Intraspecific variation in swimming- and escape performance in the labriform shiner perch, *Cymatogaster aggregata*

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Abstract

Intraspecific variation in swimming performance, morphology and escape responses was assessed in the labriform shiner perch, *Cymatogaster aggregata*. Shiner perch were videotaped while swimming in a respirometer during a critical swimming speed (U_{crit}) protocol. The degree of individual variation in both oxygen consumption rate ($\dot{M}O_2$) and kinematic performance was evaluated from this U_{crit} challenge. Fast escape performance was also evaluated in the same group of fish. There was an approximately two-fold variation in metabolic rate of fish swimming at 0.5 body lengths per second (MR@0.5 bl s^{-1}) and active metabolic rate, aerobic scope for swimming and critical swimming speed. A significant correlation was found between active metabolic rate and aerobic scope and between MR@0.5 bl s^{-1} and aerobic scope. Similarly there was a significant relationship between active metabolic rate and U_{crit}. Individual variation in swimming performance could not be explained by differences in morphology of the caudal or pectoral fins or variation in body shape or size. There were no significant relationships between stage of escape response completed and any metabolic variables indicating that anaerobic escape responses are independent of aerobic capacity of the fish.

Introduction

Locomotion in fishes, like in other animals, serves multiple purposes. Fish may swim to locate food, escape from predators, migrate, change environments or depths or engage in social interactions. Locomotion in fish can be divided into two forms; body-caudal fin (BCF) and median-paired fin (MPF) locomotion (Webb, 1998). Of the MPF swimmers, labriform locomotion is the most widespread. Labriform swimmers use their pectoral fins

for propulsion at low to medium swimming speeds but at a certain threshold speed a transition in gait from only pectoral to a combination of pectoral and caudal fin swimming occur. At high speeds caudal fin locomotion alone is utilized for rapid burst swimming. This gait transition speed is termed U_{p-c}. The transition from MPF to BCF has been believed to coincide with the switch from aerobic to anaerobic swimming (Drucker and Jensen, 1996) but a recent study on the labriform striped surfperch, *Embiotoca lateralis*, found that gait transition occurred prior to the onset of anaerobic swimming (Svendsen et al., 2010). The standard method of assessing swimming performance is the critical swimming speed (U_{crit}) test, in which the fish is allowed to swim against a water current of stepwise increasing speed until fatigue sets in and the fish fall back onto the rear grid of the flume. Swimming at low to medium speeds (pectoral fin swimming) uses red muscles that are fuelled by aerobic energy metabolism (oxidative phosphorylation). As swimming speed approaches U_{crit} a gradual transition to from aerobic to anaerobic energy production occurs (Brett, 1964; Lee et al., 2003). There is a switch to white anaerobic muscles which rely on anaerobic glycolysis for energy and thus are only used for short bursts or for rapid acceleration. Survival in many fishes is dependent on how they use the interplay of these systems to either capture prey or escape from predators.

On a physiological level a trade-off may exist between the fishes ability to perform very well at aerobically vs anaerobically. For example, individual fish that have a relatively high aerobic scope, and hence possess a higher U_{crit}, may perform relatively poorly in activities such as burst swimming and escape. Such a trade-off may exist since a potential compromise may be found between the amount of red (aerobic) and white

(anaerobic) muscle present in a single fish. This has been emphasized by Kolok (1999) but very little attention has been given to intraspecific variation in swimming performance in relation to variation in aerobic metabolic performance. Additionally where such variations have been assessed, there has been a lack of proper corrections for the effect of body mass on oxygen consumption rate ($\dot{M}O_2$) (Reidy et al., 2000).

