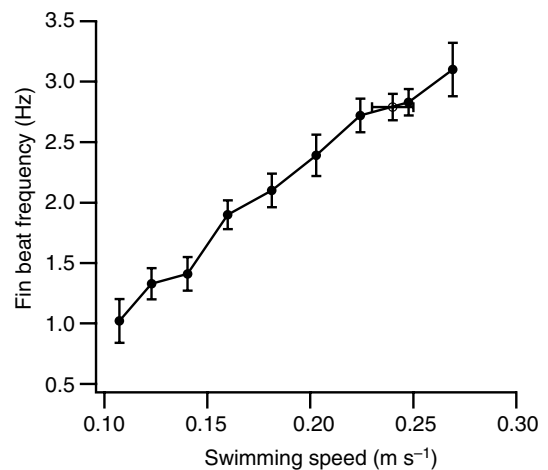

Fig. 1. Relationship between pectoral fin beat frequency and swimming speed in bluegill sunfish (filled symbols). The open symbol shows the mean pectoral fin beat frequency and speed during maximal labriform swimming. Values are means ± s.e.m. (N=6).

beat frequency was 2.79±0.11 Hz (mean ± s.e.m., N=6). This was similar to the maximum labriform fin beat frequency (2.83 Hz) previously measured for bluegill in this flume at the same temperature (Jones et al., 2007). Despite the onset of body undulations, the mean pectoral fin beat frequency increased slightly beyond the gait transition point. This upward trend does not continue at higher speeds. Pectoral fin beat frequency plateaus at approximately the frequency used at the gait transition (A. Jong and D.J.E., unpublished data).

Muscle power outputs

The maximal power output from both the adductor profundus and abductor superficialis changed significantly with cycle frequency (GLM, adductor profundus, F=8.3, P<0.001, N=12; abductor superficialis, F=16.8, P<0.001, N=12). The power output initially increased with cycle frequency in both muscles but reached a plateau spanning the gait transition at higher frequencies (Fig. 2). Stimulus parameters for maximizing fascicle power output at each cycle frequency are shown in Table 1.

Energy metabolism and cost of transport

Standard metabolic rate (SMR) was 0.34±0.02 W kg^{-1} (mean ± s.e.m., N=9). The metabolic power requirements of swimming increased with swimming speed during both labriform and undulatory swimming (Fig. 3). There were significant changes in total metabolic power (P_{gross}) during both labriform (GLM; F=14.8, P<0.001, N=44) and undulatory swimming (GLM; F=36.5, P<0.001, N=42). There were also significant changes in net metabolic power (P_{net} = total metabolic power minus SMR) during both labriform (GLM; F=14.2, P<0.001, N=44) and undulatory swimming (GLM; F=36.3, P<0.001, N=42).

Cost of transport, COT=(P/U) J kg^{-1} m^{-1}, where P is the metabolic power input in W kg^{-1} and U is the swimming speed in m s^{-1}. Speed-related changes in COT for both labriform and undulatory swimming are shown in Fig. 4. During labriform swimming, the gross cost of transport (COT_{gross}; calculated from
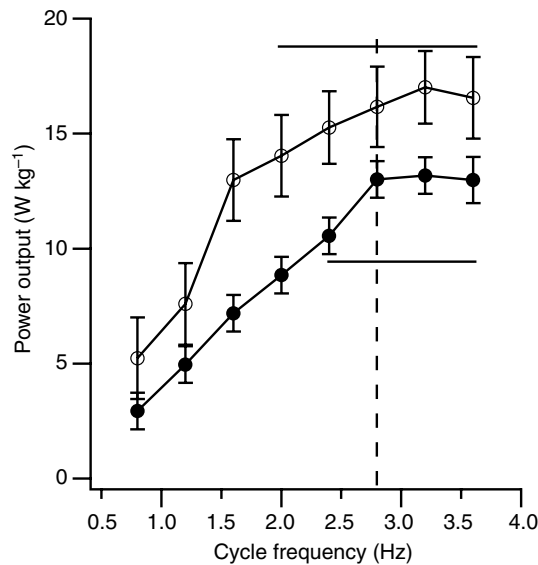
Fig. 2. Relationship between maximal pectoral girdle muscle power outputs and strain cycle frequency. Open symbols, adductor profundus; filled symbols, abductor superficialis. Values are means ± s.e.m. ($N=6$). The vertical broken line shows the cycle frequency used during maximal labriform swimming. The horizontal lines adjacent to each data set show the homogenous subsets of muscle power output values that span the gait transition (Tukey's HSD $P \geqslant 0.05$).

