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**Intraspecific differences in endurance swim performance and cardiac size in sockeye
salmon (*Oncorhynchus nerka*) parr tested at three temperatures**

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Intraspecific differences in endurance swim performance and cardiac size in sockeye salmon (*Oncorhynchus nerka*) parr tested at three temperatures

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Abstract

Pacific salmon encounter widely varying environmental conditions across populations. Performance traits and environmental tolerance limits are predicted to be related to the typical abiotic and biotic conditions encountered by each population. Endurance swim performance at three different temperatures (8, 12, 22°C) was compared across nine populations of sockeye salmon parr (*Oncorhynchus nerka* (Walbaum, 1792)) from British Columbia, Canada, reared in a common laboratory environment. In addition, relative ventricular mass (RVM) was compared between good and poor performers from each population. Populations significantly differed in endurance swim performance and these differences were related to the natal lake environment. Specifically, parr populations that reside in warm, shallow lakes (Okanagan, Scotch and Stellako) had superior swim performance at 12 compared to 8°C. All other populations from deeper, cooler lakes had equivalent swim performance at 8 and 12°C. Individual variability in swim performance within a population was not due to differences in cardiac size. Similarly, RVM did not vary across parr populations, suggesting that population differences in swim performance were not associated with cardiac size. This study provides further support that sockeye salmon parr are locally adapted to their environmental conditions.

Key words: *Oncorhynchus nerka*, sockeye salmon, local adaptation, population, heart, cardiac, endurance, aerobic swim performance, temperature

Introduction

Identifying intraspecific variability in performance traits and environmental tolerance limits is critical to understanding how species and populations will respond to a changing environment. Local adaptation occurs when individuals of a native population exhibit higher fitness within their local environmental conditions compared to other populations from a different habitat (Kawecki and Ebert 2004). Pacific salmon (*Oncorhynchus* spp.) are well-known for their natal homing and low dispersal across diverse habitats (Groot and Margolis 1991), resulting in genetically segregated populations that are postulated to be locally adapted to their environment (Taylor 1991; Fraser et al. 2011). Indeed, salmon physiology and morphology have been correlated with environmental conditions and historical temperature in adults (Beacham and Murray 1987a; Kinnison et al. 2001; Lee et al. 2003; Crossin et al. 2004; Eliason et al. 2011; Eliason et al. 2013), eggs (Beacham and Murray 1987a, 1987b, 1989; Whitney et al. 2013, 2014) and fry (Tsuyuki and Williscroft 1977; Taylor and McPhail 1985; Patterson et al. 2004; Pon et al. 2007; Chen et al. 2013; Sopinka et al. 2013).

Sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) rearing lakes are broadly distributed across British Columbia and vary in elevation, temperature, depth, duration of ice cover, lake productivity, food availability, and predation pressure (Stockner and Shortreed 1983). Aerobic swimming capacity is a critical performance metric with ecological consequences since parr must be able to migrate to different areas, maintain station against a current, avoid predators and obtain food. Furthermore, the heart is critical for delivering oxygen to the working muscles during swimming. Indeed, adult sockeye salmon with more difficult upriver migrations had significantly higher swim performance and aerobic scope and a correspondingly higher cardiac

scope, a greater relative ventricular mass (RVM) and more compact myocardium (Lee et al. 2003; Eliason et al. 2011; Eliason et al. 2013). In addition, individual variability in swim performance has been correlated with cardiac physiology and morphology. Rainbow trout (*O. mykiss* (Walbaum, 1792)) with poor aerobic swimming performance, decreased aerobic scope and low maximum metabolic rate had significantly lower maximal cardiac pumping capacity and rounded, misshapen hearts compared to high performers from the same population (Claireaux et al. 2005).

The present study sought to determine whether genetically distinct sockeye salmon parr from 9 different populations (8 from the Fraser River, 1 from the Columbia River) differ in endurance swim performance. Fish were reared in a common laboratory environment to compare genotypes while eliminating potential differences due to rearing environment. The fish were swum at 3 temperatures (8 and 12°C are within the typical environmental range while 22°C represents a high temperature challenge) to assess how populations differ in temperature tolerance. Sockeye salmon parr were predicted to be physiologically locally adapted to their specific lake environment. The second objective of this study was to assess whether population differences as well as individual variability within a population may be due to differences in cardiac size. Specifically, populations and individuals with superior swimming performance were predicted to have a greater RVM.

