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Variability in swimming performance and underlying physiology in rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*)

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ABSTRACT

We investigated intra- and interspecific variation in swimming performance and related physiological parameters in two members of the salmonid family. For our comparisons, we sourced juvenile brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) from one hatchery and a second strain of rainbow trout from another. The hatcheries maintain genetic stocks obtained several decades ago from very different environments. We tested competing hypotheses: that there would be greater interspecific (across species) variation or that there would be greater intraspecific (within species) variation, owing to regional adaptations. To test these hypotheses, individual and small schools of five fish were taken to fatigue using the critical swimming speed test (U_{crit}), and three post-exercise physiological metrics, packed red cell volume (hematocrit), citrate synthase and lactate dehydrogenase activity, were assessed. The majority of the results in swimming performance and hematocrit support that intraspecific variation was greater than interspecific variation, i.e. the location had a stronger effect than did genus. Variation in lactate dehydrogenase activity supported neither intra- nor interspecific variation as determining factors. In sum, our findings suggest that the performance of different species of salmonids from the same locale can be more similar than those of the same species from different areas.

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1. Introduction

Members of the salmonid family are widely distributed across the world and occupy a vast array of habitats. 'Landscape characteristics', such as elevation, water temperature and stream gradient have the potential to influence distribution, adaptation and genetic diversity (Gamperl et al.., 2002; Farrell, 2007; Narum et al., 2008; Eliason et al., 2011). In fact, even subpopulations of a species with niche overlap can have physiological dissimilarities that differentially prepare them for their environments (Gamperl et al., 2002; Patterson et al., 2004). An interesting question is whether subpopulations of different salmonid species isolated to a particular region can be more physiologically similar to each other than to other subpopulations of the same species in other regions.

Two of the most globally distributed salmonids are rainbow trout (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*). Phylogenetic analysis based on morphological and molecular characteristics revealed that *Salmo* and *Oncorhynchus* fish are the most phylogenetically related among the more derived salmonines (subfamily of Salmonidae) (Stearley and Smith, 1993). In addition, both have had their ranges expanded by human activities, and are considered invasive in some regions (Simon et al., 2004; Muhlfeld et al., 2009). Part of their success in populating new areas owes to their phenotypically plastic abilities that allow them to adapt to a wide range of habitats and ecological niches. There are numerous documented subspecies of both species (Behnke, 1992), with at least 50 subspecies of brown trout having been described and documented in Europe alone (Behnke, 1986). In adapting to new regions, salmonids may increase expression of enzymes that allow them to swim in more demanding water speeds (Patterson et al., 2004) and higher performing fish, even within the same species, may intrinsically have greater expression of these enzymes, including LDH and citrate synthase (CS). Enzyme expression in juveniles can be influenced by the difficulty of pre-spawning migration of females and by maternal condition, which presumably allows for greater anaerobic capacity in offspring (Patterson et al., 2004). For example, Weaver Creek sockeye make a more arduous upstream migration up the Fraser River and into natal creeks than Gates Creek sockeye, which have downstream migration. The Weaver females produced offspring with higher metabolic capacities (i.e. higher anaerobic and aerobic enzyme levels) than offspring of Gates females.

The purpose of this study was to compare intraspecific and interspecific variation in juvenile salmonids from different locations using swimming performance and its relationship to muscle use and

Abbreviations: BT, brown trout; CS, citrate synthase; DTNB, 5,5-dithiobis-(2-nitrobenzoic acid); Hct, hematocrit: red blood cell volume of the total blood volume; LDH, lactate dehydrogenase; RBT, rainbow trout.

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physiology. To do so, we compared two strains of rainbow trout bred and reared in different hatcheries from different genetic stock and brown trout, while genetically originating in a different environment, bred and reared in the same hatchery as one strain of rainbow trout. We had competing hypotheses: that either the two strains of rainbow trout would be more similar to each other than to brown trout, or that rainbow trout and brown trout from the same hatchery would be more similar.

2. Materials and methods

2.1. Fish

All juvenile fish were the same age and were held in 177 L tanks at the University of Alberta for at least 2 months prior to testing. Tanks were supplied with flow through dechlorinated municipal water at 15 °C, and all strains of rainbow trout and brown trout were fed Nu-Way Trout Grower Finisher 5 mm pellets twice daily containing 5% fiber, 8.0% fat, 36.0% protein (Unifeed Ltd., Edmonton, AB, Canada). Loading density did not exceed 35–45 fish per 0.5 m^3 and the light: dark cycle mimicked seasonal changes and fish experienced an average cycle of 16:8 during the experimentation period. Fish came from two sources; however, rearing conditions were similar.

One strain of rainbow trout and brown trout were from the Bow Habitat (Sam Livingston) Hatchery and eggs were sourced from Allison Creek Brood Trout Station. Rainbow trout are a Beity–Beaver Lake cross and brown trout a Bow River strain and both have been genetically maintained without input from wild populations since 1977 (pers. commun.[1]). Fish reared at the Bow Habitat Hatchery were reared in well water with an average hardness of 175 mg/L, pH 8.24 and alkalinity of 149 mg/L. Eggs were hatched and fry were raised to fingerlings in a flow through system with recirculation with an ambient light cycle. Brown trout were hatched and reared at 12 °C and rainbow trout were hatched at 10 °C and reared at 12 °C. Fish were fed Corey feed (1.0% fiber, 15% fat and 55% protein) until 4.5 cm in length, after which they were fed Silver Cup feed (19% fat and 45% protein) (pers. comm.[2]). At 4 months age, fish were transported to the University of Alberta aquatics facility and held for at least two months prior to the experimentation, which occurred from June–September 2010. After transport, Allison Creek fish were fed.