Table 1. *Stimulus parameters for obtaining maximum power output from bluegill sunfish abductor superficialis and adductor profundus muscles*

Cycle frequency (Hz)	Stimulation onset (proportion of strain cycle after L_0)	Stimulation duration (proportion of strain cycle duration)
0.8	0.21±0.02	0.46±0.03
1.2	0.18±0.01	0.45±0.02
1.6	0.15±0.02	0.45±0.02
2.0	0.14±0.02	0.43±0.02
2.4	0.13±0.01	0.42±0.02
2.8	0.11±0.02	0.42±0.01
3.2	0.11±0.02	0.40±0.02
3.6	0.10±0.01	0.40±0.03

Data are means ± s.e.m. ($N=12$). No significant difference was detected between the optimum stimulus durations and onsets for maximizing power output in the two muscles (GLM, $P>0.05$), so pooled mean data are presented. Stimulus onset is relative to the start of the strain cycle at resting length L_0, such that peak and minimum strain occur at 0.25 and 0.75, respectively.

P_{gross}) decreased significantly across the labriform speed range (GLM; $F=17.4$, $P<0.001$, $N=44$). By contrast, the net cost of transport (COT_{net}; calculated from P_{net}) did not change significantly with speed during labriform swimming (GLM; $F=2.2$, $P=0.094$, $N=44$). During undulatory swimming, both COT_{gross} and COT_{net} increased significantly with swimming speed (GLM; COT_{gross}, $F=12.6$, $P<0.001$, $N=42$; COT_{net}, $F=15.5$, $P<0.001$, $N=42$). We detected significant differences in both COT_{gross} (GLM; $F=5.9$, $P=0.02$, $N=86$) and COT_{net} (GLM;
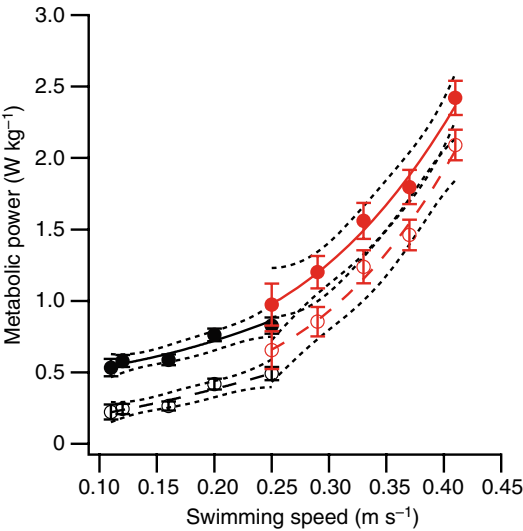

Fig. 3. Relationship between the metabolic power requirements of swimming and swimming speed for bluegill sunfish. Filled symbols, total metabolic power, P_{gross}; open symbols, P_{net} (total metabolic power minus standard metabolic rate); black symbols, labriform swimming; red symbols, undulatory swimming. Data are fitted with the following power relationships: labriform $P_{\text{gross}}=0.47+6.45U^{2.02}$; undulatory $P_{\text{gross}}=0.61+29.6U^{3.17}$; labriform $P_{\text{net}}=0.12+3.29U^{1.57}$; undulatory $P_{\text{net}}=0.35+37.4U^{3.47}$, where U is swimming speed in m s^{-1}. The broken lines show 95% confidence intervals for the fitted relationships. Values are means ± s.e.m., $N=9$, except where the speed ranges for labriform and undulatory swimming overlap at 0.25 m s^{-1}, where $N=4$ for labriform swimming and $N=5$ for undulatory swimming.

