

## SHORT COMMUNICATION

# Field swimming behavior in largemouth bass deviates from predictions based on economy and propulsive efficiency

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## ABSTRACT

Locomotion is energetically expensive. This may create selection pressures that favor economical locomotor strategies, such as the adoption of low-cost speeds and efficient propulsive movements. For swimming fish, the energy expended to travel a unit distance, or cost of transport (COT), has a U-shaped relationship to speed. The relationship between propulsive kinematics and speed, summarized by the Strouhal number ( $St=fA/U$ , where  $f$  is tail beat frequency,  $A$  is tail tip amplitude in m and  $U$  is swimming speed in  $\text{m s}^{-1}$ ), allows for maximal propulsive efficiency where  $0.2 < St < 0.4$ . Largemouth bass adopted field speeds that were generally below the range predicted to minimize their COT. This may reflect speed modulation to meet competing functional demands such as enabling effective prey detection and capture.  $St$  exceeded the optimal range for the lowest observed swimming speeds. Mechanical and physiological constraints may prevent adoption of efficient  $St$  during low-speed swimming.

**KEY WORDS:** Kinematics, *Micropterus*, Strouhal number, Cost of transport, Field behavior

## INTRODUCTION

Locomotor performance is essential to the fitness of most animals (Watkins, 1996; Miles, 2004; Walker et al., 2005). Locomotor costs dominate the daily energy budgets of many species (Kerr, 1982; Boisclair and Sirois, 1993; Irschick and Garland, 2001), and sustained locomotor behaviors may therefore experience selection pressures favoring cost reduction (Schmidt-Nielsen, 1972; Charnov, 1976; Mittelbach, 1981). In terrestrial limbed locomotion, energy costs are primarily associated with weight support and limb segment motion (Marsh and Ellerby, 2006; Pontzer, 2005; Taylor et al., 1980), while in swimmers and fliers the power costs of transferring momentum to the external medium predominate (Gerry and Ellerby, 2014; Morris et al., 2010). Cost reduction in swimmers and fliers can therefore be achieved through locomotor strategies that enable efficient lift and thrust production or by adopting speeds that minimize the energy expended in traveling a unit distance (Pennycuik, 2001). Physiological data and theoretical analyses of cost–speed relationships have identified optimal locomotor speeds for cost minimization (Brett, 1964; Tucker, 1966; Videler and Weihs, 1982; Watanabe et al., 2011). Convergence on narrow parameter spaces for propulsive kinematics may also reflect optimization of propulsive efficiency (Taylor et al., 2003;

Triantafyllou et al., 1993). The majority of the physiological and kinematic data concerning energetic and propulsive optimality were obtained under controlled, quasi steady-state conditions. The extent to which organisms pursue optimal locomotor strategies in the field remains uncertain because of a lack of suitably detailed field performance data for most species.

Locomotor performance in the field has been characterized in a variety of ways. Telemetry of physiological or mechanical parameters can serve as a proxy for activity level or behavior (Webber and O’Dor, 1986; Webber et al., 2001; Ward et al., 2002; Standen et al., 2003). Acoustic telemetry, sonar and GPS tracking provide a more direct measure of motion (Cooke et al., 2005; Hanson et al., 2010; Wilson et al., 2013; de Kerckhove et al., 2015), although may lack detail regarding the instantaneous trajectory or exact mode of propulsion. This detail is essential for estimating field metabolic rate as short-term changes in momentum may significantly increase locomotor cost (Weihs, 1981; Webb, 1991; Boisclair and Tang, 1993). Furthermore, kinematic data may reveal energy-saving strategies such as intermittent propulsion (Videler and Weihs, 1982) or convergence on efficient propulsive mechanisms (Taylor et al., 2003). Motion analysis from video images has the potential to reveal this kinematic detail and allow reconstruction of animal trajectories in three-dimensions (Krohn and Boisclair, 1994; Theriault et al., 2014). This presents challenges in the field as multiple camera points of view are required in combination with suitable calibration techniques. Techniques for calibrating large volumes have enabled detailed analyses of avian flight performance in the field (Shelton et al., 2014). The additional challenges associated with underwater videography mean that few equivalent data that integrate details of organismal trajectory and propulsive kinematics are available for aquatic organisms.