In addition to the confounding effects of body mass, many studies have shown aerobic metabolic performance in fish to be highly variable across species, populations, life-stages and under different environmental conditions (Post and Lee, 1996; Clarke and Johnston, 1999; Eliason et al., 2011). This variability leads to a diversity in species specific physiological responses with regards to activity, environmental conditions and performance. Intraspecific variation in swimming performance, as well as aerobic metabolic rate, is starting to receive more attention in fish. Kolok (1999) reviewed the literature for studies on intraspecific variation in prolonged swimming performance and concluded that individual variation in critical swimming speed is substantial and repeatable. The importance of individual variation becomes clear in the context of Darwinian fitness. Individual fish capable of swimming faster and/or longer (i.e. have greater stamina) may escape the attack of a predator better than a relatively slower conspecific. In terms of energy, fish with a greater aerobic capacity (greater absolute aerobic scope) will be less constrained by resource allocation making more energy available for routine activities.

In this study, $U_{p\text{-}c}$ was located at 1.9 bl s^{-1} but an anaerobic component was not detected before 2.3 bl s^{-1}. These swimming speeds represented 73 and 88% of U_{crit},

respectively, meaning that an anaerobic component of locomotion kicked in somewhere within this interval.

In the present study, we have assessed the extent of intraspecific variation in swimming performance, escape performance and external morphology of shiner perch, *Cymatogaster aggregata* Gibbons 1854, in relation to variation in aerobic metabolic performance.

Materials and methods

Fish

Shiner perch were collected by beach seining at Jackson Beach (48^{o}31'N, 123^{o}00'W), San Juan Island, Washington, USA and transferred to holding facilities at Friday Harbor Laboratories in august 2011. The fish were held in 60 x 22 x 115 cm flow through tanks at 12±1^{o}C, supplied with a continuous flow of unfiltered seawater at a salinity of 34 ppt. 21 fish weighing between 22.5 and 27.3 g (mean 24.7±1.61 g) with a total length between 11.61 and 13.00 cm (mean 12.39±0.45 cm) were individually tagged using fluorescent visible implant elastomer (VIE) tags (Northwest Marine Technology, Shaw Island, Washington, USA). Tagging was performed on anesthetised fish (0.1 g l^{-1} MS-222) and elastomers were injected immediately under the skin covering the left operculum using a 0.3 ml syringe. Fish were left to recover from tagging for at least 24 hours.

Respirometry

Respirometry was performed using computerised intermittent-closed respirometry (Steffensen et al., 1984). A swim tunnel with a volume of 5.3 l, containing a swimming section of 7.5 x 7.5 x 28 cm and a voltage controlled motor and propeller allowed for continuous recirculation of water at a given velocity past a swimming fish. Flow inside the respirometer was made rectilinear by a honeycomb plastic screen situated at the entrance of the swimming section. The motor was calibrated against water velocity by a handheld flow meter (Höntzsch GmbH, Waiblingen, Germany). The respirometer was immersed in an ambient tank of 41.5 l supplied with recirculating, fully aerated, water at 11.8± 0.1^{o}C and a salinity of 34 ppt from a 60 l external reservoir. Oxygen saturation was assured by bubbling with atmospheric air and water oxygen tension (P_wO_2) was calculated as $P_wO_2 = FO_2 (P_{BAR} - PH_2O)$, where FO_2 is the fraction of oxygen in the atmosphere (0.2095), P_{BAR} is the barometric pressure, and PH_2O is the water vapour pressure at given temperature and salinity. The flushing period replenished the respirometer with fully aerated water while at the same time removing metabolites. To obtain intermittent flow, the respirometer was equipped with an inlet pipe as well as an outlet chimney, allowing water to be exchanged inside the respirometer by means of a 5 l min^{-1} Eheim 1046 pump (Eheim GmbH & Co., Deizisau, Germany).

