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Cardiorespiratory performance and blood chemistry during swimming and recovery in three populations of elite swimmers: Adult sockeye salmon

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ABSTRACT

Every year, millions of adult sockeye salmon (*Oncorhynchus nerka*) perform an arduous, once-in-a-lifetime migration up the Fraser River (BC, Canada) to return to their natal stream to spawn. The changes in heart rate, stroke volume, and arterio-venous oxygen extraction (i.e., factors determining rates of oxygen delivery to the tissues by the cardiovascular system) have never been directly and simultaneously measured along with whole animal oxygen uptake in a maximally swimming fish. Here, such measurements were made using three sockeye salmon populations (Early Stuart, Chilko and Quesnel), which each performed two consecutive critical swimming speed (U_{crit}) challenges to provide a comprehensive quantification of cardiovascular physiology, oxygen status and blood chemistry associated with swimming and recovery. Swim performance, oxygen uptake, cardiac output, heart rate and stroke volume did not significantly vary at rest, during swimming or during recovery between populations or sexes. Despite incomplete metabolic recovery between swim challenges, all fish repeated their swim performance and similar quantitative changes in the cardiorespiratory variables were observed for each swim challenge. The high maximum cardiorespiratory performance and excellent repeat swim performance are clearly beneficial in allowing the salmon to maintain steady ground speeds and reach the distant spawning grounds in a timely manner.

1. Introduction

Cardiorespiratory support of locomotion can be represented by the Fick equation for circulatory oxygen convection in which the rate of oxygen delivery to tissues is determined by the product of cardiac output ($\dot{V}_b$) and the difference between arterial and venous blood oxygen contents (C_{aO2} and C_{vO2}, respectively), the latter being termed the tissue oxygen extraction ($A\text{-}\dot{V}_{O2} = C_{aO2} - C_{vO2}$). Despite an extensive literature on swimming and cardiovascular performance of fish (e.g. Stevens and Randall, 1967; Brett, 1971; Kiceniuk and Jones, 1977; Lai et al., 1990; Thorarensen et al., 1996a; Korsmeyer et al., 1997b; Gallaugher et al., 2001), to date no study has simultaneously and directly measured all the components of the Fick equation in any fish swimming maximally. Steinhausen et al. (2008) did make all the critical measurements, but with fish swimming only up to ~75% of their critical swimming speed (U_{crit}). Previous studies have either assumed or indirectly calculated one or more of the variables in the Fick equation. For example, two classic studies with salmonids (Brett, 1971; Kiceniuk and Jones, 1977) calculated $\dot{V}_b$ using the Fick equation. However, such calculations do not account for any oxygen directly consumed by the gills (thought to be 10–30% of routine oxygen uptake; see Thorarensen et al., 1996b), which likely results in an overestimate of cardiac output. Such uncertainty concerning a key cardiorespiratory variable is unacceptable if adaptations and mechanistic limitations of maximum exercise capacity are to be properly understood in fishes. Therefore, the objective of this study was to measure the integrated cardiorespiratory response of maximally swimming fish by directly and simultaneously measuring all the variables associated with

Abbreviations: $A\text{-}\dot{V}_{O2}$, tissue oxygen extraction ($A\text{-}\dot{V}_{O2} = C_{aO2} - C_{vO2}$); C_{aO2}, arterial blood oxygen content; C_{vO2}, venous blood oxygen content; COT, cost of transport ($COT = \dot{M}O_2 / (U \times 60)$); COT_{net}, net cost of transport ($COT_{net} = (\dot{M}O_2 - \dot{M}O_{2rest}) / (U \times 60)$); $COT\text{-}\dot{V}_b$, cardiovascular cost of transport ($COT\text{-}\dot{V}_b = \dot{V}_b / (U \times 60)$); $COT\text{-}\dot{V}_{bnet}$, net cardiovascular cost of transport ($COT\text{-}\dot{V}_{bnet} = (\dot{V}_b - \dot{V}_{brest}) / (U \times 60)$); EPOC, excess post-exercise oxygen uptake; f_H, heart rate; [Hb], haemoglobin concentration; Hct, haematocrit; MCHC, mean corpuscular haemoglobin concentration ($MCHC = [Hb] / (Hct / 100)$); $\dot{M}O_2$, rate of oxygen uptake; P_{aO2}, arterial blood partial pressure of oxygen; P_{vO2}, venous blood partial pressure of oxygen; RR, recovery ratio for consecutive swim challenges ($RR = U_{crit}\,2 \div U_{crit}\,1$); T_{opt}, optimal temperature for aerobic scope; T_{aO2}, arterial blood oxygen transport ($T_{aO2} = \dot{V}_b \times C_{aO2}$); T_{vO2}, venous blood oxygen transport ($T_{vO2} = \dot{V}_b \times C_{vO2}$); U_{crit}, critical swimming speed; $\dot{V}_b$, cardiac output; V_s, stroke volume ($V_s = \dot{V}_b \div f_H$).