The second group of rainbow trout was Mount Lassen strain sourced from Raven Brood Trout Station (Caroline, AB, Canada). This strain has been genetically maintained in the facility without input from wild populations since 1989 (pers. comm.[3]). Raven Creek rainbow trout were hatched and reared from embryos to fingerlings at the University of Alberta. Raven Creek rainbow trout were hatched in a flow through system in dechlorinated Edmonton municipal water at 10 °C then acclimated to 15 °C in a flow through system and subjected to a light:dark cycle that mimicked the seasons. Edmonton municipal water typically maintains a pH of 7.9, 172 mg/L hardness, and 125 mg/L alkalinity.

All fish were fasted for 24 h prior to U_{crit} testing. At the completion of testing, Allison rainbow trout were 10.4 ± 0.43 g, 9.97 ± 0.16 cm ($n = 53$), and brown trout were 4.65 ± 0.16 g, 7.98 ± 0.09 cm ($n = 50$); Raven rainbow trout were 4.16 ± 0.16 g, 7.38 ± 0.10 cm ($n = 48$). The experiments were conducted in accordance with Canadian Council of Animal Care guidelines and were approved by the University of Alberta Animal Care Committee (#7301003).

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2.2. Swimming performance assessment

Juvenile fish were tested individually, as has been done routinely in physiological studies (Kieffer, 2010), and also in schools of five. We hypothesized that a schooling test might show some physiological differences related to energy use not visible in individual trials, since biomechanical studies report a theoretical energetic benefit of schooling in fish (Lauder and Drucker, 2002; Liao et al., 2003). Swimming performance tests were carried out using a commercially available 12.5 L Brett-type design (Loligo, Denmark). Prior to testing, fish were randomly removed from holding tanks and transferred to the swim channel in a dark, 1 L container in water from the holding tank. Fish were placed in the swimming respirometer, which was filled with 15 °C dechlorinated water from the same source as the holding tanks. Fish species were tested in a randomized fashion. Oxygen levels were maintained at ≥6 mg/L. Fish were acclimated for 30 min (Peake et al., 1997) at a flow rate of 6 cm/s then were given a ramp-U_{crit} protocol in which they were brought to approximately 75% of their maximum U_{crit} in small steps of 6 cm/s of 5 min duration, after which step length was increased 20 min, for a total of approximately 10 steps (Jain et al., 1997; Plaut, 2001; Tierney, 2011). Maximum speeds were estimated from tests of fish not included in the present study. All fish were motivated to not rest at the back of the chamber using a ~2 V electrical stimulus supplied to a metal gate. The test was ended for individual fish when they were unwilling to move off of the rear gate after 5 s. In schooling tests, a fatigued individual was removed immediately upon exhaustion, without disturbance to fish swimming at the front of the respirometer. Fatigued fish were sacrificed via an MS222 overdose (0.5 mg/L tricaine methanesulfonate; Syndel) and measured for mass and length. MS222 was neutralized with an equal amount of sodium bicarbonate. Control, untested fish were removed from the holding tanks and sacrificed as above.

2.3. Physiological assessment

Immediately following sacrifice, the caudal peduncle was severed and blood was collected in 40 μl heparinized capillary tubes, which were then centrifuged at 10,000 *g* for 5 min. Hematocrit (Hct), which is a measurement of the red blood cell volume of total blood volume, was measured for each fish. Whole fish were similarly frozen for subsequent analysis. The activities of muscle LDH (EC 1.1.1.27) and citrate synthase (CS; EC 2.3.3.1) were determined from centrifuged crude extract of 100 mg of axial muscle taken below the dorsal fin using Quantichrom Lactate Dehydrogenase Assay kit (DLDH-100, BioAssay Systems) and Citrate Synthase Assay kit (CS0720; Sigma-Aldrich). Tissue was powderized in a liquid nitrogen cooled mortar and pestle and added to 1 mL of ice-cold 0.1 M phosphate buffer with 2 mM EDTA and 0.1% Triton X-100, pH 7.0. Each sample was homogenized on ice with an electric homogenizer and centrifuged for 10 min at 10000 *g* and 4 °C. Homogenization and extraction techniques were carried out according to the manufacturers' recommended protocol. Protein content was determined in the centrifuged crude extract using Bradford reagent (Sigma-Aldrich). Protein content was normalized to a bovine albumin standard curve (Sigma A2153). Each sample was assayed in triplicate for protein and duplicate for LDH and CS activity in 96-well plate format at 595 nm and 412 nm, respectively, using a VERSAmax tunable microplate reader. The lactate dehydrogenase assay kit measures the reduction of tetrazolium salt MTT in a NADH-coupled enzymatic reaction. The citrate synthase assay measures reaction of acetyl CoA and oxaloacetate to form citrate, CoA-SH, protons and water and the colorimetric reaction uses the resulting CoA-SH and 5,5-dithiobis-(2-nitrobenzoic acid) (DTNB) to produce thiobis-(2-nitrobenzoic acid (TNB) and CoA-S-S-TNB. Both assays were measured kinetically with zero-order kinetics and enzyme activity is proportional to intensity of color formed by reaction products (as per the technical bulletin of each assay). Activities of LDH and CS were

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