Automated measurements of $\dot{M}O_2$ were divided into periods of flush, wait and measurement. During the 3.5 min periods of flush, water inside the respirometer was exchanged with water from the ambient tank. This flush system was alternately turned on and off by a relay station, allowing fresh seawater to enter the respirometer. The 1.5 min wait period took into account a lag in system response assuring a linear decrease in P_wO_2

over time, and was followed by the 5 min measurement period where changes in P_wO_2 due to fish respiration were recorded by an O_2-optode and monitored at 1 Hz by the AutoResp™ software (LoligoSystems, Tjele, DK). Prior to the experiment, the O_2-optode was calibrated against an anoxic solution of sodium sulphite dissolved in seawater and fully aerated water inside the respirometer. All variables, including duration of measurement, flush and wait periods, were typed into AutoResp^{TM} software prior to the experiment. Oxygen consumption from microorganisms produced artificially high values of $\dot{M}O_2$, that was corrected for by measuring $\dot{M}O_2$ before the fish was introduced into the respirometer and again after the fish had been removed.

The respirometer was shielded from the surroundings during all measurements by means of black plastic drapings hanging from the ceiling, thereby minimising disturbance of the fish.

Escape response

An elliptical swimming arena (92 x 74 cm; 18 cm in height) marked with calibrated gridlines in the field of view was used to measure the escape response of individual fish. The arena was illuminated with two 500-watt and two 100-watt spotlights placed 1.66 m above the floor of the arena. Water level was maintained at 14 cm for all experiments and was changed every 2 hours to control for temperature (12.2-13.8^{o}C). Escape responses were initiated by a stimulus made of a 4-oz (113.4 g) ball sinker fastened to a metal disc, which was dropped from 88 cm above the water surface using an electromagnet. The stimulus fell through an ABS pipe (7.5 cm diameter; 87 cm in length) positioned at one end of the arena, 36 cm from the centre, ending 1.0 cm above the water level to prevent

fish from seeing and reacting to the falling stimulus as done by Turesson et al. (Turesson et al., 2009). A mirror (7 x 5 cm) was placed 3 cm away from the end of the tube at 45^{o} angle from the water surface so the camera would film when the stimulus made contact with the water, which was considered as initiation of stimulation.

A square piece of black plastic mesh (14 x 14 cm; mesh size 1 x 1 cm) was hung at the water surface with monofilament line, 6 cm away from the stimulus, acting as a refuge to ensure proper positioning of the fish prior to stimulation. This mesh provided some shading, which attracted the fish to remain underneath the refuge within 2.0 bl of the stimulus allowing the fish to escape in any direction and filming to occur through the mesh. Each escape response was initiated after the fish adjusted to the conditions of the arena for 30 minutes and was positioned perpendicular to the stimulus drop zone. The response was filmed at 250 frames s^{-1} using a high-speed digital camera (FASTEC Imaging, Ranger, San Diego, CA, USA).

Fin morphology

To evaluate differences in fin morphology, pictures were taken with a handheld digital camera (Olympus µTough 8000) of the caudal fin and left pectoral fin of anaesthetised fish. The fins were fully distended manually and allowed to contract to a natural position before pictures were taken. A ruler was placed beside the fins as reference for subsequent digital analysis. The length of the leading edge of the pectoral fin, height of the caudal fin and surface area of both fins were measured in individual fish using ImageJ software v 1.44 (National Institutes of Health, USA). From these measurements, the aspect ratio (AR) of the pectoral fin was calculated using the equation

$$AR = L^2/s$$

Where L is the length of the leading edge of the pectoral fin (mm) and s is the surface area of the pectoral fin (mm^2).

Experimental protocol

Shiner perch was transferred individually from the holding tanks into the swimming section of the respirometer. Transfer of the fish occurred within a water filled plastic bag, thereby avoiding aerial exposure of the fish. The fish was allowed to swim at 0.5 bl s^{-1} for 6-8 hours prior to experimental onset, allowing for estimates of routine metabolic rate (RMR) at this swimming speed. Following this, water velocity was increased in a stepwise fashion in intervals of 0.5 bl s^{-1}. Three measurements of $\dot{M}O_2$ were recorded at each swimming speed (i.e. the fish were allowed to swim for 30 min at each speed). This stepwise increase in water velocity was performed until the fish fatigued and fell back onto the grid at the back of the swimming section for more than 10 s. At this point water velocity was returned to 0.5 bl s^{-1} and the fish was removed from the respirometer following completion of the ongoing measurement period. Three measurements of background respiration were recorded before another fish was introduced to the respirometer and allowed to swim at 0.5 bl s^{-1}.

