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Biomechanics

Intermittent propulsion in largemouth bass, *Micropterus salmoides*, increases power production at low swimming speeds

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Locomotion dominates animal energy budgets, and selection should favour behaviours that minimize transportation costs. Recent fieldwork has altered our understanding of the preferred modes of locomotion in fishes. For instance, bluegill employ a sustainable intermittent swimming form with 2–3 tail beats alternating with short glides. Volitional swimming studies in the laboratory with bluegill suggest that the propulsive phase reflects a fixed-gear constraint on body–caudal-fin activity. Largemouth bass (*Micropterus salmoides*) also reportedly display intermittent swimming in the field. We examined swimming by bass in a static tank to quantify the parameters of volitional locomotion, including tailbeat frequency and glide duration, across a range of swimming speeds. We found that tailbeat frequency was not related to speed at low swimming speeds. Instead, speed was a function of glide duration between propulsive events, with glide duration decreasing as speed increased. The propulsive Strouhal number remained within the range that maximizes propulsive efficiency. We used muscle mechanics experiments to simulate power production by muscle operating under intermittent versus steady conditions. Workloop data suggest that intermittent activity allows fish to swim efficiently and avoid the drag-induced greater energetic cost of continuous swimming. The results offer support for a new perspective on fish locomotion: intermittent swimming is crucial to aerobic swimming energetics.

1. Introduction

Locomotive performance is vital to fitness [1]. Cost reduction in swimmers and fliers can be attained through locomotor strategies that enable efficient lift and thrust production or by adopting speeds that minimize the energy expended in travelling a unit distance [1]. Various behaviours have been reported in fishes that reduce the cost of locomotion, such as entrainment, group swimming and intermittent swimming. These behaviours collectively suggest that fishes can dynamically alter their gait in response to the conditions they encounter to improve efficiency.

In entrainment, fish gain benefit from the hydrodynamic conditions associated with solid objects in flow such as branches and rocks or other obstructions in moving water. These conditions allow fish to hold station in moving water with lower energetic costs compared to swimming in the open. Liao and colleagues published a series of papers on rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) employing entrainment swimming behaviours in association with flow obstructions [2–6]. These behaviours significantly reduced the metabolic cost of swimming in a respiratory swim tunnel when an obstruction is

present compared to when the obstruction is absent [7–9]. Like entrainment, swimming in groups reduces the energetic cost of locomotion, at least for some fish species [9]. Group swimming has been proposed as a mechanism for increasing swimming efficiency, as a swimming fish generates a turbulent wake of eddies similar to that of a flow obstruction [10]. A fish swimming downstream of another fish can position itself in an advantageous location in the wake of an upstream fish such that energy can be conserved [5,10,11]. Laboratory studies have demonstrated lower collective energy requirements with group swimming [9,12–15].

Intermittent swimming is a more recently described swimming behaviour in fishes proposed to reduce energy costs at steady, sustainable swimming speeds [16–18]. In field studies and laboratory observations, swimming fish will routinely employ a sustainable, aerobic muscle-powered intermittent swimming behaviour in which 2–3 tailbeats are alternated with approximately 1 s glide periods [1,19–22]. Importantly, this has been generally observed when fish are swimming volitionally in static water as opposed to induced flows in a laboratory swim tunnel. Modelling of intermittent swimming behaviour using the red or aerobic myotome in this alternating manner suggests a reduction in energetic costs [16–18]. Gliding in a straight body position reduces drag compared to an undulating body, leading to the prediction of lower muscle activity and lower energetic costs when gliding and undulation are alternated [20]. This description of intermittent swimming is distinct from the classically described high-speed burst and coast swimming that requires white or anaerobic muscle recruitment and is therefore inherently unsustainable (e.g. [23]).