Materials and Methods

This experiment was conducted under Canadian Council on Animal Care guidelines in accordance with the standards set by the University of British Columbia (AUP A11-0215).

Fish Husbandry

Adult Fraser River sockeye salmon (*O. nerka*) depart the ocean and deposit their eggs in their natal river or lake in the fall. Fry emerge from the gravel between March and June and typically spend one year rearing in a nursery lake before migrating downstream to the ocean as smolts in April and May. One major exception is the Harrison population, which migrates downstream to the Fraser River estuary shortly after emergence.

Sockeye salmon eggs and milt were collected from the spawning grounds of nine different wild populations (Fig. 1, Table 1: eight populations from the Fraser River watershed - Adams, Chilko, Gates, Harrison, Horsefly, Scotch, Stellako, Weaver, and one population from the Columbia watershed - Okanagan) in the fall of 2010. Fertilized eggs were reared at 10°C in freshwater at the University of British Columbia (Vancouver, BC). Details are provided in Whitney et al. (2013; 2014). Following emergence in early 2011, sockeye salmon fry were held in freshwater in 1000 l flow-through tanks (1 population per tank) under seasonal photoperiod and temperature. Dissolved oxygen was always maintained above 90% saturation. Fish were fed commercial salmonid feed (EWOS Canada Ltd. Surrey, Canada) daily to satiation. The fish were approximately one year-old and thus considered parr (Fig. 2; overall mean mass $\pm$ SE: 5.9 ± 0.9 g; overall mean fork length $\pm$ SE: 80.7 ± 0.4 mm) when the swimming experiments were conducted in November and December 2011. Food was withheld for 24 h before a swim test.

Swim Flume

Aerobic swimming performance is typically assessed using a critical swimming speed (U_{crit}) test (Brett 1964). U_{crit} swim tests are time consuming, as fish are usually swum

individually for several hours. This can become problematic when experimental trials need to be conducted over a brief period of time (e.g. to minimize size differences in fast-growing fish) and when many fish need to be compared. In contrast, fixed velocity endurance swim tests (Brett 1967) can be used to evaluate the time to fatigue (endurance) for groups of fish so that many individuals can be rapidly screened. Endurance swim tests have successfully been used to compare feeding regimes, fish size, water temperature, ploidy, and cardiovascular traits in sockeye salmon, rainbow trout, haddock, southern catfish, Atlantic salmon, Atlantic cod, and American plaice (Brett 1967; Winger et al. 1999; Winger et al. 2000; Martínez et al. 2003; Breen et al. 2004; Cotterell and Wardle 2004; Claireaux et al. 2005; Zeng et al. 2009).

Fixed velocity endurance swim trials were conducted in a flow-through swim flume (Fig 3, 200 cm long $\times$ 15 cm wide $\times$ 25 cm high). Water was pumped into the front of the flume, where it passed through a perforated plexiglass plate and then a honeycomb structure to maximize laminar flow through the swim area. In order to encourage fish to swim in the target swim area (mid-flume, where flow was most consistent), a bright light was directed into the area adjacent to the honeycomb, and the target swim area was shaded using black plastic. The fish tended to spread out across the width of the flume but mostly remain within the shaded area mid-flume for the duration of the swim. At the downstream end of the flume, a sliding door could be raised or lowered to adjust flow. As fish failed to swim with sufficient velocity to maintain their position in the flume, they fell to the back of the swim flume and were transferred to a recovery tank.

Swimming Protocol

Approximately 30 fish from an individual population were warmed from their holding temperature (range 6-8°C during the experiments) to their test temperature (8, 12 or 22°C) by 6°C h⁻¹. Upon reaching the test temperature, all the fish were immediately transferred into the endurance swim flume and allowed 12 min to adjust to the flume under a low velocity of approximately 1 body lengths per second (bl s⁻¹). The speed was ramped to the test velocity of 0.25-0.33 m s⁻¹ (~3 bl s⁻¹) over 11 min to allow the fish time to adjust to the increased swimming speed. If fish dropped out of the flume during this ramping period, they were immediately placed back into the flume. If an individual fish dropped out more than 3 times during the ramping period, it was removed from the flume and not included in the statistical analysis (Winger et al. 1999).