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oxygen delivery to the tissues by the cardiovascular system as described above.

Fraser River sockeye salmon (*Oncorhynchus nerka*) were chosen as the model organism for two reasons. Foremost, we wished to examine a fish with a remarkable swimming prowess, an elite athlete in the piscine world. Every year, a new generation of millions of sockeye salmon returns from the ocean to the Fraser River (British Columbia, Canada) to perform a physically demanding upriver migration to reach spawning grounds. During this highly aerobic and energetically expensive migration, sockeye salmon swim continuously against a fast flowing river for several weeks at ground speeds of 20 to 40 km day^{-1} (Hinch and Rand, 1998; English et al., 2005). The salmon have a finite amount of time (typically 3–6 weeks) and energy to complete the river migration because they cease feeding in the ocean and must spawn around a specific date. Upriver swimming, reproductive maturation (secondary sexual characteristics, gonadal growth) and spawning are fuelled entirely by limited endogenous energy stores. Given the time constraint, it is critical that sockeye salmon recover rapidly from exhaustive exercise (often used in rapids) to prevent a delay in their continuous upriver migration.

The second reason for studying Fraser River sockeye salmon is their remarkable fidelity to return to their natal stream to spawn (Burgner, 1991), which has resulted in over 100 genetically and geographically distinct populations (Beacham et al., 2005). These populations experience highly variable environmental conditions during the spawning migration depending on spawning location and river entry timing. Migration distance varies 10-fold (100 to >1100 km), elevation gain varies 100-fold (10 to 1200 m), river temperature varies from 9° to 22 °C and river flow varies 5-fold [2000 to 10,000 $m^3\ s^{-1}$ (Eliason et al., 2011)]. Furthermore, because sockeye salmon are semelparous (only spawn once), individual fish have a single opportunity to complete the journey to their spawning grounds in order to reproduce. As a corollary, there is likely strong selection pressure for successful upstream migration, which then leads to the possibility that adult sockeye salmon have adapted to the particular set of river migration challenges that they face.

The present experiments focused on the cardiorespiratory performance of three interior sockeye salmon populations (Early Stuart, Chilko and Quesnel). All three populations must traverse major hydrological barriers in the Fraser Canyon (including Hells Gate, located 180 km upstream from the mouth of the Fraser River). Hells Gate and its adjacent river reaches are the most energetically costly sections of the river and likely require maximum aerobic scope as well as anaerobic swimming to be negotiated (Hinch et al., 1996; Hinch and Rand, 1998; Hinch and Bratty, 2000). These three populations travel between 642 and 1071 km upstream to spawn at elevations of between 690 and 1174 m while encountering similar modal and median (16–17 °C) river temperatures (Eliason et al., 2011). Previous work demonstrated that these populations have a similar optimal temperature for aerobic scope (T_{opt}: ~17 °C), and similar maximum aerobic scope, cardiac scope and scope for heart rate (Eliason et al., 2011). However, Eliason et al. (2011) did not systematically report on how these populations mechanistically support their impressive swimming performance and aerobic scope.

We performed a detailed investigation of how the sockeye salmon cardiorespiratory system supports swimming performance during two sequential U_{crit} critical swimming speed challenges at T_{opt} for aerobic scope. In addition to investigating the general question of how cardiac function is affected by repeated bouts of exercise, we examined five specific hypotheses: 1) oxygen delivery to the tissues is supported by equivalent increases in V_b and $A\text{-}V_{O2}$; 2) increased cardiac stroke volume is the primary means of increasing arterial oxygen delivery to tissues; 3) arterial oxygen saturation is maintained during maximal swimming; 4) the concentration of oxygen returning in venous blood to the heart remains well in excess of the oxygen needs of the heart when it is working maximally to support locomotion; and 5) cardiorespiratory support of aerobic scope is similar among three populations facing a long, arduous migratory challenge.

