Swimming at the Edge: Testing the Endurance-Exhaustion Hypothesis in Shiner Perch (*Cymatogaster aggregata*)

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Abstract

Fish escape responses are a type of fast start used by fish to avoid predation. Better escape performance leads to increased fitness due to increased ability to avoid predation. However, predators of fish can employ a number of behaviors and tools to increase their ability to catch prey fishes. One behavior employed by predators is prolonged chasing, which should exhaust fishes when they are forced into an oxygen debt while swimming at speeds that require burst swimming and the use of anaerobic muscles. It is hypothesized that more exhausted fishes will be worse at escaping from predators. In this study we aim to determine if exhaustion level effects escape performance. Shiner perch, (*Cymatogaster aggreagata*), a labriform swimming shore fish from the Pacific coast of North America, was used to test this hypothesis. We used critical swimming speed tests to determine gait transition (U_{p-c}) and critical swimming speed (U_{crit}). We then rested the fish overnight and transferred the fish to a large flume and tested their escape response while swimming for 20 minutes at 1 BL/s, U_{p-c}, and U_{crit}. Mean U_{p-c} was reached at 4.24 ± 0.45 BL/s and mean U_{crit} was reached at 4.92 ± 0.51 BL/s (mean ± standard deviation). Mean aerobic scope was 682 ± 174 $mgO_2/kg/h$ with most variation occurring in maximum metabolic rate (MMR). Shiner perch optimal swimming speed was 3.21 BL/s. Responsiveness to escape response stimulus increased with exhaustion, but not significantly. Onset of escape response was significantly longer at U_{p-c} and U_{crit} speeds compared to 1 BL/s, turning angle did not significantly differ among the levels of exhaustion. Our results indicate that escape performance may not be substantially altered while swimming at different levels of exhaustion.

Introduction

In this study, we aim to determine if exhaustion level impacts escape response in shiner perch (*Cymatogaster aggregata*). Shiner perch are small, euryhaline surfperches common from Alaska to Baja California (Odenweller, 1975). Shiners are an important prey species for birds, fishes, and marine mammals (Odenweller, 1975; Acevedo-Gutiérrez and Luxa, 2013). It has been hypothesized that large marine mammals attempt to exhaust prey before capture, presumably because a tired fish is less capable of escape (Guinet *et al.*, 2007). Escape response has been measured in relation to swimming speeds (*e.g.* Anwar *et al.*, 2016; Diamond *et al.*, 2016; Nadler *et al.*, 2018), but the responses to extended levels of exhaustion have not been measured. Shiner perch are labriform swimmers and with an easily identified gait transition, the swimming speed at which pectoral-caudal gait transition occurs (U_{p-c}), defined as the transition from primarily aerobic swimming (pectoral fins) to swimming requiring anaerobic caudal fin bursts. While swimming at 1 BL/s, fish are able to maintain velocity indefinitely because they are able to balance oxygen uptake and oxygen use while using aerobic muscles. When fish transition from aerobic swimming with median paired fins to anaerobic caudal fin beats, they begin to acquire an oxygen debt. At U_{p-}

$_c$, labriform swimmers are able to maintain their speed for a prolonged period of time, but not indefinitely, and while swimming at their critical swimming speed (U_{crit}), fish are only able to maintain their speed for 30 minutes. The level of oxygen debt should be very high after 20 minutes while swimming at U_{crit}, mid at U_{p-c}, and no oxygen debt should occur at 1 BL/s. These treatments produce a gradient of exhaustion from U_{crit}, U_{p-c}, to 1 BL/s. We hypothesize that as exhaustion increases, escape response performance will decrease.

Methods

Collection and Husbandry

Shiner perch were collected via seine net at Jackson Beach, San Juan Island, WA, USA (N 48°31′11″, W 123°0′45″) in July and August of 2025. 26 fish were kept in an approximately 160 L flow through seawater table at Friday Harbor Laboratories (University of Washington, USA). Fish were kept at 13.122 ± 0.520°C (mean ± SD) for the duration of the study. Fish were fasted at least 24 hours prior to respirometry trials.