The fish were swum at a constant velocity for up to 90 min. As individual fish dropped out, the time was recorded. The swim trial was terminated at 90 min and any remaining fish were recorded as “censored” (see analysis section below), removed from the flume and all fish were allowed to recover for 3 h at their test temperature. This recovery duration was chosen to enable the fish to fully recover between tests (Brett, 1964). The identical test was then repeated a second time. As individual fish dropped out during the second test, the time was recorded and body mass and fork length were measured by lightly anaesthetizing the fish with buffered MS-222 (0.05 g l⁻¹ MS-222 with 0.1 g l⁻¹ NaHCO₃; Sigma-Aldrich, Oakville, Canada). Following the second 90 min swim test, all the fish were cooled back to their holding temperature. Preliminary analysis indicated that swim performance was similar between swim 1 and swim 2. However, the first swim test was used as a training test and thus only the results from the second swim test were included in the final analysis. All populations were tested at 8 and 12°C. In addition, four populations (Adams, Chilko, Harrison, Weaver) were also tested at 22°C.

Relative Ventricular Mass

During the second swim at 12°C, individual fish that quit swimming first (<60 min into the swim test) were categorized as “poor” performers and individual fish that completed the entire swim test were categorized as “good” performers. Five poor performers and five good performers were selected from each population. The fish were euthanized by cerebral concussion and mass and fork length were measured. The heart was removed and the ventricle was isolated from the atrium and bulbous arteriosus using a dissecting microscope and weighed.

Calculations and Statistical Analysis

Condition factor (CF) was calculated as: $CF = (\text{body mass}/\text{fork length}^3) \times 100$ where body mass is in g and fork length is in cm. The actual swim speed for each individual fish was determined as: water velocity/fork length. Relative ventricular mass (RVM) was determined as: $RVM = \text{ventricle mass}/\text{body mass} \times 100$.

All statistics were performed using Sigmaplot 11.0. Failure time analysis, also known as survival analysis, was used to statistically compare endurance swim performance. See Winger et al. (1999) for a discussion of the benefits of using survival analysis (includes censored data), over regression analysis (excludes censored data). Endurance swim time was compared among populations and among temperatures using Kaplan-Meier LogRank survival analysis. A Bonferroni multiple comparison test was used to distinguish among groups. A Cox proportional hazards model (Cox 1972; Cox and Oakes 1984; Winger et al. 1999) was used to evaluate the effect of covariates (population, body mass, fork length, swim speed and condition factor) on endurance swim time for each test temperature. The hazard rate was only significantly affected

by population. Therefore, a Cox regression stratified model was used to evaluate the effect of covariates (body mass, fork length, swim speed, condition factor) on endurance swim time using population as a stratification variable. Relative ventricular mass was compared across populations and between good and poor swimmers using two-way ANOVA.

Results

Endurance swim test

At 8°C, Okanagan fish had significantly reduced endurance swim performance compared with Adams, Harrison, Horsefly, Gates, Scotch and Weaver fish (Fig 4). In addition, Adams fish had superior endurance swim performance compared with Gates and Stellako fish at 8°C. Harrison fish had superior endurance swim performance compared with Stellako fish at 8°C. At 12°C, Stellako fish had superior swim performance compared with Chilko, Gates and Harrison fish (Fig 4). All other populations were statistically indistinguishable at 12°C. At 22°C, there were no significant differences among the four populations tested (Fig 4).

Within a population, endurance swim performance did not significantly differ between 8 and 12°C for most populations (Table 2; Adams, Chilko, Gates, Harrison, Horsefly, Weaver). Notably, swim performance was higher at 12 compared to 8°C for Okanagan, Scotch and Stellako fish. In addition, swim performance was significantly lower at 22°C for Adams and Harrison fish, but not for Chilko fish.

Box plots for body mass, fork length, condition factor and swim speed for each population are provided in Fig 2. The covariates (body mass, fork length, swim speed and

condition factor) did not significantly affect the failure time at any of the test temperatures (Table 3).

Relative Ventricular Mass

RVM did not significantly differ among populations or between fish with good vs poor swim performance (Table 4; 2-Way ANOVA, $p > 0.05$). The overall mean RVM across all fish was $0.121 \pm 0.001\%$.