$F=4.5$, $P=0.03$, $N=86$) in relation to changing gait. However, at the transition point of 0.25 m s^{-1}, there was no clear change in COT with the gait transition.

Discussion

The metabolic power expended during swimming increases with swimming speed during both labriform and undulatory swimming and across the gait transition between the two modes (Fig. 2). The power available from the adductor profundus and abductor superficialis muscles reaches a maximum at the gait transition and, even though pectoral fin beat frequency initially increases with the transition to undulatory swimming, the pectoralis muscles cannot supply additional power (Fig. 3). This strongly suggests that a major factor in the transition from labriform to undulatory swimming is a need to recruit additional myotomal muscle mass to meet the increasing power requirements of high-speed swimming.

Is economy also a factor driving this gait transition? In many terrestrial animals, gaits are selected to minimize cost within a particular range of speeds (Hoyt and Taylor, 1981; Alexander, 1989). Overall, the cost of transport is significantly higher during undulatory swimming than during low-speed labriform swimming (Fig. 4). Where there is overlap in the speed range within the two gaits, however, there is no clear difference in COT between the gaits (Fig. 4). The absence of a decrease in COT on transitioning to undulatory swimming indicates that the gait shift is not a means of maximizing swimming economy. Energetic factors are therefore not important in driving the gait
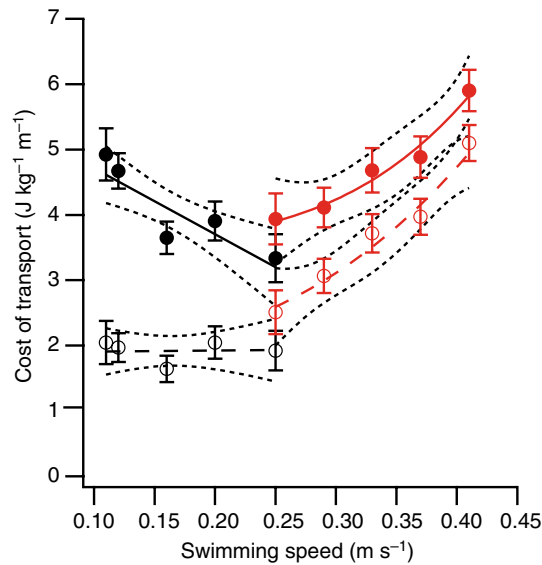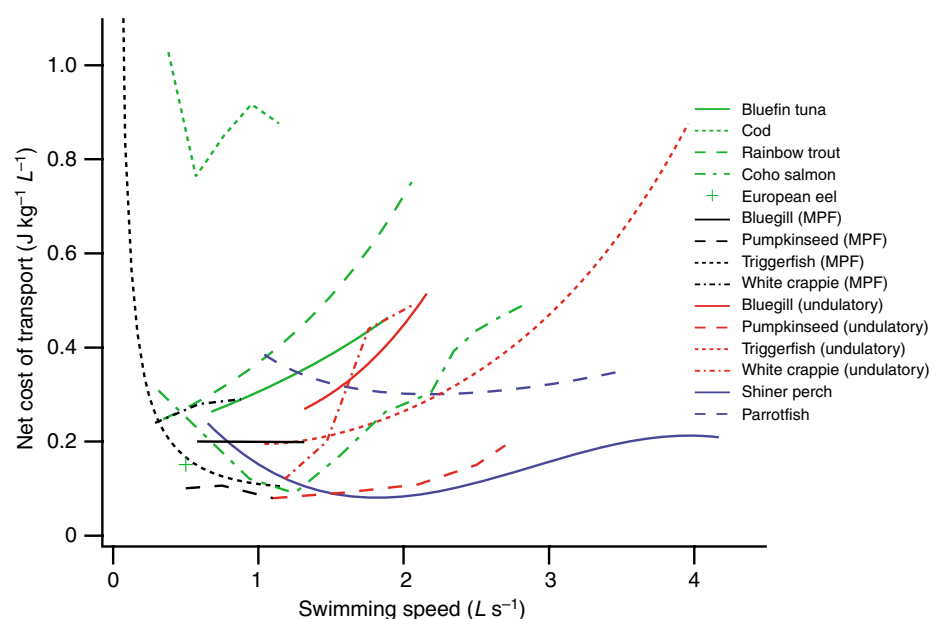
Fig. 4. Relationship between the cost of transport (*COT*) and swimming speed for bluegill sunfish. Filled symbols, COT_{gross}; open symbols, COT_{net}; black symbols, labriform swimming; red symbols, undulatory swimming. Data are fitted with the following relationships: labriform $COT_{gross}=5.73-10.1U$; undulatory $COT_{gross}=3.59+76.3U^{3.96}$; labriform $COT_{net}=1.9+0.13U$; undulatory $COT_{net}=1.83+39.2U^{2.84}$. The broken lines show 95% confidence intervals for the fitted relationships. Values are means ± s.e.m., *N*=9, except where the speed ranges for labriform and undulatory swimming overlap at 0.25 m s^{-1}, where *N*=4 for labriform swimming and *N*=5 for undulatory swimming.