2. Materials and methods

2.1. Fish collection

Wild adult sockeye salmon were collected in 2007, 2008 and 2009 from the lower Fraser River while en-route to their spawning grounds using a beach seine or gill net. The salmon were collected early in their river migration (after only ~100 km), which translates to 1–3 days after entry into freshwater from temperatures of ~10–12 °C in the ocean. Following capture, the fish were transported 25–75 km by land to the Department of Fisheries and Oceans Cultus Lake Salmon Research Laboratory (Cultus Lake, BC, Canada). All fish were given a unique PIT (Passive Integrated Transponder, Biomark Inc., Boise, Idaho, USA) tag for individual identification, and <0.1 g of the adipose fin was clipped for population identification via DNA analysis (Beacham et al., 2005). Since the DNA analysis takes several days to complete, experiments commenced without knowledge of the specific populations to which the fish belonged. Many different populations of sockeye salmon enter the Fraser River at the same time, co-migrate upriver and cannot be visually distinguished, thus it is impossible to guarantee in advance which population will be captured. While it would have been desirable to compare populations across a broader range of migration difficulties, sufficient fish were captured from only three interior populations with highly challenging upriver migrations: Early Stuart population (N = 9, distance: 1071 km, elevation: 690 m), Chilko population (N = 13, distance: 642 km, elevation: 1174 m) and Quesnel population (N = 6, distance: 796 km, elevation: 728 m). Other characteristics associated with each of the adult migrations (e.g. peak Fraser River entry, peak spawning ground arrival, migration rate, migration duration, work, river slope, migration effort) are detailed in Eliason et al. (2011). All procedures were approved by the University of British Columbia's Animal Care Committee (Animal use protocols A06-0328 and A08-0388) in accordance with guidelines recommended through the Canadian Council on Animal Care.

Fish were held at 11–12 °C for 1–4 weeks in outdoor 8000–12,000 L circular aquaria supplied with filtered and UV sterilised freshwater (LS-PermaBead Filtration System, Integrated Aqua Systems Inc., Escondido, CA, USA) under seasonal photoperiod. The fish were not fed because they had ceased feeding naturally before entering the Fraser River. Three days before the swimming challenge, fish were placed in 1400 L circular aquaria and the temperature was progressively increased to the test temperature (15–20 °C) by no more than 5 °C day^{-1}. The fish were maintained at this temperature for 24–48 h before experiments.

2.2. Surgical procedures

Individual fish were anaesthetised with buffered tricaine methanesulfonate in freshwater (0.2 g L^{-1} $NaHCO_3$ and 0.1 g L^{-1} MS-222, Sigma-Aldrich, St. Louis, MO, USA), weighed and transferred onto wet foam on a surgical table where their gills were continually irrigated with aerated, chilled freshwater with a lower dose of buffered anaesthetic (0.15 g L^{-1} $NaHCO_3$ and 0.075 g L^{-1} MS-222). Surgical procedures have been detailed elsewhere (Steinhausen et al., 2008). To sample arterial blood, a PE-50 cannula was inserted into the dorsal aorta (Soivio et al., 1973). To measure V_b, a 3 mm SB flow probe (lateral cable exit, Transonic Systems, Ithaca, NY, USA) was positioned around the ventral aorta without opening the pericardium (Steffensen and Farrell, 1998). To sample venous blood, a PE-50 cannula was inserted into the ductus of Cuvier and advanced towards the heart into the sinus venosus (Farrell and Clutterham, 2003). Both cannulae were filled and regularly flushed with heparinised saline solution (150 IU mL^{-1}). The flow probe and cannulae leads were secured together and sutured to the dorsal line of the fish's body using 2-0 silk. The fish were placed individually in one of two Brett-type swim tunnels (described in Lee et al., 2003b; Steinhausen et al., 2008) and allowed to recover overnight at their test temperature