Discussion

The present study found that endurance swim performance differs across sockeye salmon parr populations and with temperature, and some of these performance differences can be related to variation in the historical environmental conditions of the rearing lakes. This finding is in line with the increasing body of knowledge showing strong correlatory evidence that genetically distinct salmon populations are locally adapted to their environments (e.g. Taylor 1991; Crossin et al. 2004; Eliason et al. 2011). Cardiac size (RVM) was compared to assess whether population and individual differences in swim performance were related to genetic differences in cardiac capacity. However, differences in swim performance in the present study were not due to differences in RVM.

Population Differences in Swimming Performance

Genetically and geographically segregated sockeye salmon populations are hypothesized to be locally adapted to their specific environmental conditions (Taylor 1991; Fraser et al. 2011).

Numerous abiotic and biotic variables could be exerting selection pressure at the parr life stage, including temperature, dissolved oxygen, flow conditions, predator pressure, interspecific competition, and prey availability. As predicted, endurance swim performance significantly differed across parr populations in the current study. However, it is challenging to relate these performance differences to specific natal lake characteristics since the lakes are complex environments with high inter and intra-seasonal variation, and environmental data is largely incomplete.

Intraspecific variation in swimming performance and morphology has been related to local environmental conditions in many species of fish including sockeye salmon, rainbow trout, coho salmon (*O. kisutch* (Walbaum, 1792)), steelhead trout (*O. mykiss* (Walbaum, 1792)), Atlantic salmon (*Salmo salar* L., 1758), brown trout (*Salmo trutta* L., 1758), Arctic charr (*Salvelinus alpinus alpinus* L., 1758), and blacknose dace (*Rhinichthys atratulus* (Hermann, 1804)) (Tsuyuki and Williscroft 1977; Riddell et al. 1981; Taylor and McPhail 1985; Nelson et al. 2003; Keeley et al. 2005; Langerhans 2008; Janhunen et al. 2009; Pavey et al. 2010; Drinan et al. 2012). Differences were hypothesized to be largely associated with habitat complexity, predation pressure, and foraging opportunities, where a streamlined body shape allows for enhanced prolonged swimming performance which may be advantageous in an open environment when fish cruise in schools, are not aggressive toward each other and feed on plankton in open water. In contrast, deeper, more robust body shapes are suggested to improve burst swimming performance and movements in structurally complex environments and enhance predator avoidance (Keeley et al. 2005; Langerhans 2008; Pavey et al. 2010).

In the present study, Adams and Scotch sockeye salmon had the highest overall endurance swim performance. Both populations rear in Shuswap lake, a deep but warm lake with

greater species diversity of both zooplankton and fish compared to some of the other natal rearing lakes (e.g. Chilko Lake) (Goodlad et al. 1974). Furthermore, Harrison sockeye salmon, which demonstrated superior swim performance at 8°C, migrate directly to the turbid Fraser River estuary shortly after emergence. Turbid water is predicted to reduce predation pressure (Gregory 1993; Gregory and Levings 1998), which may allow for enhanced endurance swim performance over burst performance. Gates and Chilko sockeye salmon, which had the poorest endurance swim performance overall, reside in natal lakes that are deep and clear, which may necessitate increased burst swimming capacity and predator avoidance strategies as the risk of predation is higher (Abrahams and Kattenfeld 1997).

Effect of Temperature on Swimming Performance

Temperature plays a central role determining species and population distributions. Since fish are ectotherms, temperature strongly affects physiological processes such as metabolic rate and thus swim performance. Sockeye salmon parr were predicted to have superior swim performance at the temperatures that they typically encounter in their environment. Supporting this hypothesis, fish from Okanagan, Scotch, and Stellako populations had superior swim performance at 12 relative to 8°C and all three populations rear in relatively shallow, warm lakes (mean depth is <100 m, Table 1). In particular, Okanagan fish can encounter extremely warm temperatures in Osoyoos lake (summer surface temperatures can exceed 24°C; Hyatt et al. 2015) and they had the lowest swim performance among all populations tested at 8°C but very high performance at 12°C. In contrast, the other populations rear in deeper, cooler lakes (mean depth = 100-169 m, Table 1) and swim performance was equivalent between 8 and 12°C.

