

## Research



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## Biomechanics

# Swimming from coast to coast: a novel fixed-gear swimming gait in fish

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Bluegill sunfish use intermittent propulsion during volitional swimming. The function of this propulsive mode during routine swimming has not been well quantified. At low speeds, propulsive cycle frequencies and amplitudes were constant, and average speed and power output were controlled by modulating coasting duration. This fixed-gear gait may accommodate muscle level constraints on power production. At higher speeds bluegills switched to a mixed power-modulation strategy, increasing speed and power through increased propulsive cycle frequency and reduced coasting time.

## 1. Introduction

Locomotion and fitness are intrinsically linked in most animals. Locomotor costs dominate energy budgets, and mobility is required for effective foraging, predator avoidance and migration [1,2]. Most performance and energy cost data have been obtained under quasi-steady-state conditions [3,4]. The applicability of these data to understanding locomotion in the field is questionable as the routine, volitional locomotor behaviour of most animals is intrinsically unsteady [5,6]. Recently obtained data suggest that the disparity between laboratory and field performance is particularly acute in bluegill sunfish, where routine, volitional swimming is achieved via intermittent propulsion but forced swimming in flumes favours constant propulsion [5].

Intermittent propulsion is a feature of routine locomotion in many birds [7], and in fish is a consistent feature of swimming at high, imposed velocities where it coincides with the recruitment of anaerobic muscle [8]. Although also observed during volitional swimming in fish [9,10], its use at lower speeds is not well understood. This stems in part from the scarcity of data for unconstrained, volitional swimming. The combined availability of large-volume calibration techniques recently applied to quantify avian flight performance in the field [11] and low-cost underwater cameras has enabled the collection of field performance data for fish [5,12] with higher temporal and spatial resolution than has previously been possible [1]. This approach has revealed the use of intermittent propulsion during routine, sustained locomotion at aerobically sustained speeds and propulsive cycle frequencies, but with insufficient detail to indicate why this swimming style is used [5].

Several factors may favour the use of intermittent propulsion during swimming. If the drag incurred during the non-propulsive coasting phase is significantly lower than during propulsive movements, intermittency could reduce average power and energy requirements [13]. Recovery during non-propulsive coasting phases also has the potential to minimize muscle fatigue. Finally, modulation of coasting duration could allow for control of average power output while maintaining relatively constant propulsive kinematics. This may be advantageous as for any given muscle, power output and efficiency are maximal within a relatively narrow parameter space for activation patterns and strain trajectories [14,15]. Explanations for intermittent propulsion during swimming may therefore be akin to the 'fixed-gear' hypothesis for intermittent flight in

birds, which proposes that wing beat frequencies and amplitudes are restricted to an optimal range for muscle power output [7]. A truly fixed-gear swimmer will therefore modulate their average locomotor power output and speed by varying the relative duration of propulsive and non-propulsive phases rather than propulsive cycle frequency or amplitude.

Our goal was to test whether intermittent propulsion in bluegill sunfish represented a fixed-gear locomotor strategy. We hypothesized that propulsive kinematics would not change detectably with swimming speed, and that average speed and power output would be controlled through modulation of the non-propulsive coasting duration. This would be distinct from the kinematic patterns expected if cost and fatigue minimization were the major underlying factors. Both mechanisms need a coasting phase for drag reduction or metabolic recovery respectively, but neither explicitly requires modulation of coasting duration or invariant propulsive kinematics.