Following respirometer experiments, the fish were placed in a recovery tank for a minimum of 24 h prior to measuring escape responses as described above.

Data analysis

Linear regressions between P_wO_2 and time were calculated automatically by the AutoResp^{TM} software for each period of measurement and slopes (k) derived from these regressions were used to calculate oxygen consumption by the fish according to the equation

$$\dot{M}O_2 = k\ V_{resp}\ \beta_wO_2\ M^{-1}$$

where $\dot{M}O_2$ is the oxygen consumption rate (mg kg^{-1} h^{-1}), k is the change in P_wO_2 over time (kPa h^{-1}), V_{resp} is the volume of the respirometer minus volume of the fish (l), and β_wO_2 is the solubility coefficient of oxygen in water at given temperature and salinity (mg l^{-1} kPa^{-1}) (Dejours, 1981). Presence of fish in the respirometer caused water velocity to increase. This solid blocking effect was corrected for by the AutoResp^{TM} software as described by Steffensen et al. (Steffensen et al., 1984). The three measurements of $\dot{M}O_2$ at each swimming speed were averaged and a mean value of background respiration over the entire experimental period was subtracted to give the actual $\dot{M}O_2$ of the fish. Aerobic scope for swimming was calculated as AMR – $\dot{M}O_2$@0.5 bl s^{-1}. This method of presenting aerobic scope was used to avoid confounding effects of extrapolation back to SMR ($\dot{M}O_2$@0 bl s^{-1}).

Data of $\dot{M}O_2$ *versus* swimming speed (U) were fitted to the power function

$$\dot{M}O_2 = a + bU^c$$

where a is an estimate of SMR ($\dot{M}O_2$@0 bl s^{-1}), and b and c are parameter estimates derived from the fitting procedure using TableCurve™2D4 (Jandel Scientific Software, AISN Software Inc.) as suggested by Korsmeyer et al. (Korsmeyer et al., 2002).

Cost of transport (COT) was calculated as

$$COT = \dot{M}O_2\ U^{-1}$$

wherefrom the optimal swimming speed (U_{opt}) was obtained as the minimum COT value.

Critical swimming speed (U_{crit}) was calculated according to Brett (Brett, 1964) as

$$U_{crit} = U_p + (t_p/t_i)\ U_i$$

where U_p is the velocity at which the fish swam for the entire 30 min period (bl s^{-1}), t_p is the duration from obtaining maximum swimming speed to crash of the fish (min), t_i is the duration of the individual swimming periods at a given velocity (30 min) and U_i is the stepwise increase in swimming speed (0.5 bl s^{-1}).

Relationships between oxygen consumption variables were compared using linear regression.

Sequential video images of each escape response of individual fish were uploaded to a computer running WINanalyze (v1.5) 3D Software. The centre of mass and the center of the head were digitized frame by frame from a dorsal view. The software produced coordinates, calibrated to the grids, per frame that were used to calculate maximum velocity (m s^{-1}), turning radius (cm), turning rate (degrees s^{-1}), and time to respond to

stimulus (ms). During each escape response the completion of stages 1 through 3 were qualitatively described and the maximum velocities during each stage were estimated for each fish.

Results

Oxygen Consumption Variables

All oxygen consumption data is summarized in Table 1. All significant relationships between oxygen consumption variables are shown in Figures 1-4. As seen in Table 1, there was large variation in absolute aerobic scope and active metabolic rate between individuals. These two variables showed a strong positive relationship (Fig. 1).

Table 1. Oxygen consumption rate and swimming performance measures.

