

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

E.J. Eliason, M.K. Gale, C.K. Whitney, A. Lotto, and S.G. Hinch

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 (*Oncorhynchus nerka* (Walbaum, 1792)) parr 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 °C compared with 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.

Résumé : Les saumons du Pacifique sont exposés à des conditions ambiantes qui varient fortement selon la population. Il est prédit que les caractères associés à la performance et les limites de tolérance aux conditions ambiantes seraient reliés aux conditions abiotiques et biotiques typiques auxquelles une population donnée est exposée. Une comparaison de la performance de nage d'endurance à trois températures différentes (8, 12, 22 °C) a été effectuée entre neuf populations de tacons de saumon rouge (*Oncorhynchus nerka* (Walbaum, 1792)) de la Colombie-Britannique (Canada) élevés dans le même environnement de laboratoire. Une comparaison de la masse ventriculaire relative (MVR) a également été effectuée entre individus caractérisés par une bonne et une mauvaise performance de nage d'endurance pour chaque population. Des différences significatives de la performance de nage d'endurance ont été relevées entre les populations, ces différences étant reliées à l'environnement du lac natal. Plus précisément, les populations de tacons résidant dans des lacs chauds et peu profonds (Okanagan, Scotch et Stellako) présentaient une meilleure performance natatoire à 12 °C qu'à 8 °C. Toutes les autres populations de lacs plus profonds et plus frais présentaient des performances natatoires équivalentes à 8 et 12 °C. La variabilité de la performance natatoire entre individus d'une même population n'était pas due à des variations de la taille du cœur. De même, la MVR ne variait pas entre les populations de tacons, ce qui porte à croire que les variations de la performance natatoire entre populations ne sont pas associées à la taille du cœur. L'étude soutient la thèse voulant que les tacons de saumon soient adaptés aux conditions ambiantes locales. [Traduit par la Rédaction]

Mots-clés : *Oncorhynchus nerka*, saumon rouge, adaptation locale, population, cœur, cardiaque, endurance, performance natatoire aérobie, température.

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 with other populations from a different habitat (Kawecki and Ebert 2004). Pacific salmon (genus *Oncorhynchus* Suckley, 1861) 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, 2013), eggs (Beacham and Murray 1987a, 1987b, 1989; Whitney et al. 2013, 2014), and fry (Tsuyuki and Willisicroft 1977; Taylor and McPhail 1985; Patterson et al. 2004; Pon et al. 2007; Chen et al. 2013; Sopinka et al. 2013).

Received 14 October 2016. Accepted 19 January 2017.