We have obtained swimming performance and kinematic data from field video recordings of largemouth bass, *Micropterus salmoides* (Lacépède 1802). We hypothesized that fish would adopt swimming speeds that minimized their cost of transport (COT), the energy expended to travel a unit distance, thus maximizing their net rate of energy return as predicted by optimal foraging models (Charnov, 1976; Mittelbach, 1981). Swimmers and fliers may also maximize propulsive efficiency by adopting a relationship between propulsive kinematics and speed, summarized by the Strouhal number ( $St$ ), that is constrained within a narrow range of values (Nudds et al., 2014).  $St=fA/U$ , where  $f$  is tail beat frequency,  $A$  is tail tip amplitude (m) and  $U$  is swimming speed ( $\text{m s}^{-1}$ ). For oscillating propulsors, efficiency peaks at  $0.2 < St < 0.4$  (Triantafyllou et al., 1991, 1993). Despite this, fish may use inefficient  $St$  during flume swimming (Hunter and Zweifel, 1971; Webb, 1971; Lauder and Tytell, 2006). This could be an artifact arising from the imposition of swimming speeds rarely utilized in the field. We hypothesize that, in contrast, during volitional field swimming, bass will adopt a range of speeds and swimming kinematics that maintain  $St$  within a narrow range consistent with maximizing propulsive efficiency.

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Received 20 February 2017; Accepted 27 June 2017

Concerns have been raised regarding the extent to which laboratory performance data can be linked to organismal fitness (Hertz et al., 1988; Irschick, 2003; Vanhooydonk and Van Damme, 2003; Irschick et al., 2005; Nathan et al., 2008). To be informative, it is essential that performance data are obtained under conditions that are relevant to field behavior. The field data obtained will allow an assessment of how applicable steady-state performance data are to estimated field metabolic rate and interpreting locomotor behavior in the field for this species.

## MATERIALS AND METHODS

Video was collected in Lake Waban, MA, USA, in July 2015 at a 60 Hz frame rate with four GoPro video cameras (GoPro, Hero 3 Silver, San Mateo, CA, USA). These were mounted in pairs on a camera head with overlapping fields of view. Cameras were deployed in locations with approximately 3 m water depth, and the camera head located 50 cm below the water surface. Water temperature ranged from 20 to 22°C. Fish length ( $L$ ) was estimated from the video images by tracking the snout and tail trailing edge positions on a minimum of 10 frames for a given individual and taking the average snout–tail distance as the length for that fish. Mean ( $\pm$ s.d.)  $L$  was  $152 \pm 12$  mm ( $n=21$ ). For largemouth bass,  $\log_{10}$  body mass =  $3.13 \log_{10} L - 5.16$  (Schneider et al., 2000). On this basis, mean ( $\pm$ s.d.) estimated body mass for the tracked fish was  $45.9 \pm 11.4$  g ( $n=21$ ). Each tracked fish was considered a distinct individual and the resulting data treated as independent for statistical purposes. As video collection was carried out at three separate locations on different days, and several identifiable individuals could be concurrently followed through the imaged volumes, the chances of resampling an individual were considered low.