	Mean	Minimum	Maximum	Factorial variation	CV (%)
MR@0.5	84.5±3.43	46.2	108.1	2.34	18.6
AMR	676.1±18.11	463.8	802.1	1.73	12.3
ASS	591.6±19.92	370.6	755.8	2.04	15.4
FAS	8.5±0.63	5.0	17.3	3.46	34.0
U_{p-c}	3.9±0.14	2.5	5.0	2.00	16.0
U_{crit}	4.6±0.08	3.6	5.0	1.39	8.1
U_{opt}	2.3±0.13	1.5	3.5	2.33	25.8

MR@0.5, metabolic rate at 0.5 bl s^{-1}; AMR, active metabolic rate; ASS, aerobic scope for swimming; FAS, factorial aerobic scope; U_{p-c}, swimming speed at gait transition; U_{crit}, critical swimming speed; U_{opt}, optimal swimming speed; CV, coefficient of variation.
Means are presented ± s.e.
Factorial variation is maximum divided by minimum.

Metabolic rate at 0.5 bl s^{-1} varied less between fish but there was still a significant relationship with aerobic scope (Fig. 2). Individuals that had a higher metabolic rate at 0.5 bl s^{-1} had a lower aerobic scope for swimming (Fig. 2). Also correlated with aerobic scope was U_{crit}. In general fish with a larger scope for activity were found to have a higher critical swim speed (Fig. 3). In addition, U_{crit} was also found to have a positive relationship with active metabolic rate (Fig. 4). Other variables calculated from oxygen consumption do not show significant relationships with each other and generally show less individual variation (Table 1).

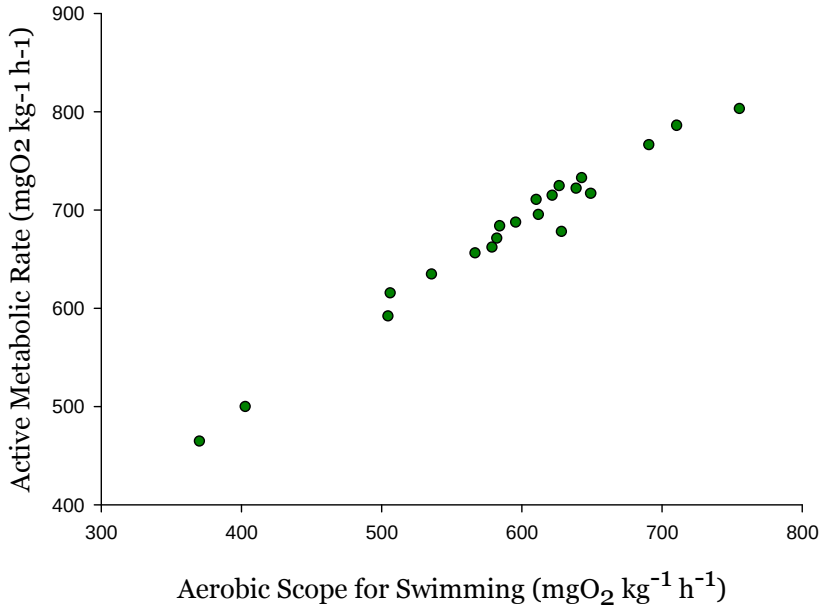

Figure 1. Relationship between aerobic scope and active metabolic rate for individual fish. N = 21, $p < 0.001$, $r^2 = 0.977$.