Respirometry

Critical swimming speed (U_{crit}) was determined for 26 shiner perch in a 5.26 L Steffenson MK III intermittent flow swimming tunnel respirometer at 13.5°C. Fish were measured for total length (cm), mass(g), height (cm), and width (cm) before being placed into the swim tunnel respirometer; Table 1 shows mean and standard deviation of subject sizes. As the fish were added, the swim tunnel was set to 0.5 BL/s and metabolic rate was measured for at least 3.5 hours before U_{crit} testing began. Critical swimming speed was measured using 0.6 BL/s increments ramped every 30 minutes (0.2BL/s per minute ramp speed). The swim tunnel was blocked from outside activity by a tarp sheet blocking the tunnel from the rest of the lab. A webcam was used to live monitor the test. From the live webcam, gait transition (U_{p-c}) was noted when the fish had sustained caudal fin beats of 0.3 Hz (Drucker and Jensen, 1996; Svendsen et al., 2010), and the end point of the U_{crit} test was when the fish was unable to remove itself from the back grate for at least 5 seconds (Johansen and Jones, 2011). After U_{crit} was reached, the tunnel was quickly returned to 0.5BL/s for at least 30 minutes to measure exercise-post oxygen consumption (EPOC). Speeds for U_{p-c} and U_{crit} were calculated using Brett (1964) U_{crit} calculation: $U + Ui * (t/ti)$. U was the speed where the U_{crit} end point or gait transition occurred, U_i was the incremental change in speed (0.6 BL/s), t was the length of time at the final speed increment, and t_i was the time speed at the final increment (Brett, 1964; Johansen and Jones, 2011). Solid blocking was corrected directly in the ResPyroMetry software, used to record all temperature and oxygen measurements in the chamber.

Escape Response

After respirometry, the fish were allowed to recover from the swim trials for a minimum of 18 hours in their individual holding tanks (while still being fasted). Following the recovery period, fish were individually transported to a bigger flume to quantify escape performance. The open flume used for escape trials had transparent acrylic side panels and a designated swimming compartment of 50 cm long, 36.5 cm wide, and 26 cm deep. A high-speed camera (Olympus Tough TG-6) set to record at 240 frames per second was installed over the flume to provide a top view of the swimming compartment.

A 6.5cm-diamter black tennis ball was used as visual stimulus against a white background. Two holes were made in the tennis ball, and the ball was subsequently attached to a nylon string and guided over a white PVC pipe installed on the outside of the flume. Prior to each trial, the ball was pulled up over the flume and securely attached until triggered to release. The PVC pipe was placed so that the ball, when released, dropped in a straight vertical line into the visual field of the fish. Care was taken to keep the stimulus system isolated from the flume, to avoid additional mechano-acoustic stimuli. A mirror was set at a 45° angle on the other side of the swimming compartment to time when the ball came to a full stop at the bottom of the PVC pipe (14 cm behind the front grid of the swimming compartment, and 10 cm from the bottom of the flume). The time between release from the top of the PVC pipe and coming to a full stop at the bottom of the pipe was 500 ± 4 ms (120 ± 1 frames).

Fish were swum at three different speeds for 20 minutes each (i.e., 1 BL/s, $U_{p\text{-}c}$, and U_{crit}). After 20 minutes at any of the three given swimming speeds, the ball was triggered to release and escape responses recorded. All three swimming speeds were tested in all fish in randomized sequences, and fish were allowed to recover at 1 BL/s in the flume for 20 minutes between trials.

The onset of the escape response (C-start) was measured relative to the time when the ball was released (i.e., when the ball in motion could potentially be visible by the fish). Cumulative escape distance travelled by the centre of mass (COM) was calculated over the first 100 ms following the onset of the response. The COM was identified as 0.35 x BL from the snout (Roche *et al.*, 2023). Distance travelled was corrected for flow speed by moving the coordinates of the COM at 100ms post-response forward accordingly (i.e., at 1 BL/s, the final COM coordinates were moved towards the front grid by 1/10 x BL; at $U_{p\text{-}c}$, the final coordinates were moved forward by 1/10 x $U_{p\text{-}c}$ x BL; at U_{crit}, the final coordinates were moved forward by 1/10 x U_{crit} x BL). Escape distance was calculated as the distance between the two COM coordinate points in BL. Finally, turning angle was calculated as the angle between the snout and the caudal peduncle, relative to the COM. Video analyses were performed in Kinovea.