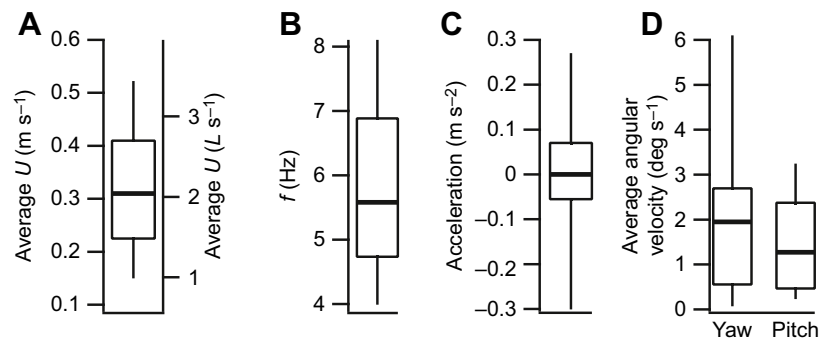
Camera pairs were calibrated using a wand calibration technique and the direct linear transform (DLT) method (Tsai, 1987). Videos of wand movements defined a series of coordinates throughout the imaged volume based on wand end positions, and were used to generate 11 DLT coefficients for each camera pair (Therault et al., 2014). Lens distortion coefficients were also quantified using a checkerboard imaging technique (Bouguet, Camera Calibration Toolbox for MATLAB; <http://www.vision.caltech.edu/bouguetj/index.html>). Fish center of mass (COM) locations were tracked through the calibrated volumes with a MATLAB-based digitizing program (MATLAB 2014a, The Mathworks Inc., Natick, MA, USA) developed by Hedrick (2008). Position data were smoothed using a smoothing spline interpolation in the application Igor Pro (v6.2, Wavemetrics, Lake Oswego, OR, USA). This method is similar to the cubic spline algorithm recommended by Walker (1998) for calculating velocities and accelerations from position data. The level of smoothing applied by the algorithm was defined by the standard deviation of the data. Smoothed COM position–time data were differentiated to obtain COM velocity, and velocity was differentiated to obtain COM acceleration. As an index of deviation from a linear swimming path, tortuosity, the ratio of total path length to the linear distance between the beginning and end points, was calculated. Tortuosity values of 1 would therefore indicate linearity. Perpendicular velocity vector magnitudes were used to calculate the tangents of heading angles. The tangent of the path angle in the horizontal plane was calculated as the ratio of the perpendicular velocity vector magnitudes in the horizontal plane. The tangent of the vertical path angle was calculated as the ratio of the resultant horizontal and the vertical velocity vector magnitudes. Path angles were calculated as the arctangents of the velocity vector ratios. Angles were differentiated with respect to time to calculate angular

velocities in pitch and yaw. Tail beat frequency ( $f$ ) was recorded for tracked sequences. Tail tip amplitude ( $A$ ) could not be measured directly from the video images as there was insufficient spatial resolution. Mean  $A$  for largemouth bass remains constant at  $0.13L$  across a similar relative speed range, although for some individuals there may be an increase in amplitude with speed (Jayne and Lauder, 1993), similar to the amplitude modulation observed in other species (Hunter and Zweifel, 1971; Webb, 1971; Nudds et al., 2014). To ensure that we did not overestimate changes in  $St$  with respect to speed, we calculated  $St$  both with constant amplitude and with amplitude modulation such that  $A$  as a proportion of  $L$  is  $0.162 - 0.126e^{-5.08U}$ , where  $U$  is swimming speed in  $\text{m s}^{-1}$  (Jayne and Lauder, 1993). Spearman's rank correlation coefficient was used to test for changes in  $St$  with respect to swimming speed. Statistical analyses were carried out using PASW Statistics (v18, SPSS, Chicago, IL, USA).

## RESULTS AND DISCUSSION

The swimming speeds used by largemouth bass in the field were generally lower than would be consistent with minimizing their COT (Figs 1 and 2). COT–speed relationships in fish are typically U-shaped. The curvilinear relationship between total cost and speed (Fig. 2A) means that COT increases at the upper end of the sustainable speed range (Fig. 2B). COT also increases at low speeds as the finite cost associated with non-locomotor processes ensures that COT must asymptotically approach infinity as speed approaches zero (Fig. 2B). For largemouth bass, the minimum COT speed based on flume oxygen consumption data falls in the  $0.4\text{--}0.5$   $\text{m s}^{-1}$  range (Fig. 2B). The majority of fish swam at speeds below this range, with median and 75th percentile speed distribution values of  $0.31$  and  $0.41$   $\text{m s}^{-1}$ , respectively (Figs 1 and 2B). This contrasts with our initial hypothesis derived from optimal foraging models and with data from other fish species where volitional speeds appear to minimize COT (Hinch and Rand, 2000; Tudorache et al., 2011).