Intermittent swimming has been well described in the centrarchid bluegill sunfish, *Lepomis macrochirus*, swimming volitionally in both natural and laboratory settings [19,20]. Across a range of low, sustainable swimming speeds, bluegill employ a fixed-gear propulsive strategy with short propulsive bouts at a constant tailbeat frequency alternating with periods of glide. The duration of glide between propulsive bouts determines swimming speed [20]. Similar behaviour has been described in the field for another centrarchid fish, the largemouth bass, *Micropterus salmoides* [21], although never carefully evaluated in the laboratory under controlled conditions. In the present study, we hypothesized that bass employ intermittent swimming behaviour when swimming volitionally. We collected data to characterize such intermittent swimming in a laboratory setting by largemouth bass. We then asked if intermittent swimming benefits muscle function in largemouth bass during swimming. This is the first study to examine intermittent muscle function in *in vitro* muscle mechanics experiments. We hypothesized that muscle intermittent oscillatory activity improves muscle power production at low swimming speeds compared to steady or continuous activity.

2. Methods

Largemouth bass were obtained from the Kurtz Fish Farm, Elverson, PA, and were maintained in a 250 gal aquarium in freshwater maintained at 20°C with recirculating filtration. They were fed a diet of pelleted trout food (Ziegler Bros, Gardners, PA); partial water changes were made three times weekly. All fish procedures were approved by the Widener University Institutional Animal Care and Use Committee and followed the Guide for Care and Use of Laboratory Animals of the National Research Council.

(a) Swimming studies

For volitional swimming trials, individual fish were collected from the holding tank and placed into a static tank (1.5 m long × 1.0 m wide × 0.2 m deep). The centre of the static tank was filmed using a Fastec IL5 camera (Fastec Imaging, San Diego, CA) at 100 fps with a 12.5 mm wide-angle lens. Fish were allowed to acclimate to the static tank for 1 h and then were filmed for 1 h while swimming volitionally about the static tank. A total of six fish were used with a mean (±s.d.) total length of 18.6 ± 1.0 cm. Video sequences ($n = 26$ total, 4–5 per fish) of bass swimming intermittently were isolated and analysed for swimming speed, propulsive and glide durations, tailbeat frequency, tailbeat amplitude and Strouhal number (*St*) as described in Gellman *et al.* [20]. Tailbeat frequency and amplitude were determined during the swimming bouts. Intermittent swimming was defined as a locomotive sequence involving alternating patterns of propulsion and gliding. Video sequences (approx. 3–5 s long) were selected when there was little observed turning in the bout of intermittent swimming [20]. Gliding was defined as any discernible period of the tail stopping at the midline; glide durations in this study ranged from approximately 0.25–3 s. Glide duty factor of one swimming event was calculated as time spent gliding divided by the total duration of the swimming sequence across the static tank. Video analysis was carried out using DLTdv software in MATLAB [24]. For the glide duty factor, tailbeat frequency and tailbeat amplitude, there was no effect of fish identity on each variable (ANOVA, $p > 0.05$ for each variable). The effect of swimming speed (in body lengths per second, BL s^{-1}) on each variable was analysed using a linear mixed model analysis to account for the effect of individual and for differences in sample size (SPSS 27.0).

(b) Muscle mechanics and work loops

Muscle mechanic experiments were performed on the largemouth bass red or slow-twitch myotomal muscle ($n = 6$). Bass were euthanized via pithing. Longitudinal strips of muscle were cut directly above and below the lateral line at approximately 75% of the total fish length from the tip of the snout. Muscle was maintained in physiological saline [25]. Muscle bundles composed of two myomeres with an approximate cross-section of 0.5 × 0.5 mm were isolated. Bundles were tied into a muscle mechanics apparatus composed of a servomotor, force transducer, temperature-controlled chamber filled with recirculating physiological saline, platinum-stimulating electrodes and a Windows PC with custom Lab-View software and input/output computer board [26]. Muscle bundle dimensions were measured to determine muscle tension corrected for the cross-sectional area, and power output was corrected for muscle mass [27].