A high temperature swim test, at the top of the range encountered in the wild, was used to test whether populations differ in their upper thermal tolerance. As expected, swim performance was reduced when Adams and Harrison fish swam at 22°C compared to 8 and 12°C. In contrast, Chilko fish exhibited equally poor swim performance at all 3 test temperatures indicating that Chilko fish may have been less sensitive to the high temperature challenge. Interestingly, endurance swim performance was equivalent at 22°C for all 4 populations, and the trajectory of when fish quit swimming was very similar, which contrasts sharply with the patterns observed for the 8 and 12°C swims (Fig 4).

Relative Ventricular Mass

The heart plays the critical role of delivering oxygen to muscles to support aerobic swimming. Larger hearts can generate a larger cardiac output and greater cardiac power and thus have an increased capacity for oxygen delivery (Farrell 1996). RVM was similar in parr from all nine sockeye salmon populations and did not differ between individuals with good and poor swim performance, suggesting that differences in endurance swim performance were not due to differences in cardiac size in sockeye salmon parr. In contrast, Claireaux et al. (2005) found that cardiac performance and morphology was linked to individual differences in swim performance in rainbow trout and they found that differences could be detected using an endurance swimming test. However, they used hatchery-reared fish that were much larger (~145 g during initial screening test and ~1100 g during physiology and morphology assessments). Prolonged exposure to hatchery and aquaculture conditions are known to negatively affect cardiac morphology (Gamperl and Farrell 2004). In addition, Claireaux et al. (2005) screened 600 fish to identify 60 good and 60 poor swimmers (i.e. top and bottom 10%) while the present study only screened 30

fish per population and identified the top and bottom 17%. It is possible that insufficient numbers of fish may have been screened in the present study to detect differences in cardiac morphology across individuals. Future research should investigate other traits that support aerobic swim performance such as enzyme activity [e.g. citrate synthase and lactate dehydrogenase activity (Patterson et al. 2004)] and alternative cardiac performance metrics (e.g. cardiac scope, cardiac power output, hematocrit, and hemoglobin concentration). The influence of extraneous, non-genetic influences such as pathogen load should also be considered.

Conclusions

Endurance swim performance significantly differed across the nine sockeye salmon populations examined in the present study. Some of these intraspecific differences can be linked to variation in the local rearing lake environment, though our knowledge of the biotic and abiotic factors for each rearing lake is incomplete. Individual variability in swim performance could not be attributed to differences in relative ventricular mass, thus alternative factors should be considered.

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Table 1. Environmental characteristics for the rearing lakes of eight populations of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)); Harrison fry migrate straight to the ocean shortly after emergence, so they are not included in the table.

Population	Adams	Adams	Adams/ Scotch	Chilko	Gates	Horsefly	Okanagan	Stellako	Stellako	Weaver
Rearing Lake	Adams Lake	Little Shuswap	Shuswap Lake	Chilko Lake	Anderson Lake	Quesnel Lake	Osoyoos Lake	Francois Lake	Fraser Lake	Harrison Lake
Outlet River	South Thompson River	South Thompson River	South Thompson River	Chilko River	Portage Creek	Horesfly River	Okanagan River	Nautley River	Nautley River	Harrison River
Elevation (m)	407	347	347	1172	258	725	278	715	670	10
Area (km ²)	138	18	310	200	28	270	23	260	55	218
Max Depth (m)	>183	64	162	366	215	>506	63	240	31	279
Mean Depth (m)	169	14	62	108	140	158	14	87	13	151
Drainage area (km ²)	3080	16200	16200	2110	730	5930	8158	3600	6030	8440
Summer secci depth (m)	8.0-8.5	8.0	8.5-11.0	3.0-7.0	11.0	9.0-13.0	3.3	8.2	4.0	3.0-5.5
Mean temperature May 15- Oct 15 (0-9 m)		13.3	14.2	9.0					12.2	
Mean epilimnetic temp (°C)	14.6		14.9	8.2	14.2	12.4		13.3	15.3	12.6
Epilimnetic depth (m)			10.0	21.4		12.2				
Thermocline depth (m)	7.5		10	24.2	18.2	12.4		17.2	10.6	21.4
Euphotic zone depth (m)	13.3		12.3	20.9	22.6	15.5		10.9	7.4	11.2
Reference	1,2,7	1,2,4	1,2,3,4,5,6,7	1,2,3,4,5,6,7	1,2,7	1,2,3,5,6,7	1,8	1,2,5,7,	1,2,4,5,7,	1,2,7