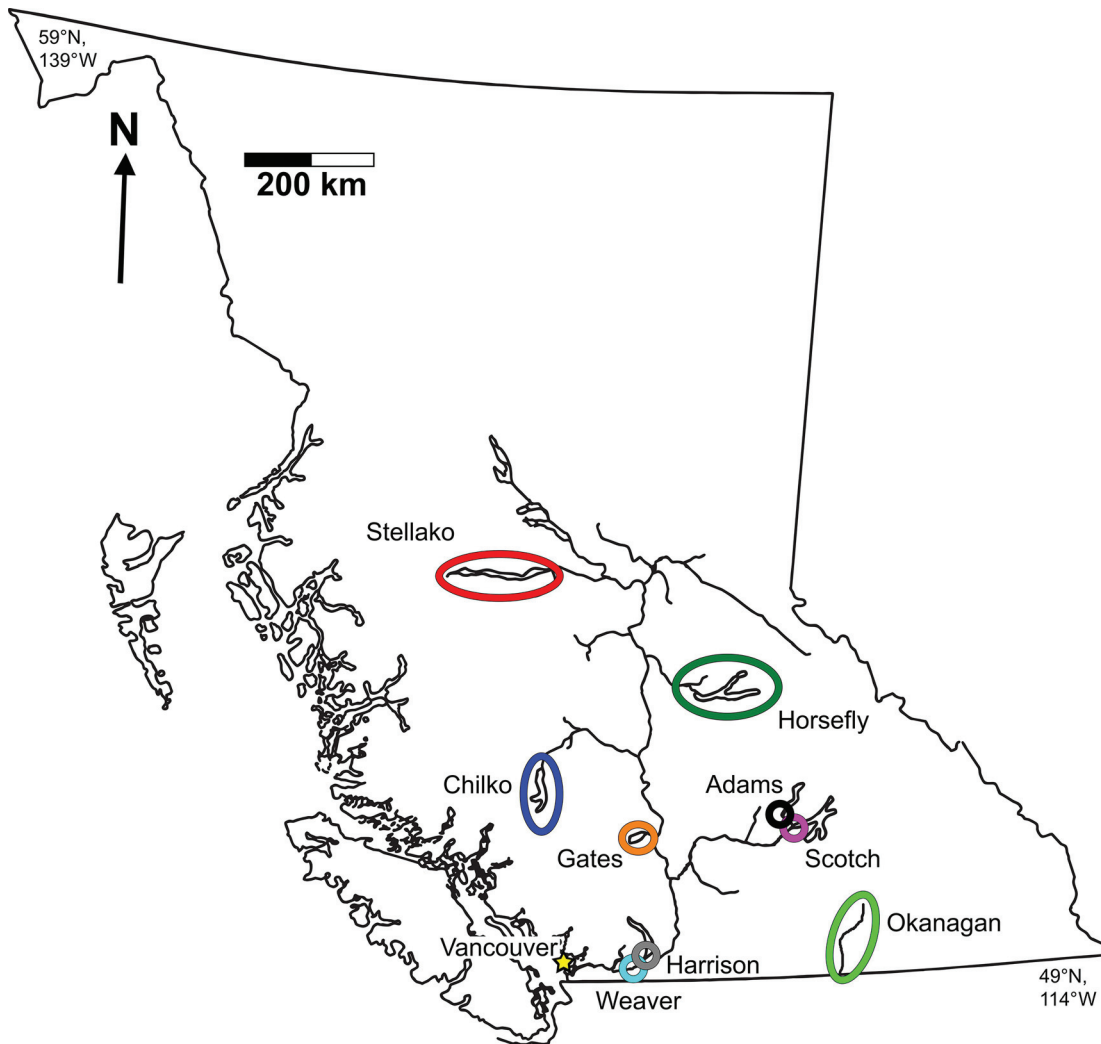
E.J. Eliason,* M.K. Gale, C.K. Whitney, A. Lotto, and S.G. Hinch. Department of Forest and Conservation Sciences, The University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4, Canada.

Corresponding author: E.J. Eliason (email: erika.eliason@lifesci.ubc.edu).

*Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, Santa Barbara, CA 93106-9620, USA.

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from [RightsLink](https://www.ubcpress.com/permissions).

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. Figure appears in colour on the Web.



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 a more compact myocardium (Lee et al. 2003; Eliason et al. 2011, 2013). In addition, individual variability in swim performance has been correlated with cardiac physiology and morphology. Rainbow trout (*Oncorhynchus 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 with high performers from the same population (Claireaux et al. 2005).

The present study sought to determine whether genetically distinct sockeye salmon parr from nine different populations (eight from the Fraser River, one 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 three temperatures (8 and 12 °C are within the typical environmental range, whereas 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 and 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 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 1 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, British Columbia, Canada). 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 (one 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, British Columbia, Canada) daily to satiation. The fish were approximately 1 year old and thus considered parr (Fig. 2; overall mean (±SE) mass = 5.9 ± 0.9 g; overall mean (±SE) fork length = 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 (*Melanogrammus aeglefinus* (L., 1758)), southern catfish (*Silurus meridionalis* Chen, 1977), Atlantic salmon (*Salmo salar* L., 1758), Atlantic cod (*Gadus morhua* L., 1758), and American plaice (*Hippoglossoides platessoides* (Fabricius, 1780)) (Brett 1967; Winger et al. 1999, 2000; Martinez 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 × 15 cm wide × 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. 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 length·s⁻¹. The speed was ramped to the test velocity of 0.25–0.33 m·s⁻¹ (~3 body length·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, then they were immediately placed back into the flume. If an individual fish dropped out more

Table 1. Environmental characteristics for the rearing lakes of eight populations of sockeye salmon (*Oncorhynchus nerka*).