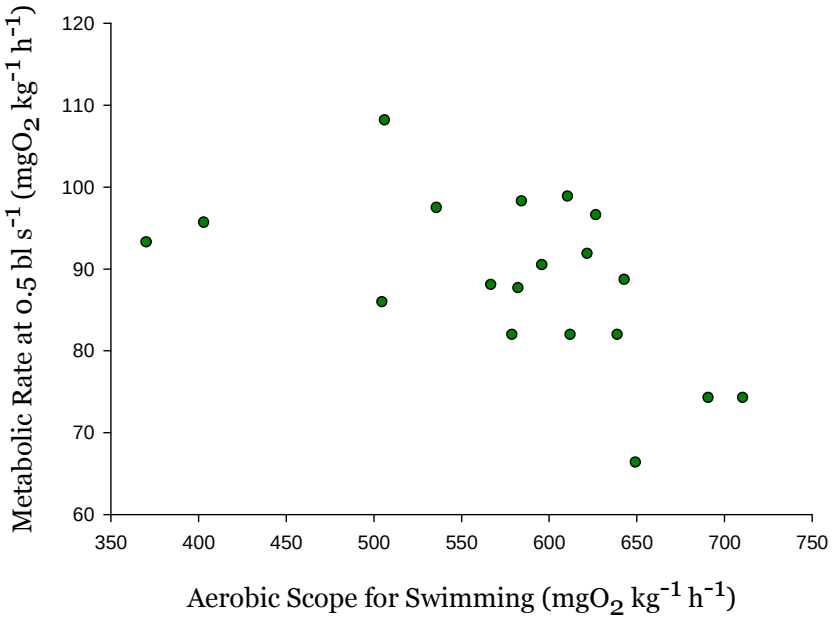

Figure 2. Relationship between aerobic scope and metabolic rate at 0.5 bl s^{-1} for individual fish. N = 21, p = 0.005, r^2 = 0.4.

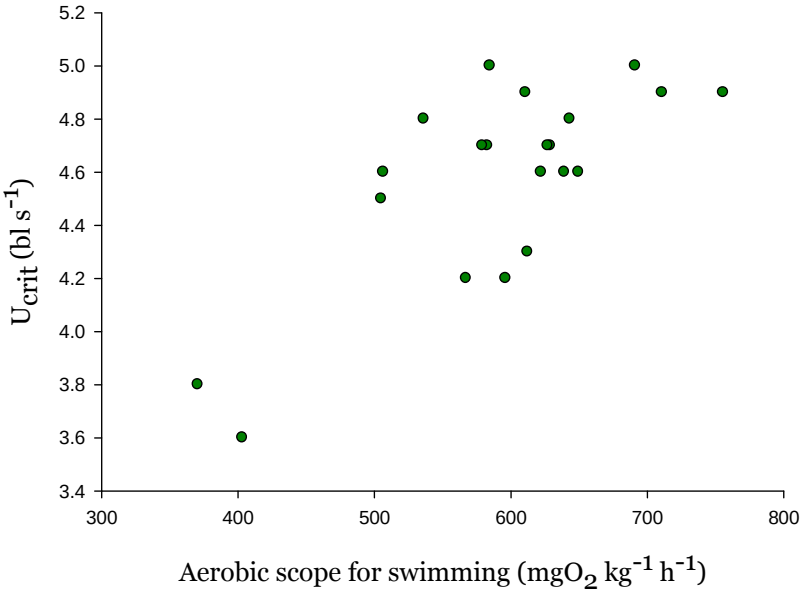

Figure 3. Relationship between aerobic scope and U_{crit} for individual fish. N = 21, p < 0.001, r^2 = 0.6.