1 Gustafson et al. 1997; 2 Stockner and Shortreed 1983; 3 Hume et al. 1996; 4 Goodlad et al. 1974; 5 Shortreed et al. 1996; 6 Stockner and Shortreed 1991; 7 Shortreed et al. 2001; 8 Hyatt et al. 2015

Table 2. Kaplan-Meier LogRank survival analysis of the swimming endurance of nine populations of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) swum at 3 temperatures, differing letters indicate a statistically significant difference between test temperatures within a population.

Population	Statistic	DF	P-value	8°C	12°C	22°C
Adams	9.143	2	0.010	a	a	b
Chilko	1.305	2	0.521	a	a	a
Gates	0.244	1	0.621	a	a	-
Harrison	7.977	2	0.019	a	ab	b
Horsefly	0.302	1	0.582	a	a	-
Okanagan	42.748	1	<0.001	a	b	-
Scotch	4.432	1	0.035	a	b	-
Stellako	26.396	1	<0.001	a	b	-
Weaver	6.499	2	0.039	a	a	a

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Table 3. Failure time analysis of the swimming endurance of nine populations of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) using a Cox regression stratified model including four covariates (body mass, fork length, condition factor, and swim speed) and population as the stratum.

Covariate	Coefficient	SE	χ^2	P-Value
<i>8°C</i>				
fork length	0.0191	0.190	0.0101	0.920
body mass	-0.225	0.381	0.348	0.556
swim speed	-1.933	3.126	0.382	0.536
condition factor	-0.264	2.730	0.00935	0.923
<i>12°C</i>				
fork length	-0.0783	0.257	0.0932	0.760
body mass	-0.189	0.588	0.104	0.748
swim speed	-2.463	3.670	0.451	0.502
condition factor	3.147	3.391	0.861	0.353
<i>22°C</i>				
fork length	-0.0635	0.229	0.0767	0.782
body mass	0.00829	0.454	0.000334	0.985
swim speed	-0.935	3.420	0.0748	0.784
condition factor	0.869	2.281	0.145	0.703

Table 4. Mean ($\pm$ SE) relative ventricular mass (RVM = ventricular mass $\div$ body mass $\times$ 100) for parr from nine populations of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)).

Population	RVM (%)
Adams	0.130 $\pm$ 0.007
Chilko	0.118 $\pm$ 0.004
Gates	0.122 $\pm$ 0.004
Harrison	0.116 $\pm$ 0.002
Horsefly	0.116 $\pm$ 0.004
Okanagan	0.121 $\pm$ 0.004
Scotch	0.120 $\pm$ 0.005
Stellako	0.120 $\pm$ 0.003
Weaver	0.124 $\pm$ 0.004

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Figure Captions

Fig. 1. Map of the spawning locations and rearing lakes in British Columbia, Canada for the sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) populations investigated in the current study.

Fig. 2. Body mass, fork length, condition factor (body mass/fork length³ × 100) and swim speed during the endurance swim test for nine populations of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)). The black line shows the median value for a population, the boundaries of the box indicate the 25th and 75th percentiles, the whiskers above and below the box indicate the 90th and 10th percentiles, and the circles indicate outlying points.

Fig 3. Schematic of the endurance swim flume.

Fig. 4. Population comparison of sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) endurance swim performance at 8, 12, and 22°C. Statistical results are provided in the text.

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Fig. 1. Map of the spawning locations and rearing lakes in British Columbia, Canada for the sockeye salmon (*Oncorhynchus nerka*) populations investigated in the current study.

202x190mm (300 x 300 DPI)

Fig. 2. Body mass, fork length, condition factor (body mass/fork length³ × 100) and swim speed during the endurance swim test for nine populations of sockeye salmon (*Oncorhynchus nerka*). The black line shows the median value for a population, the boundaries of the box indicate the 25th and 75th percentiles, the whiskers above and below the box indicate the 90th and 10th percentiles, and the circles indicate outlying points.

229x170mm (300 x 300 DPI)

Fig 3. Schematic of the endurance swim flume.

210x71mm (300 x 300 DPI)

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