A variety of ecological, physiological and phylogenetic factors can influence field swimming speed. Use of minimum COT speeds during submerged swimming is likely to be most strongly associated with increased fitness in air-breathing divers, where this should prolong dive depth and duration (Thompson et al., 1993). COT minimization in this functional group has been supported across a range of scales by comparison of field speed data with predictions derived from a biomechanical model of swimming cost (Watanabe et al., 2011), although elevation of metabolic capacity in endotherms relative to ectotherms can raise the minimum COT speed independently of scaling effects, and variation in field speeds between some taxa remain unexplained. Other factors, such as predation risk or the sensory and mechanical constraints associated with foraging may also shift behaviors away from predictions based on economy alone (Werner et al., 1983; Higham et al., 2015). In the present study, tracked fish were moving through open water and so were potentially exposed to predators. However, if predation risk minimization was a factor, observed speeds were more likely to exceed the minimum cost speed while allowing the fish to rapidly reach refuge (Werner et al., 1983). Fish were occasionally observed ingesting small food items, likely *Daphnia* (Applegate and Mullan, 1967), from the water column. The observed low speed swimming may therefore enhance the detection and capture of prey items (Higham et al., 2015), thus raising the rate of energy intake rather than maximizing energy economy. The selection of low speeds also reduces the energy expended per unit time (Fig. 2A). This could also be consistent with optimal foraging strategies to maximize the rate



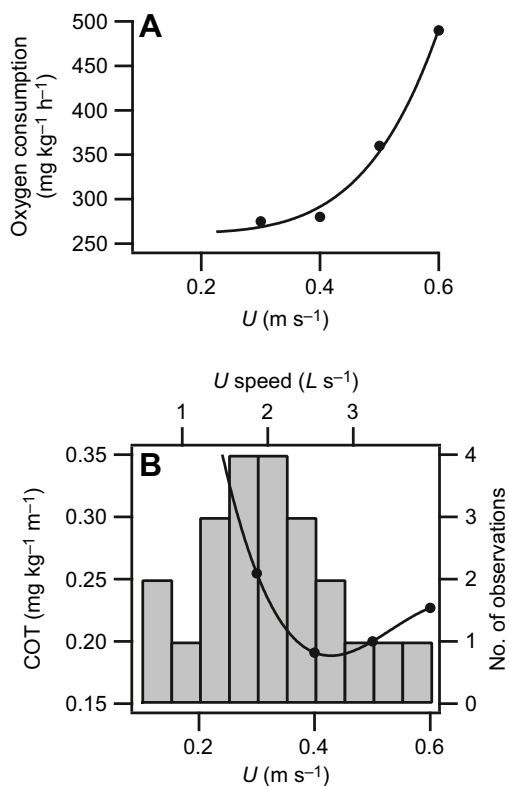
**Fig. 1. Field swimming performance of largemouth bass.** (A) Average swimming velocity ( $U$ ).  $L$ , body lengths. (B) Tail beat frequency ( $f$ ). (C) Acceleration. (D) Average angular velocity in yaw and pitch. Horizontal bars show the median values, boxes the 25th and 75th percentiles, and whiskers the 10th and 90th percentiles of the distributions.  $n=21$ .

of energy return if prey encounter rates are sufficiently high (Mittelbach, 1981).