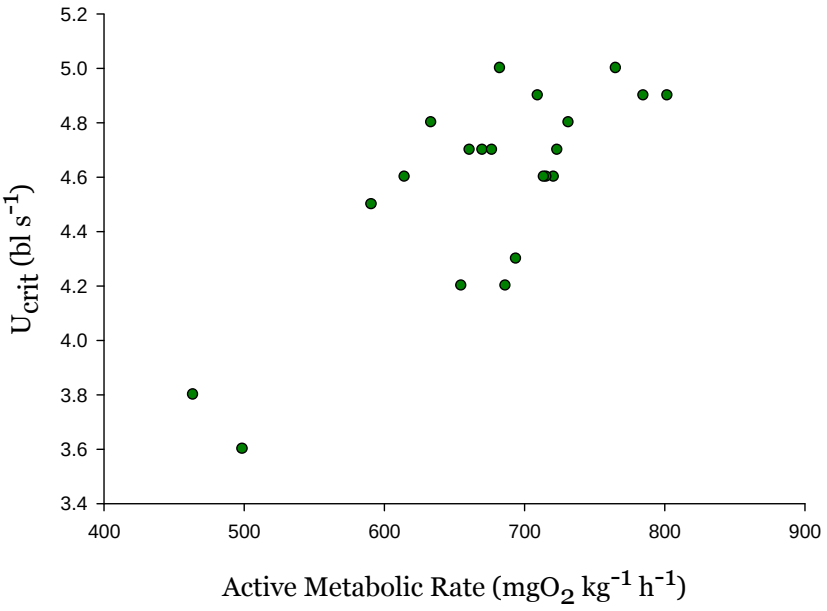

Figure 4. Relationship between U_{crit} and active metabolic rate for individual fish. N = 21, $p < 0.001$, $r^2 = 0.56$.

Escape Responses

Less than 10% of fish failed to respond to the stimulus, 43% completed a stage 1 response, 24% responded with a stage 1 and 2 response and the final 24% completed stages 1, 2, and 3. There were no significant correlations between escape responses and the fishes aerobic scope for activity (Fig. 5).

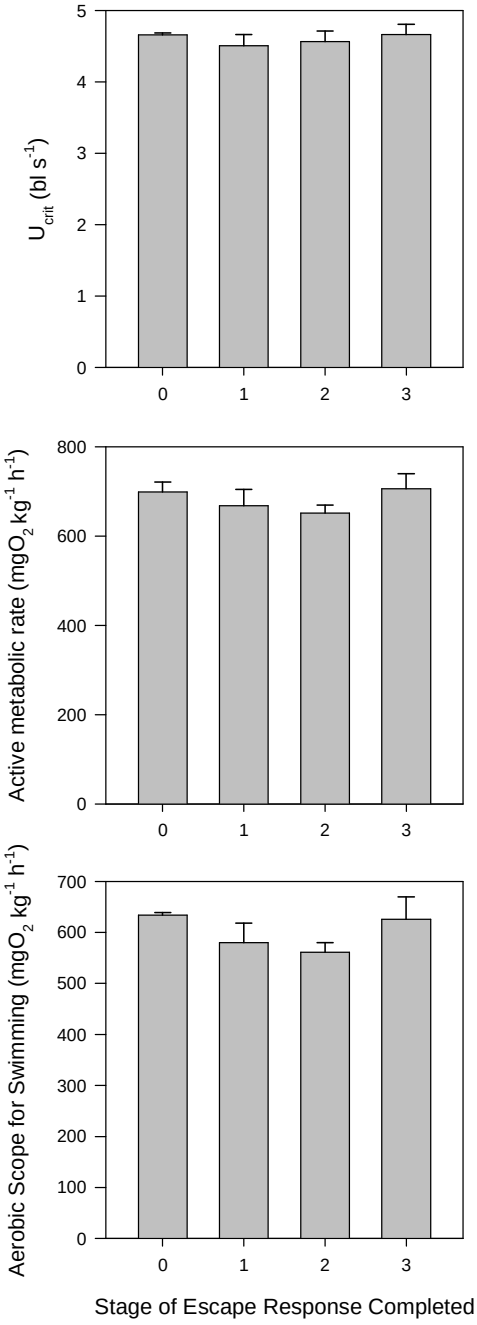

Figure 5. Measures of aerobic variables at different stages of the escape response.

Body and Fin Morphology

Tables 4 and 5 summarize the general morphological characteristics of both body and fin size. No significant relationships were found between oxygen consumption variables and size or between fin characteristics and oxygen consumption variables.

Table 4. General morphological parameters.

	Mean	Minimum	Maximum	CV (%)
M (g)	24.7±0.33	22.5	27.3	6.1
TL (cm)	12.43±0.10	11.61	13.00	3.5
Depth (cm)	3.55±0.02	3.38	3.74	2.8
Width (cm)	1.46±0.01	1.34	1.60	4.5
Fineness ratio	3.50±0.03	3.15	3.76	4.3

M, body mass; TL, total length; CV, coefficient of variation.