transition in this species. Overall, it is clear that the labriform–undulatory gait change in bluegill sunfish is driven by a need to supply additional mechanical power rather than to minimize swimming costs.

This may also be the case in some other gait-transitioning species for which data are available. In the pumpkinseed sunfish (*Lepomis gibbosus*) (Brett and Sutherland, 1965) and triggerfish (*Rhinecanthus aculeatus*) (Korsmeyer et al., 2002), the pattern is similar to that measured in bluegill in that there is no clear change in *COT* at the gait transition speed, suggesting that limits to muscle power also drive the gait changes in these species. This pattern is not common to all species for which data are available. By contrast, the white crappie (*Pomoxis annularis*) (Parsons and Sylvester, 1992) shows a clear decrease in *COT* on switching from labriform to undulatory swimming. This does not rule out mechanical factors, but maximizing economy appears to be an important factor driving gait change in this particular species.

How do bluegill compare to other fish species in terms of swimming economy? Fig. 5 shows the relationships of net *COT* to swimming speed in a number of MPF (one species for which data are shown uses ballistiform swimming, flapping of dorsal and anal fins while maintaining a rigid body axis, rather than labriform swimming at low speeds) and undulatory swimmers. Comparing the economy of different swimming styles is complicated by a number of factors. Mass-specific metabolic rate in fish scales with body mass$^{-0.25}$ (Schmidt-Nielsen, 1972). This prevents a direct comparison of swimming styles based on metabolic cost, particularly as many MPF swimmers are relatively small, while specialized undulatory cruisers like the thunniform scombrids are several orders of magnitude larger. To allow a fair comparison between species of different body masses, the data sets have been transformed using this relationship so that they represent the predicted metabolic power and *COT* for a standard 1 kg fish such that the standardized cost of transport, $COT_{stand}=COT_{meas}(1/M)^{-0.25}$, where COT_{meas} is the measured *COT* value and *M* is the body mass in kg. The data are also presented in relation to body-length-specific speeds, and *COT* is expressed as the energy required to travel a unit body

Fig. 5. Fish cost of transport (*COT*) in relation to swimming speed. Green traces: specialist undulatory swimmers; bluefin tuna, *Thunnus orientalis* (Blank et al., 2007); cod, *Gadus morhua* (Reidy et al., 1999); rainbow trout, *Oncorhynchus mykiss* (Webb, 1971); coho salmon, *Oncoryhnchus tshchawystcha* (Gallaugher et al., 2001); European eel, *Anguilla anguilla* (van Ginneken et al., 2005). Black traces: species that utilize median paired fin (MPF) swimming only at low speeds, switching to undulatory swimming at higher speeds; bluegill sunfish (present study); pumpkinseed, *Lepomis gibbosus* (Brett and Sutherland, 1965); triggerfish, *Rhinecanthus aculeatus* (Korsmeyer et al., 2002); white crappie, *Pomoxis annularis* (Parsons and Sylvester, 1992). Red traces: high-speed undulatory swimming in species that use MPF swimming at low speeds; bluegill sunfish (present study); pumpkinseed (Brett and Sutherland, 1965);