Prior to statistical analyses, data were checked for normality and equal variance. The test parameter of statistical significance was set at $\alpha = 0.05$. Responsiveness across the three swimming speeds was compared using a chi-squared test. Other kinematics data were compared using one-way analyses of variance (ANOVAs).

Statistical Analysis

Swimming aerobic scope was calculated using our oxygen consumption rates measured at 0.5 BL/s as our swimming routine metabolic rate (RMR) and maximum metabolic rate (MMR) was the highest oxygen consumption rate measured during the U_{crit} test. RMR was calculated as the mean of the lowest 10 MO2 measurements during swimming at 0.5BL/s (Norin and Malte, 2011). U_{crit} testing has been shown to produce reliable MMR data (Raby *et al.*, 2020). Optimal swimming speed (U_{opt}) was calculated using the formula $Uopt = -\frac{b}{2a}$. A quadratic model was used to fit the curve, b was the linear term of the model, and a was the quadratic term of the model.

Table 1. Shiner perch total length, weight, height and width, used for solid blocking corrections in respirometry data.

Sample parameters (N = 25)	
Total length (mean ± SE)	12.76 ± 0.17 cm
Wet weight (mean ± SE)	25.84 ± 0.93 g
Height (mean ± SE)	3.62 ± 0.05 cm
Width (mean ± SE)	1.27 ± 0.03 cm

Results

Swimming and Respirometry

The shiner perch reached $U_{p\text{-}c}$ at 4.24 ± 0.45 BL/s and U_{crit} at 4.92 ± 0.51 BL/s (means ± standard deviations) (Figure 1). Shiner perch mean RMR while swimming at 0.5 BL/s was 162 ± 25.6 mg/kg/h, mean MMR was 845 ± 168 mg/kg/h and mean aerobic scope between RMR and MMR was 682 ± 174 mg/kg/h. Figure 2 shows aerobic scope, MMR, and RMR. Optimal swimming speed (U_{opt}) was 3.21 BL/s, shown in figure 3.

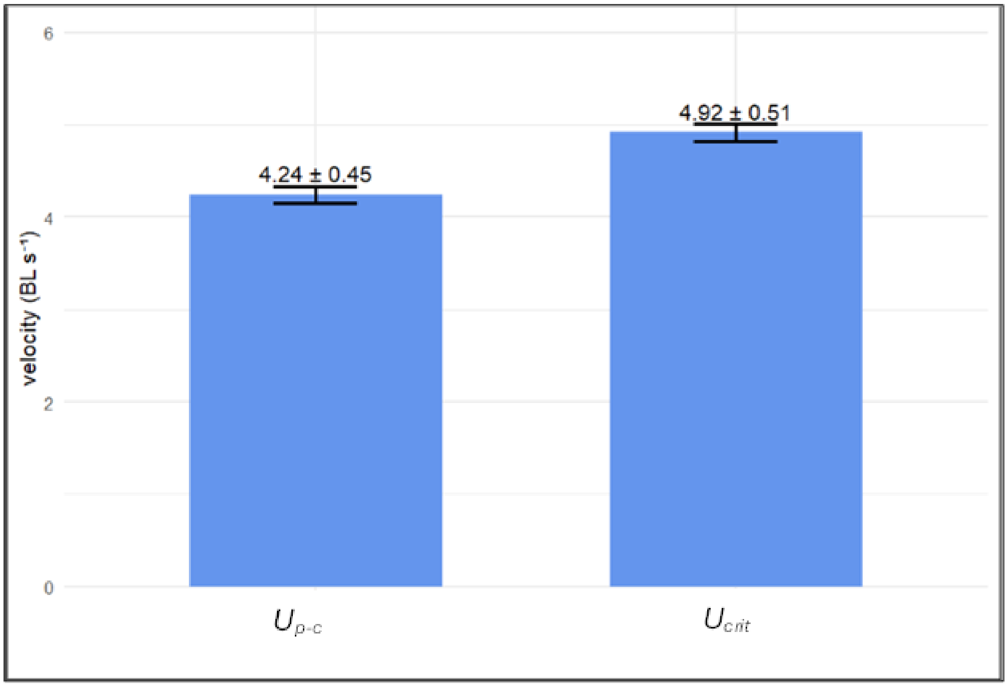

Figure 1. Pectoral-caudal gait transition ($U_{p\text{-}c}$) and critical swimming speed (U_{crit}) in shiner perch (*Cymatogaster aggregata*).