For each muscle mechanics experiment, bundles were isometrically stimulated across a range of muscle lengths until the optimal length at which the tetanic force maximized was found. Subsequently, stimulus amplitude (V) was optimized to maximize twitch force at the optimal length. Workloop experiments were carried out to assess power output of muscle bundles operating under both steady oscillatory activity and intermittent oscillatory activity. Workloops were sinusoidal and employed a standardized ±3% length change and 4 s trials. The length change was selected based on the length change observed at that approximately 75% body position in swimming bass [28,29]. For steady activity, workloop measurements of power output were carried out for optimized conditions (muscle activation duration and phase during sinusoidal loops) that

maximized power output for oscillatory frequencies of 1, 2, 3, 4, 5 and 6 Hz. Simulations of intermittent swimming were then carried out at oscillatory frequencies of 2.67, 3.2 and 4 Hz. The intermittent stimulation involved stimulating for either two or three simulated tailbeats followed by a 1 s pause representing the glide period. These six intermittent muscle activity conditions (three frequencies × two tailbeat conditions) were modelled on prior observations of intermittent swimming in centrarchids [19,21]. The intermittent tailbeat frequencies used were within the range of what is reported here for volitional swimming in largemouth bass in the laboratory and included the median observation of bass swimming in the field [21]. Power output was determined as average power during continuous muscle activity or during a bout of intermittent swimming including the glide period. Normalized power output data are plotted for the approximate swimming speed for fish employing either steady or intermittent activity. For steady swimming, swimming speed is reported as a function of oscillation (tailbeat) frequency based on the published relationship of tailbeat frequency and swimming speed in bass [30]. For intermittent activity, intermittent muscle power output is plotted at the mean observed speed of volitional swimming in this study. The intermittent muscle activity conditions would have resulted in a range of swimming speeds, but the exact speeds cannot be accurately predicted from the *in vitro* muscle mechanics experiments, so the mean observed intermittent swimming speed from the volitional swimming experiments was used as a reference point. The mean is found in middle of the range of observed volitional swimming speeds in this study: 0.4 to 1.5 BL s^{-1}.

3. Results

Across a range of swimming speeds, the glide duty factor of intermittently swimming bass decreased significantly with increasing speed (figure 1*a*, $F_{1,13} = 6.791$, $p = 0.025$) However, across the same range of intermittent swimming speeds, tailbeat frequency was constant (figure 1*b*; $F_{1,13} = 2.337$, $p = 0.142$). Tailbeat amplitude increased slightly with swimming speed (figure 1*c*; $F_{1,13} = 28.053$, $p < 0.001$). *St* during intermittent swimming by largemouth mass was 0.36 ± 0.03 (mean ± s.e.). *In vitro* power production by bass red muscle under intermittent conditions was comparable to steady swimming power output for speeds at which intermittent swimming was observed (figure 2*a*). Under intermittent conditions, muscle operates at a higher oscillatory frequency than during steady swimming at the same approximate speed, leading to greater work per oscillatory cycle during intermittent activity (figure 2*b–d*). Workloops from muscle operating under steady conditions but at low frequencies (e.g. 1 and 2 Hz) show limited work per cycle due to a failure to maintain force during shortening. Muscle operating at higher frequencies displays more robust work per cycle as force is greater during much of the shortening phase of the oscillatory cycle.