triggerfish (Korsmeyer et al., 2002); white crappie (Parsons and Sylvester, 1992). Blue traces: species that use labriform swimming across a wide range of speeds, with no gait change to sustained undulatory swimming; shiner perch, *Cymatogaster aggregata* (Webb, 1974); parrotfish, *Scarus schlegeli* (Korsmeyer et al., 2002).

length, minimizing variation due to differences in absolute speed across a large fish size range. Differences in water temperature between studies impose additional variability that is not related to swimming style *per se*. SMR in ectotherms changes with temperature, so for a given speed any temperature change will alter the proportion of total metabolism supporting non-locomotor functions. Total metabolic costs and gross cost of transport are therefore likely to change with temperature. Changes in temperature are unlikely to change the net metabolic costs of swimming in adult fish for two reasons. First, temperature-related changes in viscosity are only a significant factor for larval fish swimming in viscous, low Reynolds number flow regimes (Fuiman and Batty, 1997). Second, muscle efficiency in ectotherms does not change significantly with temperature (Smith et al., 2005). The net metabolic costs of swimming in relation to speed should therefore remain relatively constant irrespective of changes in temperature. This is confirmed by direct metabolic measurements of *COT* across a range of water temperatures (Claireaux et al., 2006). The COT_{net} data presented in Fig. 5 should therefore allow a comparison of swimming economy where any variability is primarily due to differences in swimming style rather than scale or temperature.

It has been proposed that MPF swimming is more economical 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). MPF swimmers that maintain a rigid body axis may therefore be more economical than undulatory swimmers. The undulatory specialists exhibit a wide range of *COT* values. The European eel, bluefin tunas and coho salmon, species that undertake lengthy migrations requiring sustained swimming performance, have the lowest *COT* within this group. This may represent an adaptation to minimize energy expenditure during migration. It has previously been suggested that eels may be four to six times more economical at swimming than other fish species (van Ginneken et al., 2005). After accounting for scale effects, however, this appears not to be the case. It is difficult to draw a clear conclusion about the relative economy of MPF and undulatory swimmers as there is considerable overlap between the ranges of *COT* values for each group (Fig. 5); however, the two most economical species are both MPF swimmers.

It has also been hypothesized that specialization for MPF swimming may lead to reduced undulatory swimming performance (Webb, 1982). In terms of economy, the low-speed MPF swimmers do not appear to perform poorly in comparison with the undulatory specialists once they shift to an undulatory gait at higher speeds (Fig. 5). In terms of this gait shift, two distinct MPF strategies are apparent. Some species utilize MPF gaits only at speeds below approximately $1.3 L \ s^{-1}$, while others exhibit MPF swimming across a much greater speed range (Fig. 5). This may be related to differences in the mechanism of thrust generation. Labriform swimmers exhibit a continuum of swimming styles (Walker and Westneat, 2002). At one extreme are rowers like the stickleback, where there is a distinct propulsive movement, followed by 'feathering' of the fin like an oar during the recovery stroke (Walker, 2004). At the other extreme are 'fliers', with pectoral fin kinematics analogous to the flapping wing of a bird, exemplified by species like the parrotfish (Korsmeyer et al., 2002). Bluegill exhibit pectoral fin kinematics that suggest a combination of drag- and lift-based mechanisms for generating thrust (Gibb et al., 1994). The two species for which energetic data are available and that utilize labriform swimming across a wide speed range happen to both be fliers (Fig. 5) (Webb, 1974; Korsmeyer et al., 2002). The alternative strategies cannot entirely be due to kinematic differences, however, as the stickleback (*Gasterosteus aculeatus*) (Walker, 2004) can maintain speeds of over $5 L \ s^{-1}$ using a rowing stroke.