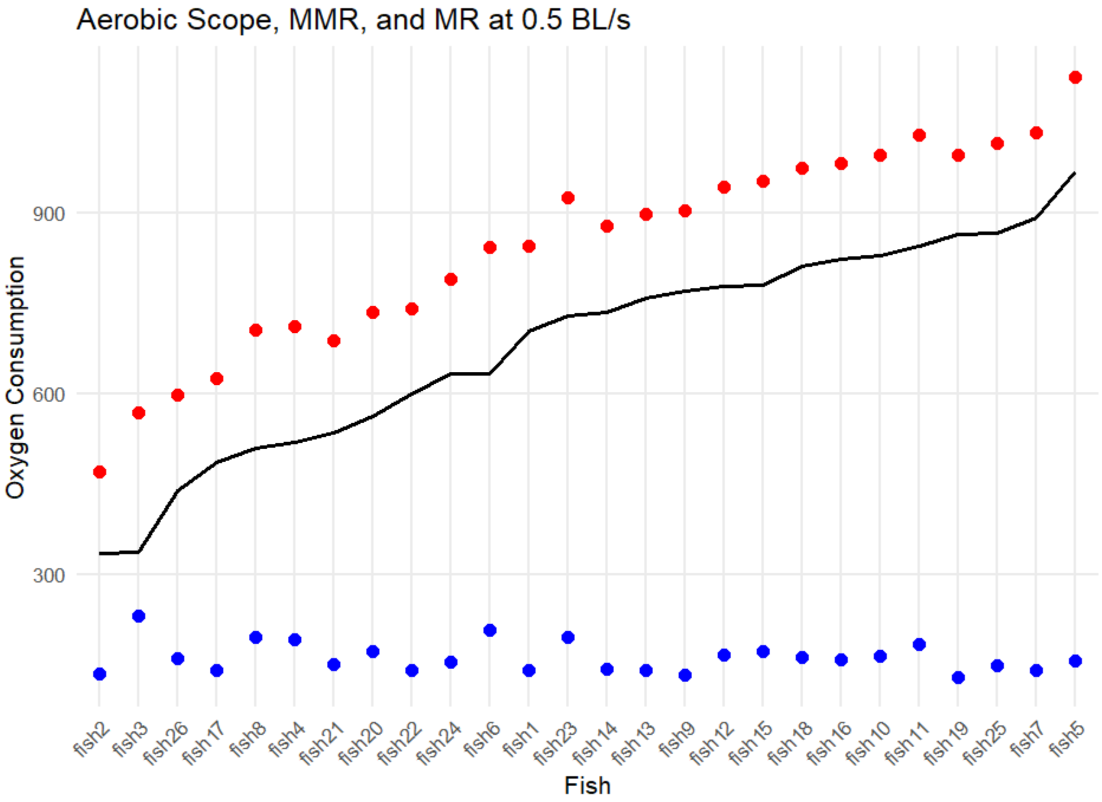

Figure 2. Oxygen consumption data from 26 shiner perch. Blue dots indicate RMR at 0.5 BL/s, red dots show MMR