4. Discussion

Largemouth bass swam with an intermittent mode of locomotion when allowed to swim volitionally in a static tank. Across the range of slower, sustainable speeds, swimming speed was primarily modulated by the duration of glide periods (figure 1*a*). Across this range of swimming speeds, tailbeat frequency showed no relationship with swimming

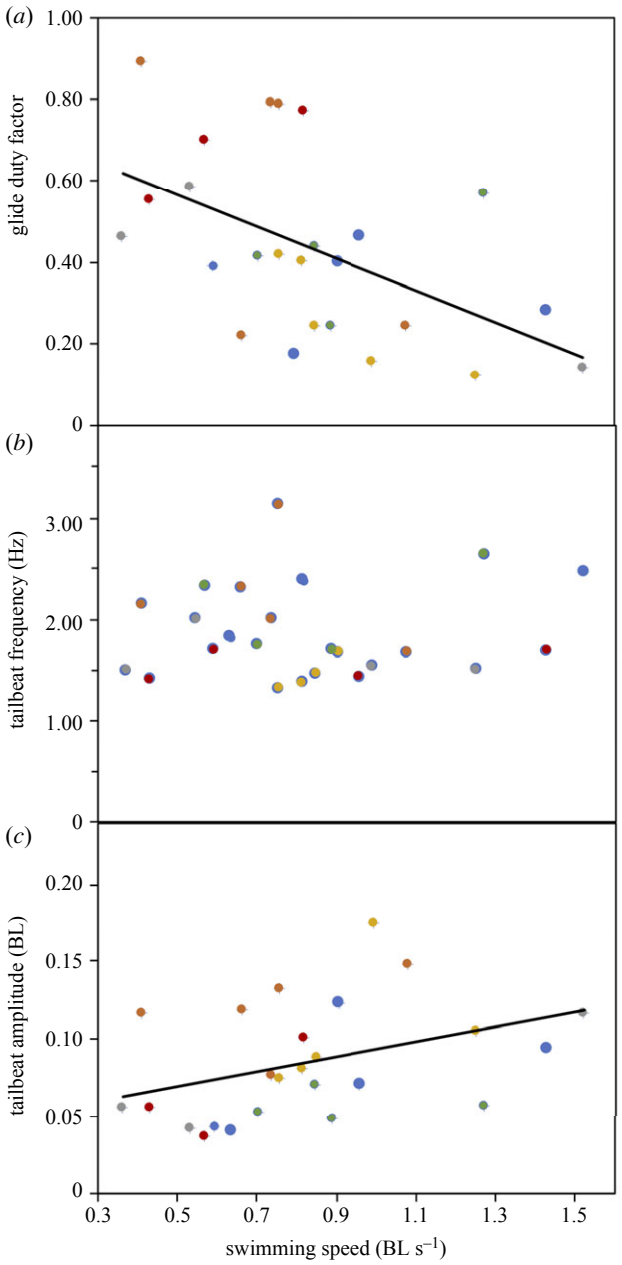

Figure 1. Glide duty factor (*a*) decreases with increasing swimming speed, while tailbeat frequency (*b*) does not. Tailbeat amplitude (*c*) does vary with swimming speed across a range of volitional swimming speeds. Each fish in the study is represented by a different colour. Fish identity did not affect any of the three variables.

speed (figure 1*b*). Conversely, tailbeat frequency increases linearly with swimming speed during steady swimming in bass [28]. Tailbeat amplitude did increase somewhat with swimming speed (figure 1*c*). The results reported here are similar to those for bluegill in terms of the impact of glide duty factor on swimming speed [20], but differed in the significant relationship of speed and tailbeat amplitude in bass. This later observation suggests different forms of intermittent swimming in these two species. However, intermittent swimming allows both species to operate at a single tailbeat frequency over a range of swimming speeds, maintaining a narrow range of Strouhal numbers that correspond to higher propulsive efficiency [21]. During the intermittent swimming bouts, the bass swam with a mean *St* of 0.36 (electronic supplementary material figure S1), which was within the range predicted to maximize propulsive efficiency