Differences in muscle mass distribution are an alternative explanation for the different gait-shift patterns. In *Cymatogaster aggregata*, the pectoral girdle muscles are 2.6% of the total body mass (Webb, 1974), compared with only 1.3% of total body mass in bluegill and pumpkinseed (Jones et al., 2007). A greater relative investment in pectoral girdle muscle mass is likely to enable a fish to maintain labriform swimming across a greater speed range. Also, labriform swimmers that exhibit a wide labriform speed range lack significant numbers of aerobic myotomal muscle fibers (Webb, 1974; Korsmeyer et al., 2002). This limits the ability of these species to switch to sustained undulatory swimming.

It is not just the availability of muscle power but also the ability of the fish to transfer this power to the water as thrust that may be an additional factor in setting the limits to labriform swimming performance. Bluegill sunfish are one of the few species for which data concerning wake structure are available (Drucker and Lauder, 1999; Drucker and Lauder, 2000; Lauder et al., 2007) in addition to metabolic and muscle power measurements. In bluegill, as labriform swimming speed increases, the jet flow associated with the pectoral fin downstroke becomes increasingly laterally oriented (Drucker and Lauder, 2000). This is in contrast to the surfperch (*Embiotoca jacksoni*), a species that can maintain labriform swimming at twice the length-specific speed of bluegill, where jet flow becomes increasingly oriented downstream as speed increases (Drucker and Lauder, 2000). These differences in wake structure mean that even if the bluegill could generate additional pectoral muscle power, this could not be transferred to the water as additional thrust. Wake structure, in addition to physiological and morphological factors, is therefore an important factor in determining the limits of labriform swimming performance (Drucker and Lauder, 2000).

The structural complexity of the habitats inhabited by the different species may also be a determinant of swimming style. Differences in wake structure may reflect a functional trade-off, with more effective thrust production coming at the expense of decreased maneuverability and stability at low speeds (Drucker and Lauder, 2000). There are relatively few data available on turning performance in labriform swimmers, although there is clearly a wide range of abilities in terms of turning performance. At one extreme, the rowing boxfish can perform a hovering turn with effectively a zero turning radius (Walker, 2000), whereas some fliers cannot hover (Gerstner, 1999; Korsmeyer et al., 2002), turning primarily by modulating pectoral fin kinematics during forward motion. Differences in maneuvering performance are likely to dictate whether a species is restricted to open water or can exploit more structurally complex habitats.

The wake structure of bluegills suggests specialization for maneuverability rather than speed during labriform swimming

(Drucker and Lauder, 2000). A number of studies have investigated bluegill foraging preferences and efficiency (Mittelbach, 1981; Werner et al., 1981; Devries et al., 1989; Harrell and Dibble, 2001), and bluegills are attracted to structurally complex habitats such as weed beds (Johnson, 1993). These are rich sources of the invertebrates that constitute much of the bluegill's diet (Beckett et al., 1992). The labriform gait likely allows bluegill to forage economically in patches of vegetation while maintaining maneuverability. Gait choice in open water may be determined by a number of factors. The balance between minimizing either cost or travel time between food patches will depend on the amount of available food and the level of predation. If minimizing cost is the primary factor, a speed close to the gait transition speed is the most economical choice (Fig. 4), although this may not maximize energy gain from foraging due to the relatively high travel time between patches (Pettersson and Hedenström, 2000). In open water, bluegills are more vulnerable to predation (Mittelbach, 1981; Chips et al., 2004). High predation levels may therefore favor the use of the faster, but less economical, undulatory gait to minimize travel times between patches of vegetation.

In conclusion, the labriform–undulatory gait transition in bluegill sunfish is primarily driven by a need to recruit additional myotomal muscle mass rather than to maximize swimming economy. When compared to undulatory swimming specialists, labriform swimmers are relatively economical. In bluegill, the labriform gait may enable economical low-speed foraging in structurally complex habitats.

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