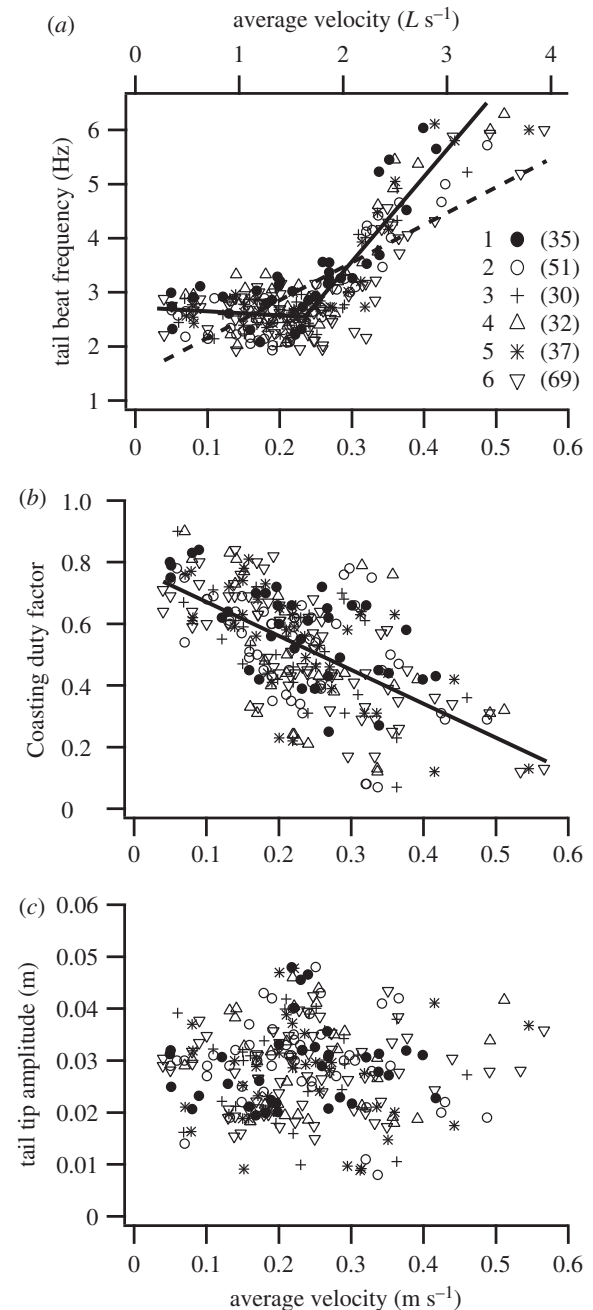
## 2. Material and methods

Bluegill sunfish were collected under Massachusetts Department of Fish and Game licence from Lake Waban, MA, fed daily on earthworms, bloodworms and brine shrimp, and maintained on a 12 L:12 D cycle at 20°C. Kinematic data were obtained from bluegill sunfish swimming volitionally in a  $2.4 \times 1.5 \times 0.6$  m tank with a 0.2 m water depth (body mass =  $61.6 \pm 7.7$  g, total length,  $L = 0.145 \pm 0.007$  m, mean  $\pm$  s.e.m.,  $N = 6$ ). Video was collected at a 60 Hz frame rate using two JVC GC PX-100 cameras (JVC, Yokohama, Japan) mounted perpendicularly above the tank. This maximized spatial resolution (0.4 mm per pixel) and fish track length across large, partially overlapping fields of view. Centre of mass and tail tip location were tracked with a MATLAB-based digitizing program (MATLAB 2014a, The Mathworks Inc., Natick, MA, USA) [16]. Position data were smoothed using a smoothing spline interpolation in the application Igor Pro (v. 6.2, Wavemetrics, Lake Oswego, OR, USA). This method is similar to the cubic spline algorithm recommended for calculating velocities and accelerations from position data [17]. Average velocity ( $U$ ), proportion of time spent coasting ( $q$ ) and average tail beat frequency ( $f$ ) and amplitude ( $A$ ) were measured across contiguous propulsive/coasting cycles. All work was carried out with the approval of the Wellesley College Institutional Animal Care and Use Committee.

As multiple observations were obtained per fish, the relationships between kinematic variables and speed were explored with linear mixed effects regression models where a fish identifier was included as a random factor. Analyses were implemented in R-statistics [18] using a linear mixed effects model package which iteratively determined if the model fit was improved by a break point dividing the relationship into segments with significantly different slopes [19]. If a break point was determined, linear and break point models were compared using the Akaike information criterion (AIC) as an indicator of goodness of fit [20]. If on this basis a segmental model was preferred, relationships between kinematic variables and speed were further explored above and below the break point using linear mixed models again incorporating fish identity as a random factor. Confidence intervals for model parameters were established by a bootstrapping procedure [19].

## 3. Results

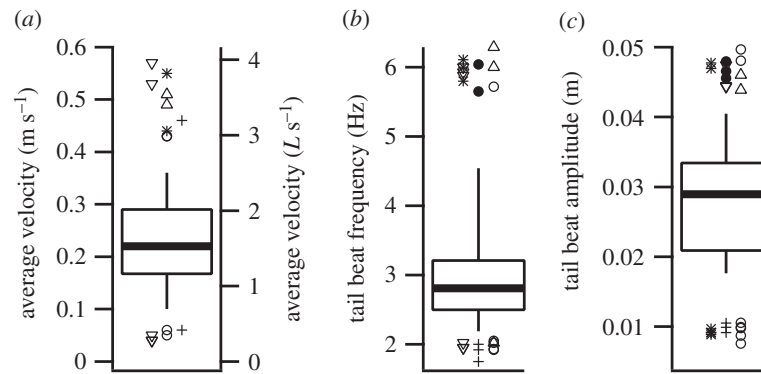
Sustained swimming tracks where fish traversed more than half the tank length consisted of alternating bouts of BCF propulsion and coasting similar to those previously observed in bluegill in a large static tank [21] (example video files, electronic supplementary material).



**Figure 1.** Relationships of (a) tail beat frequency, (b) coasting duration and (c) tail beat amplitude to average swimming velocity maintained across multiple contiguous propulsive/coasting cycles. The relationship between tail beat frequency and velocity was best described by a segmented mixed regression model. The dashed line in (a) shows a mixed linear regression for comparison. Coasting duration in (b) is expressed relative to total time as a duty factor. Data were obtained from six fish. The inset in (a) shows the symbols associated with each fish and the number of observations per individual in brackets.