Another possibility underlying the mismatch between predicted and observed behaviors is that flume energetic data are not useful in interpreting field behavior and predicting field metabolic rate. In the present study, although the field performance and energetic comparison was between comparably sized bass at similar temperatures, differences in their geographical origins or physiological condition could undermine the comparability of the data. The potential discrepancy between volitional locomotor behavior and forced locomotion in the laboratory is a more general concern regarding comparisons of this type. The available metabolic cost data for fish swimming were primarily obtained through indirect calorimetry based on the rate of oxygen consumption within a sealed volume of water. This requires a low

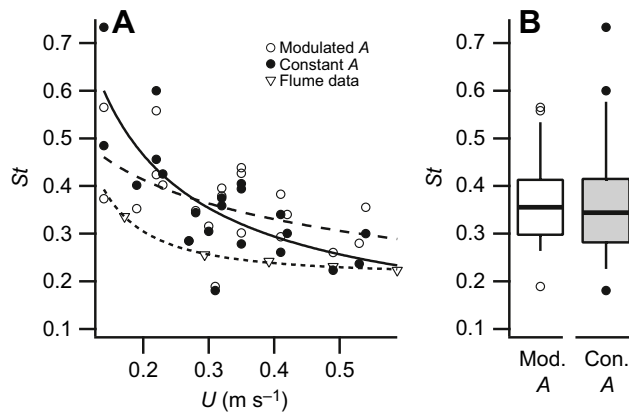
relative water volume to ensure fairly accurate and rapid resolution of changes in oxygen concentration (Ellerby and Herskin, 2013). This is achieved by forcing fish to swim against a current within sealed, recirculating flumes (e.g. Brett, 1964) or, more rarely, by allowing fish to swim volitionally within a restricted volume (Tang and Boisclair, 1995; Tang et al., 2000; Steinhausen et al., 2010). These approaches produce mechanically quite different behaviors between quasi-steady-state swimming in flumes versus unsteady maneuvering within the physical constraints of a small, static volume (Steinhausen et al., 2010). Volitional swimming behavior may be intrinsically unsteady (Webb, 1991), and unsteady locomotion is typically costlier than steady-state motion because of the additional energy expended in altering the organism's trajectory (Daniel, 1984). Consequently, correction factors have been developed that apply a cost increment to steady-state cost-speed data to estimate the cost of volitional swimming in the field (Boisclair and Tang, 1993). The observed swimming behavior for bass deviated minimally from steady-state conditions. Accelerations, decelerations and turning rates (Fig. 1C,D) fell within the range measured during sustained flume swimming at an applied average velocity (Plew et al., 2007; Thiem et al., 2015), and were low in comparison to maximal accelerations and angular velocities during maneuvers, which approach  $30 \text{ m s}^{-2}$  and  $1000 \text{ deg s}^{-1}$ , respectively, in juvenile bass and other centrarchids of similar body mass (Webb, 1978, 1986; Ellerby and Gerry, 2011). The fish also followed relatively straight paths as indicated by a mean ( $\pm$ s.d.) tortuosity value of  $1.13 \pm 0.14$  ( $n=21$ ). This suggests that for this species and behavioral context, quasi-steady-state performance data are a reasonable basis for estimating field metabolic rate and interpreting field behavior. This may not apply in other contexts, such as swimming through more complex physical environments and foraging for evasive prey, or for other species with differing locomotor behavior. Enhanced estimates of the activity component of fish energy budgets in general therefore require more detailed data concerning field locomotor performance.

Data of this type also allow an assessment of whether organisms adopt efficient propulsive kinematics in the field. The efficiency of thrust production by an oscillating propulsor in a fluid peaks within a relatively narrow parameter space for the relationship between propulsor kinematics, wake structure and speed such that  $0.2 < St < 0.4$  (Taylor et al., 2003). During flume swimming at imposed velocities, the  $St$  of swimming fish often exceeds this range at low speeds (Lauder and Tytell, 2006). Our initial hypothesis was that during volitional swimming where fish were freed from the constraints of flume swimming, they would prefer speeds and propulsive kinematics that optimized propulsive efficiency. This was not the case at all speeds.  $St$  changed significantly with speed when calculated both with constant  $A$  (Fig. 3A; Spearman's  $\rho = -0.71$ , d.f.=19,  $P < 0.01$ ) and with modulation of  $A$  (Spearman's



**Fig. 2. Aerobic cost of swimming in largemouth bass.** (A) Rate of oxygen consumption in relation to swimming speed ( $U$ ). (B) Cost of transport (COT) in relation to swimming speed. Data from 43 g fish at  $20^\circ\text{C}$  are replotted from Beamish (1970). Gray bars show a frequency histogram of field swimming speeds from the present study, with the number of observations within a speed bin show on the right-hand y-axis.