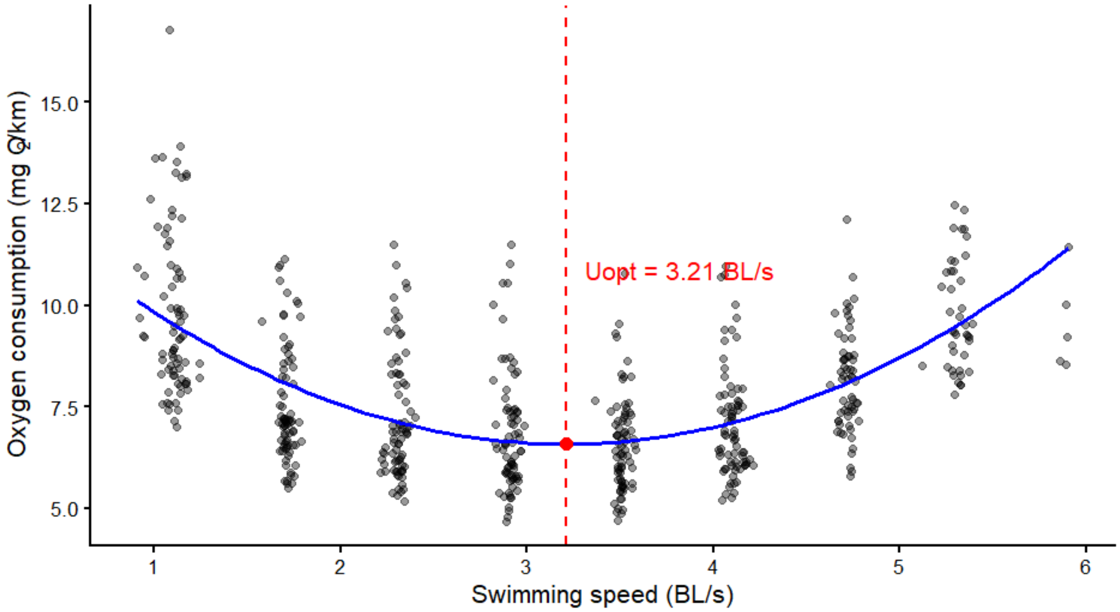

Figure 3. Shiner perch oxygen consumption per distance (mgO_2/km) at speeds used during U_{crit} testing. The optimal swim speed is labeled with a dashed red line at 3.21 BL/s.

Escape Response

Responsiveness to the visual stimulus increased with increasing swimming speed, albeit not significantly (Figure 4A). The onset of an escape response was not significantly different among swimming speeds (Figure 4B). Cumulative distance travelled by the COM during 100ms from the onset of the escape was significantly longer at U_{p-c} (mean ± sd; 0.67 ± 0.17 BL, $p = 0.005$) and U_{crit} (0.64 ± 0.15 BL, $p = 0.01$), compared to at 1 BL/s (0.38 ± 0.21 BL) (Figure 4C). Turning angle did not significantly differ among swimming speeds (Figure 4D).