Changes in tail beat frequency with average speed were best described by a segmented regression with a break point at  $0.24 \pm 0.01 \text{ ms}^{-1}$  ( $\pm 95\%$  CI, figure 1a). The AIC for the segmented mixed model of 279 indicated a substantially better fit to the data than a linear mixed model (AIC, 540). The segmented model did not detect break points in the overall relationships of  $q$  and  $A$  to speed.

Below the break point  $q$  changed with speed ( $t_{144} = -8.3, p < 0.01$ ) while there were no detectable changes in  $f$  and  $A$  ( $f, t_{144} = 0.21, p = 0.83$ ;  $A, t_{144} = 1.84, p = 0.07$ ). By contrast, above the break point  $f$  changed with speed ( $t_{93} = 16.2, p < 0.01$ ) while  $q$  and  $A$  did not ( $q, t_{93} = -1.51, p = 0.13$ ;  $A, t_{93} = 1.05, p = 0.29$ ).



**Figure 2.** Distributions of volitional swimming velocity and propulsive kinematics. (a) Average speed across multiple, contiguous propulsive and coasting cycles (b) propulsive tail beat frequency and (c) amplitude. Bold bars indicate median values. Boxes and whiskers indicate 25th to 75th and 10th to 90th percentiles, respectively. Symbols for outliers and sample sizes associated with the six fish are as in figure 1. Symbols are offset laterally to improve visibility.

The majority of  $U$ ,  $f$  and  $A$  values fell within a narrow range (figure 2). Outliers at the upper end of the velocity range were associated with corresponding high tail beat frequency values.

## 4. Discussion

Bluegills employed a fixed gear at low speeds, modulating average velocity and power output by altering their coasting duty factor while maintaining tail beat frequency and amplitude within a narrow range (figure 1). To our knowledge, this fixed-gear gait has not previously been described in fish. During body-caudal fin propulsion, tail movements are produced by posteriorly moving waves of myotomal muscle contraction that develop progressive waves of axial curvature [22]. Muscle shortening velocities and strain amplitudes are closely related to axial wave and amplitudes and frequencies [23]. Low variation in axial kinematics (figure 2) therefore strongly implies a limited range of propulsive muscle strain trajectories. This is consistent with a fixed-gear strategy arising from muscle level constraints on performance, and potentially allowing optimization of muscle function to maximize power output or efficiency [14,15].

At the upper end of the observed speed range tail beat frequency increased, presumably to meet the increased power requirements of higher speed swimming (figure 1). The persistence of intermittent propulsion at higher speeds and power requirements (figure 1) requires explanation. Why not meet the power requirements at the upper end of the observed volitional speed range with constant propulsion at a lower average cycle frequency? Cost reduction may be a factor, through drag minimization during the coasting phase [13]. Fatigue minimization may also favour coasting by allowing a recovery period for physiological processes that sustain long-term muscle activity, e.g. calcium cycling, replenishment of muscle ATP, creatine phosphate and glycogen levels, and removal of ATP breakdown products [24]. To maintain the same average speed, intermittent propulsion must require higher cycle frequencies and rates of power production during the propulsive

phase than constant propulsion based on uninterrupted tail beats. Even so, the lack of recovery time between successive propulsive cycles during constant propulsion may lead to a more rapid onset of fatigue than during intermittent propulsion.

The observed volitional kinematic patterns differed from those typically observed in fish during steady-state swimming, where speed and power modulation are mainly achieved through changes in tail beat frequency [3]. This could be associated with inter-specific differences, but the majority of data being obtained at imposed, constant velocities is a likely factor. This is illustrated by the contrast in steady-state and volitional swimming behaviours in bluegills. During sustained, aerobic flume swimming, bluegills do not exhibit coasting and employ a wide range of fin beat frequencies. Further, low-speed, flume swimming is powered by the pectoral fins [25] while in the field, pectoral fin propulsion is mainly reserved for station-holding and manoeuvring [5]. The difference may arise from spatial constraints during flume swimming that limits opportunities for coasting [8].

## 5. Conclusion

Bluegills use intermittent propulsion during volitional swimming across a wide range of speeds. At low speeds, this allows maintenance of a fixed gear, potentially enabling optimization of muscle function. Retention of a coasting phase at high speeds may reduce muscle fatigue or reduce energetic cost during low drag coasting. Confirmation will require *in vitro* measurements of muscle contractile properties and energy use.

**Data accessibility.** The raw data on which the figures are based is provided as a spreadsheet (electronic supplementary material).

**Authors' contributions.** All authors contributed to the experimental design and data analyses and made substantial contributions to the drafting of the manuscript. All authors also agree to be held accountable for the content therein and approve the final version of the manuscript.

**Competing interests.** We declare we have no competing interests.

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