Population	Adams	Adams	Adams	Adams-Scotch	Chilko	Gates	Horsefly	Okanagan	Stellako	Stellako	Weaver
Rearing lake (L.)	Adams L.	Little Shuswap L.	Shuswap L.	South Thompson R.	Chilko L.	Anderson L. Portage Cr.	Quesnel L. Horesfly R.	Osoyoos L. Okanagan R.	Francois L. Nautley R.	Fraser L. Nautley R.	Harrison L. Harrison R.
Outlet river (R.) or creek (Cr.)	South Thompson R.	South Thompson R.	South Thompson R.	South Thompson R.	Chilko R.	258	725	278	715	670	10
Elevation (m)	407	347	347	347	1172	28	270	23	260	55	218
Area (km ²)	138	18	310	310	200	215	>506	63	240	31	279
Maximum depth (m)	>183	64	162	62	366	140	158	14	87	13	151
Mean depth (m)	169	14	62	16	108	730	5 930	8 158	3 600	6 030	8 440
Drainage area (km ²)	3 080	16 200	16 200	8.5–11.0	2 110	11.0	9.0–13.0	3.3	8.2	4.0	3.0–5.5
Summer Secchi depth (m)	8.0–8.5	8.0	14.2	14.2	3.0–7.0						
Mean temp. from 15 May to 15 Oct. (0–9 m)	13.3	13.3	14.9	14.9	9.0	14.2	12.4		13.3	12.2	12.6
Mean epilimnetic temp. (°C)	14.6	13.3	14.9	14.9	8.2	14.2	12.4		13.3	15.3	12.6
Epilimnetic depth (m)	7.5	10.0	10.0	10.0	21.4	18.2	12.2		17.2	10.6	21.4
Thermocline depth (m)	13.3	12.3	10	10	24.2	22.6	12.4		10.9	7.4	11.2
Euphotic zone depth (m)	1, 2, 7	1, 2, 3, 4, 5, 6, 7	1, 2, 3, 4, 5, 6, 7	1, 2, 3, 4, 5, 6, 7	1, 2, 3, 4, 5, 6, 7	1, 2, 7	15.5	1, 8	1, 2, 5, 7	1, 2, 4, 5, 7	1, 2, 7
References											

Note: Fry from Harrison River migrate straight to the ocean shortly after emergence, so they are not included in the table. References are as follows: 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.

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, respectively; the circles indicate outlying points.