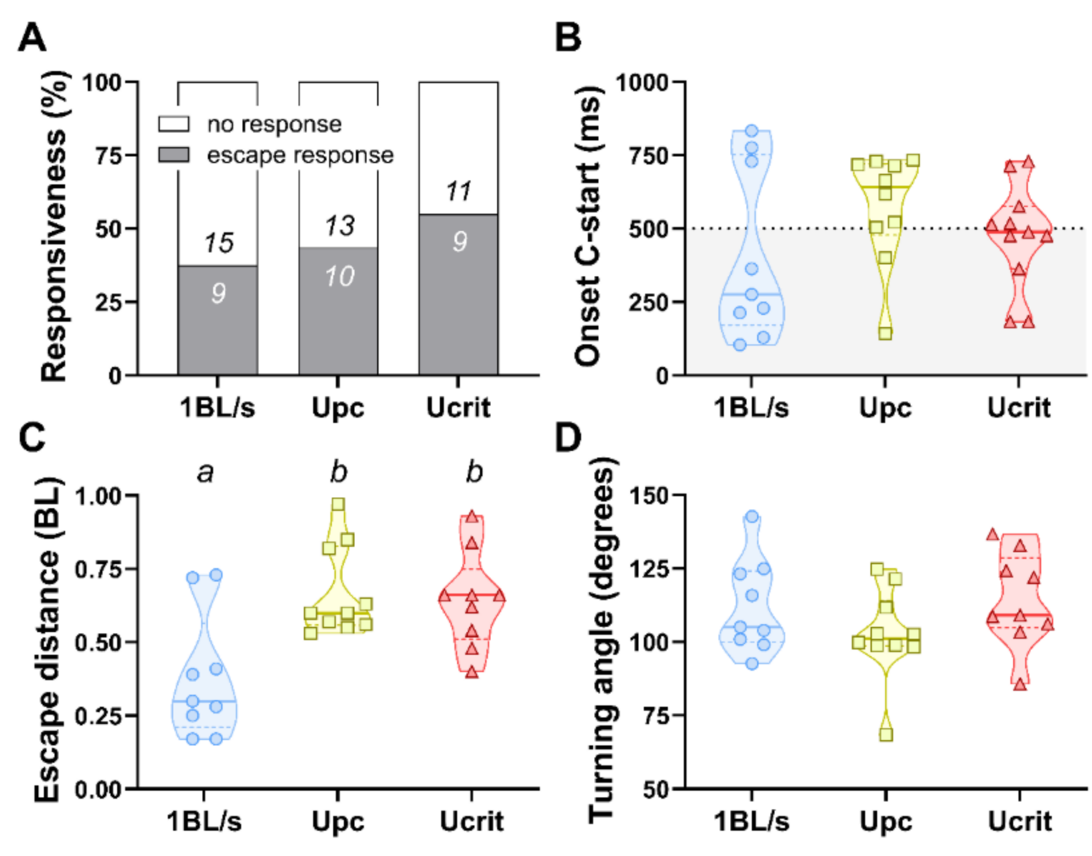

Figure 4. – Escape response kinematics at 1BL/s (blue circles), Upc (yellow rectangles), and U_{crit} (red triangles). A, the responsiveness of the tested fish to the visual stimulus (bar height reflects fractions in %, numbers inside each bar reflect actual successful vs unsuccessful trials). B, the onset of the C-start relative to the time when the ball was released. The grey area represents the time when the ball was in motion, the horizontal dashed line at 500ms is when the ball came to a full stop at the bottom of the pipe. C, cumulative escape distance over 100ms from the onset of an escape response. D, turning angle during the escape response. Full lines in the violin plots are median values. Sample sizes are reflected by the number of successful escape responses at each swimming speed. Letters indicate significant differences.

Discussion

Our recorded $U_{p\text{-}c}$ and U_{crit} values were higher than those reported by Roche *et al.*, (2014: $U_{p\text{-}c}$ = 3.1, U_{crit} = 3.8) but similar to U_{crit} reported by Christensen *et al.*, 2018; U_{crit} = 5.1 BL/s). It is noteworthy that the aforementioned two studies applied slightly different protocols; Roche et al. (2014) increased flow velocity at 0.5 BL/s in 30 minute intervals at 12°C, whereas Christensen et al. (2018) increased flow velocity at 0.5 BL/s in 45 minute intervals at 12.5°C (cf. our study increased flow velocity at 0.6 BL/s in 30 minute intervals at 13.5°C). In our study, U_{crit} was typically reached one step higher than U_{p-c} (i.e., 0.6 BL/s).

Aerobic scope varied between individuals in our trials from 335.5 mgO_2/kg/h to 967.8 mg/kg/h. More variability was observed in MMR (469.9 to 1124.9 mg/kg/h) than in RMR at 0.5 BL/s (130.0 to 230.3 mgO_2/kg/h), so differences in aerobic scope are mostly related to differences in MMR. Fish with higher aerobic scope and MMR also had higher critical swimming speeds. In the future we will explore the intersection between individual fishes with more aerobic capacity and their escape performance (e.g. Metcalfe *et al.*, 2016). Mean optimal swimming speed was 3.21 BL/s, identical to the optimal speed found previously in shiner perch by Christensen *et al.* (2018).

Responsiveness to the visual stimulus increased with increasing swimming speed, but the observed differences were not statistically significant. We observed large inter-individual variations in escape kinematics parameters. Escape distance is the only parameter that differed significantly among treatments, with higher swimming speeds resulting in a longer escape distance following stimulation; yet no difference was observed between U_{pc} and $U_{crit.}$ The longer escape distances at U_{p-c} and U_{crit} can likely be explained by the reduced acceleration required when the fish perceives the stimulus, since the fish are already swimming close to their maximum burst swimming speeds, compared to fish swimming at 1BL/s. This is in contrast with our hypothesis that exhaustive swimming would decrease escape performance.

We did not take the sequence of tested swimming speeds into account yet. However, a previous study documented repeatable individual escape performances to sequential stimuli, suggesting minimal differences in escape responses across the three trials for similar swimming speeds (Marras *et al.*, 2011).

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