**Fig. 3. Estimated Strouhal number in largemouth bass.** (A) Relationships between the Strouhal number ( $St$ ) of largemouth bass and swimming speed. Field  $St$  was calculated using a constant tail tip amplitude ( $A$ ) and with  $A$  modulated with respect to swimming speed such that  $A$  as a proportion of body length ( $L$ ) is  $0.162 - 0.126e^{-5.08U}$ , where  $U$  is swimming speed in  $m\ s^{-1}$ . Field constant  $A$  and field-modulated  $A$  data are shown by filled and open circles, respectively. Flume data (Jayne and Lauder, 1993) are represented by inverted triangles. Data were fitted with the following relationships: field with constant  $A$  (solid line),  $St = 0.07 + 0.11^{-0.81U}$ ; field with modulated  $A$  (dashed line),  $St = -0.25 + 0.49^{-0.19U}$ ; flume (dotted line),  $St = 0.21 + 0.0045^{-1.87U}$ . (B) Distribution of  $St$  values for field swimming. Horizontal bars show the median values, boxes the 25th and 75th percentiles, and whiskers the 10th and 90th percentiles of the distributions. Individual circles indicate outliers. Open symbols and box indicate  $St$  values calculated assuming modulation of  $A$ , and filled symbols and box indicate  $St$  values calculated assuming constant  $A$ .  $n = 21$ .

$\rho = -0.49$ ,  $d.f. = 19$ ,  $P < 0.05$ ), and the fitted  $St$ –speed relationships exceeded the predicted optimum range of  $0.2 < St < 0.4$  at speeds below  $0.22$  and  $0.25\ m\ s^{-1}$  for constant and modulated  $A$ , respectively (Fig. 3A). This pattern was similar to that observed during flume swimming in a range of species (Hunter and Zweifel, 1971; Webb, 1971; Lauder and Tytell, 2006). This low speed deviation from ideal propulsive kinematics could at least in part underlie the increase in COT at low speeds (Figs 2 and 3). The minimum COT range also coincided with estimated  $St$  values that fall within the optimum propulsive range (Figs 2 and 3), suggesting an interaction between propulsive efficiency and COT. Uncertainties remain as it is possible that  $A$  is modulated differently in field swimming compared with forced swimming in a flume, such that a narrow  $St$  range is achieved at all speeds. These can only be resolved by collection of more detailed performance and kinematic data in this and other species. However, given that swimming movements arise from the interacting properties of the musculature, skeletal and connective tissues, propulsive fins and surrounding water (Altringham and Ellerby, 1999; Long and Nipper, 1996), constraints arising from these interactions may simply prevent fish from achieving high propulsive efficiency when they swim slowly.

#### Acknowledgements

We are grateful to Kelsey Cathcart and Selina Shin for their work in developing the video data processing protocols used.

#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: D.J.E.; Methodology: A.X.H., C.B., D.J.E.; Validation: C.B., D.J.E.; Formal analysis: A.X.H., C.B., D.J.E.; Writing - original draft: A.X.H., C.B., D.J.E.; Writing - review & editing: A.X.H., C.B., D.J.E.; Supervision: D.J.E.; Funding acquisition: D.J.E.

#### Funding

The work was funded by the National Science Foundation [1354274 to D.J.E.].

#### Data availability

Raw data are available from the Dryad Digital Repository (Han et al., 2017): <http://dx.doi.org/10.5061/dryad.0qr68>

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