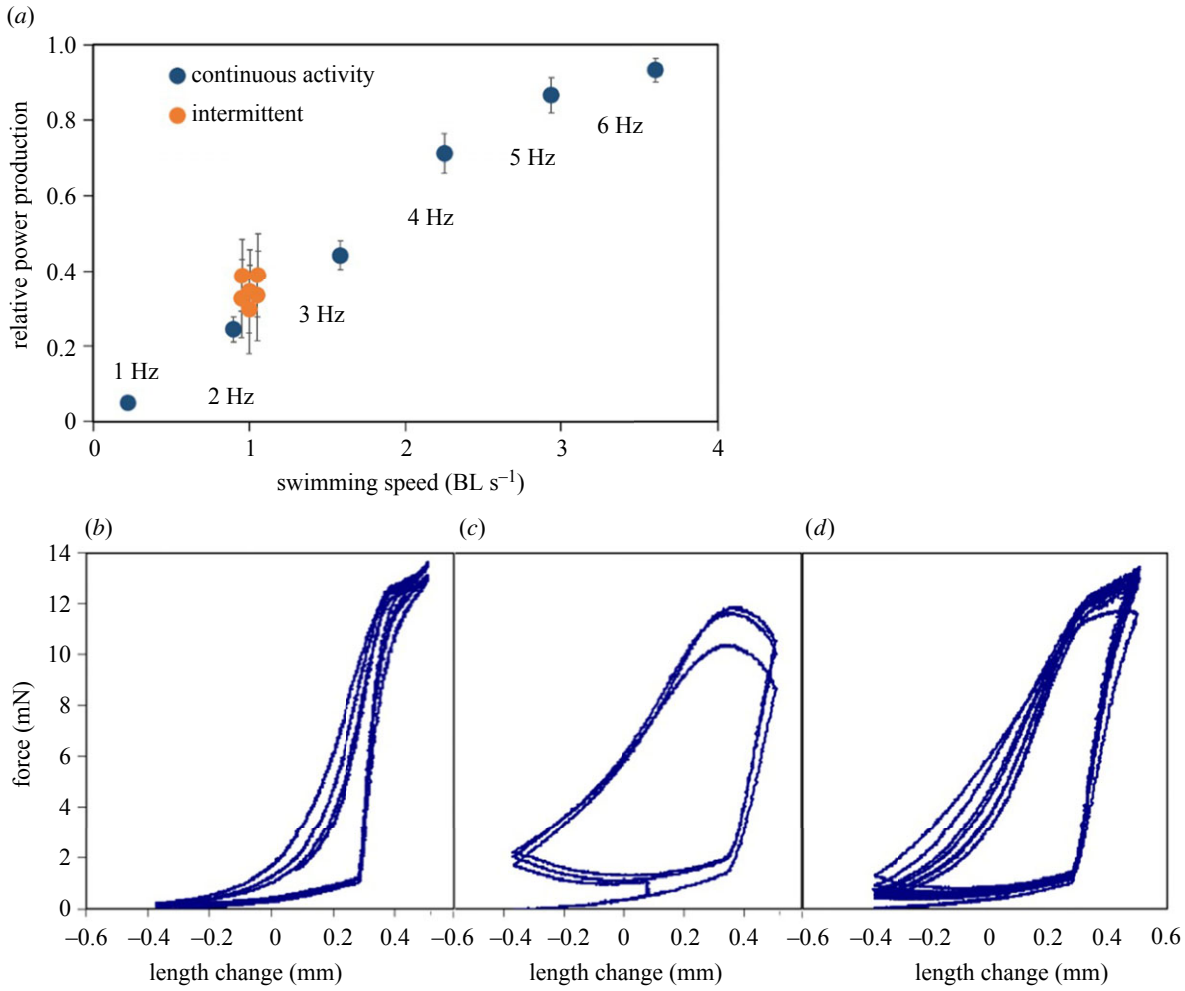

Figure 2. *In vivo* power output for myotomal muscle operating under steady versus intermittent conditions. For continuous oscillatory activity, power output increases with oscillation frequency (*a*), plotted below against corresponding swimming speed for each oscillation frequency. For intermittent conditions, power output at the corresponding swimming speed exceeds that produced through steady conditions for the same speed. Sample workloops for steady or continuous activity at low oscillation frequencies show relatively low work per oscillatory cycle (*b*,*d*) ((*b*) 1 Hz continuous, (*c*) 3.2 Hz intermittent and (*d*) 2 Hz continuous) compared to intermittent muscle activity (*c*).