Means are presented ± s.e.

Table 5. Pectoral and caudal fin characteristics.

	Mean	Minimum	Maximum	CV (%)
Pectoral fin				
Length (mm)	24.1±0.25	21.7	27.3	4.8
Area (mm^2)	282.8±6.63	217.2	344.5	10.8
AR	4.1±0.07	3.6	4.7	8.0
Caudal fin				
Height (mm)	28.7±1.09	15.9	39.5	17.4
Area (mm^2)	310.6±10.99	204.5	428.1	16.2

AR, aspect ratio; CV, coefficient of variation.

Pectoral fin length refers to the leading edge of the fin. Means are presented ± s.e.

Discussion

Individual variation is a field that has been well studied in humans but only little is known about intraspecific variation in other vertebrates (Burton et al. 2011). One of the major objectives of this study was to investigate the degree of individual variation in swimming and escape performance in a labriform fish, the shiner perch. With regard to swimming and metabolic performance we showed an approximately two-fold variation in almost all of the parameters tested (Table 1).Variation also existed when the fish performed anaerobically during the escape response trials. This observed variation seems to be unsubstantiated by differences in morphology since none of the morphological parameters investigated (fineness ratio, pectoral fin length, area and aspect ratio, as well as caudal fin height and area) could explain the variation in swimming performance. Such lack of correlation between external morphology and swimming performance is also reported by Reidy et al. (2000) where total fin surface area of Atlantic cod (*Gadus morhua*) showed no relations with neither aerobic, nor anaerobic, swimming performance.

Aerobic scope for swimming of the shiner perch was found to correlate very tightly with active metabolic rate, and less so with metabolic rate at 0.5 bl s^{-1}. This means that it was the metabolic ceiling (i.e. active metabolic rate) that was responsible for most of the two-fold variation in aerobic scope observed.

The positive correlation between aerobic scope for swimming and U_{crit} observed here in the shiner perch also agree with the findings of Reidy et al. (2000). These authors found a similar correlation between aerobic scope and U_{crit} in the Atlantic cod supporting the notion that metabolism is fuelled mainly aerobically throughout the swimming trial

(Nelson et al., 1996). Further support for this comes from a study on striped surfperch, *Embiotoca lateralis* (a labriform swimmer similar to the shiner perch from the present study), where no indication of any anaerobic component of swimming was present below swimming speeds between 73 and 88% U_{crit} (Svendsen et al., 2010).

In addition to the positive correlation between U_{crit} and aerobic scope for swimming, the study by Reidy et al. (2000) also found a significant negative correlation between U_{crit} and burst performance. Since burst swimming is mainly anaerobic, this finding suggests a trade-off between aerobic and anaerobic swimming performance within individual fish. In our study on shiner perch we also tested for potential interactions between aerobic and anaerobic swimming performance by evaluating the number of stages completed during a fast escape response. We did not find any interactions between such anaerobic escape performance and either U_{crit}, active metabolic rate or aerobic scope for swimming. This lack of correlation could indicate that the two components of the locomotory machinery, the red aerobic and the white anaerobic muscle, does not trade off within the individual shiner perch. It is possible that the fish with a higher aerobic capacity (aerobic scope for swimming) were able to obtain a higher U_{crit} because they possessed more red muscle than their conspecifics but, since red muscle comprise less than a few percent of total muscle mass (Thorsen and Westneat, 2005), such increase in red muscle mass does not necessarily lead to a noticeable reduction in the amount of white muscle and thereby anaerobic locomotor performance.

In conclusion, a high degree of intraspecific variation was found within the group of shiner perch, with both aerobic metabolic performance and swimming performance varying approximately two-fold. Aerobic scope for swimming correlated with U_{crit} but no

relations were observed between aerobic and anaerobic swimming performance. The variation in aerobic scope for swimming was explained mainly by variation in active metabolic rate. None of the morphological parameters correlated with any measure of swimming performance.

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