($0.2 < St < 0.4$) [21]. Therefore, these observations of swimming fish suggest that the fish are employing their caudal fin (and the muscle that powers its movement) efficiently.

Muscle mechanics experiments suggest that power output under intermittent conditions at a fixed oscillation frequency exceeds the power output under continuous or steady activity that corresponds to the same swimming speed (figure 2*a*). Intermittent muscle activity with 2–3 tailbeats at 3.2 Hz alternating with 1.0 s glide periods produces the same power as steady muscle activity at 1–2 Hz. At low tailbeat frequencies, the red muscle bundles did not maintain force levels during shortening, resulting in smaller workloop areas (lesser work per oscillatory cycle) (e.g. figure 2*b*). During the shortening period of the oscillatory cycle, force levels dropped rapidly after the onset of shortening, declining to less than 10% of peak force by halfway through the shortening period.

Intermittent swimming may therefore offer parallel adaptive advantages. Intermittency allows the fish to adopt a higher tailbeat frequency for a given average speed. Our *in vitro* muscle performance data suggest that the higher oscillatory frequency (corresponding to higher tailbeat frequency), combined with a fixed gear (i.e. a limited range of muscle oscillation frequencies), enhances power output relative to sustained propulsive cycles at a lower cycle frequency, as previously suggested by Gellman *et al*. [20]. Alternating between periods of propulsion and gliding may also be favoured by the low gliding drag. Drag is at least two times greater during a propulsive period than during the glide period of intermittent swimming [31]. However, recent modelling studies suggest that intermittent swimming can be energetically more expensive [32]. When muscle physiology is taken into consideration, the pause in muscle activity during gliding may be important for deferring the onset of fatigue. These combined effects are likely to reduce energetic costs and improve energy efficiency, although this requires direct confirmation from respirometry data or metabolic measurements at the muscle level. An additional benefit of intermittent swimming is the decoupling of muscle activity and movement from sensory function. Glide periods may permit swimming fish to perceive the hydrodynamic and visual world with greater sensitivity [33–35]. Although the glide period during intermittent swimming does not involve actual stopping, as in saltatory searching (e.g. [34]), decoupling motor and sensory functions may benefit foraging behaviour [35].

We describe intermittent swimming in largemouth bass, and not only expanded the list of species that undergo this sustainable swimming mode that is powered by the red or aerobic myotomal muscle, but demonstrated the consistency

of this behaviour in terms of the modulation of glide duration and the fixity of tailbeat frequency and tailbeat amplitude during the short propulsive phases. More so, this is the first study to document the *in vitro* power output of the aerobic muscle under steady versus intermittent conditions. Our results suggest a mechanistic explanation based in muscle physiology for predictions in the literature that intermittent swimming minimizes cost of transport (e.g. [18]). Empirical measurements of power output from isolated muscle bundles allow us to make predictions for future metabolic studies of muscle function and swimming behaviours in fishes. As our understanding of intermittent swimming grows, so too does the realization that fishes employ a wide variety of swimming behaviours to reduce the cost of transport. Entrainment, group swimming and intermittent swimming all differ from 'steady-swimming' described by many flume-based studies, reflecting the complex locomotory behaviours possible by fishes.

Ethics. The use of fish was approved by the Widener University IACUC (2019-001).

Data accessibility. The data that support the findings of this study are openly available at the Center for Open Science at https://osf.io/978y3/?view_only=796c04499143466d9a93289c0193bf15.

Authors' contributions. D.J.C.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, writing—original draft and writing—review and editing; J.D.C.: formal analysis, investigation and writing—original draft; D.J.E.: conceptualization, funding acquisition, methodology, resources and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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