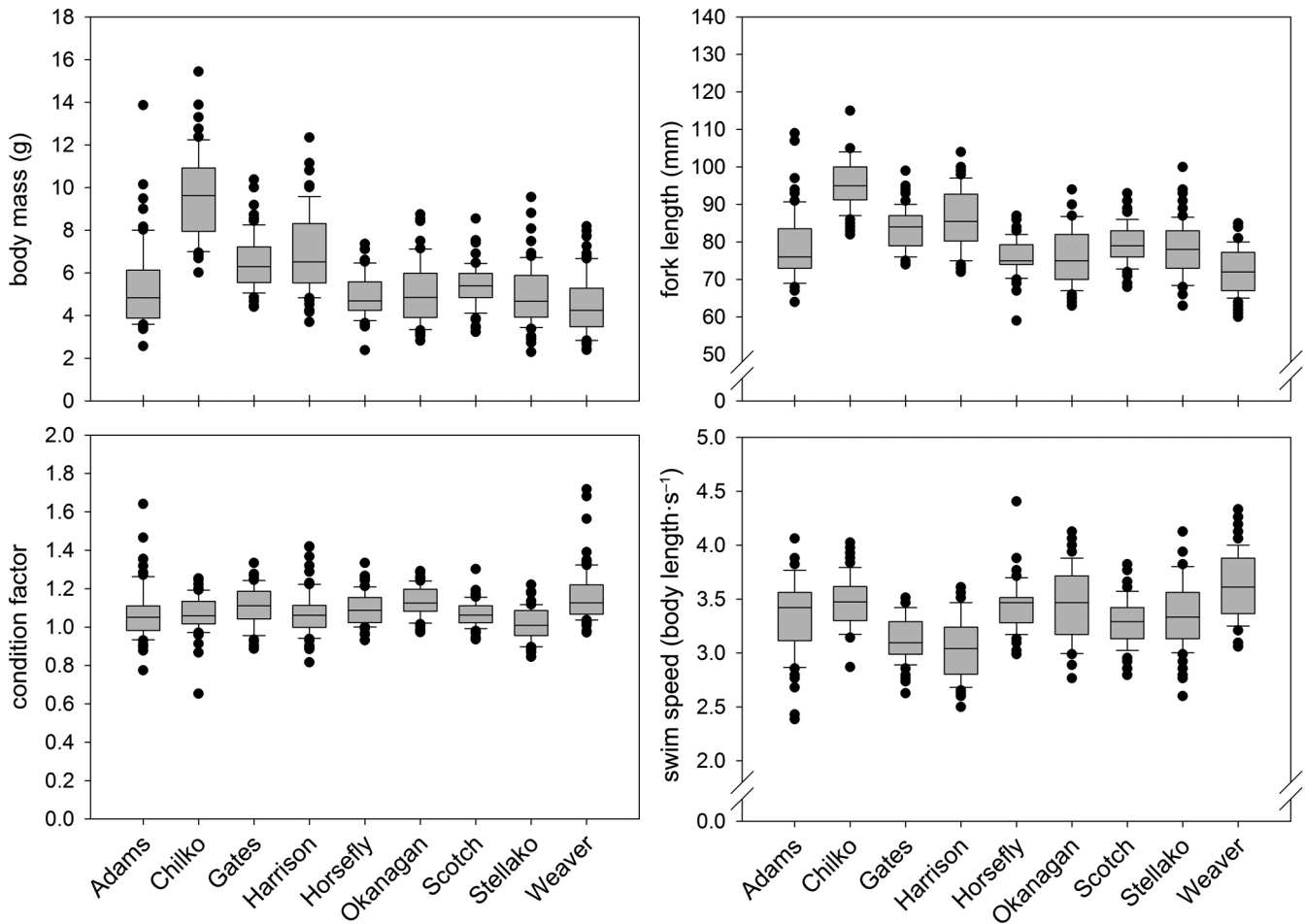
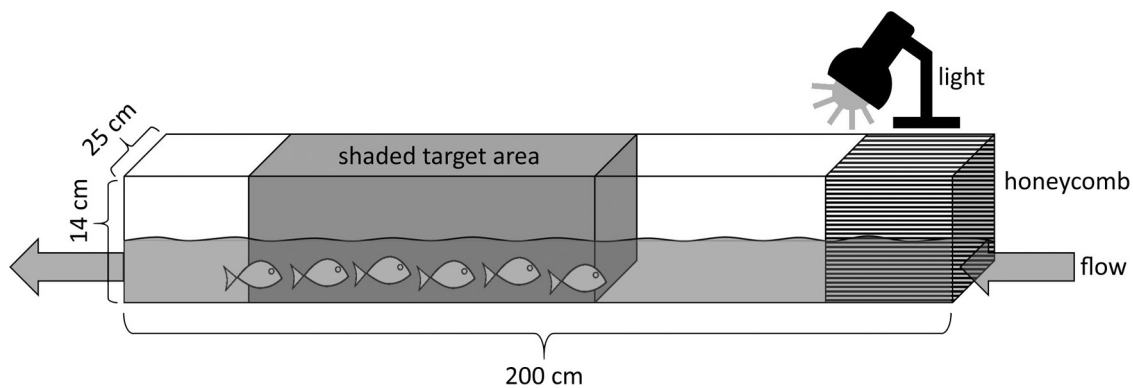


Fig. 3. Schematic of the endurance swim flume.

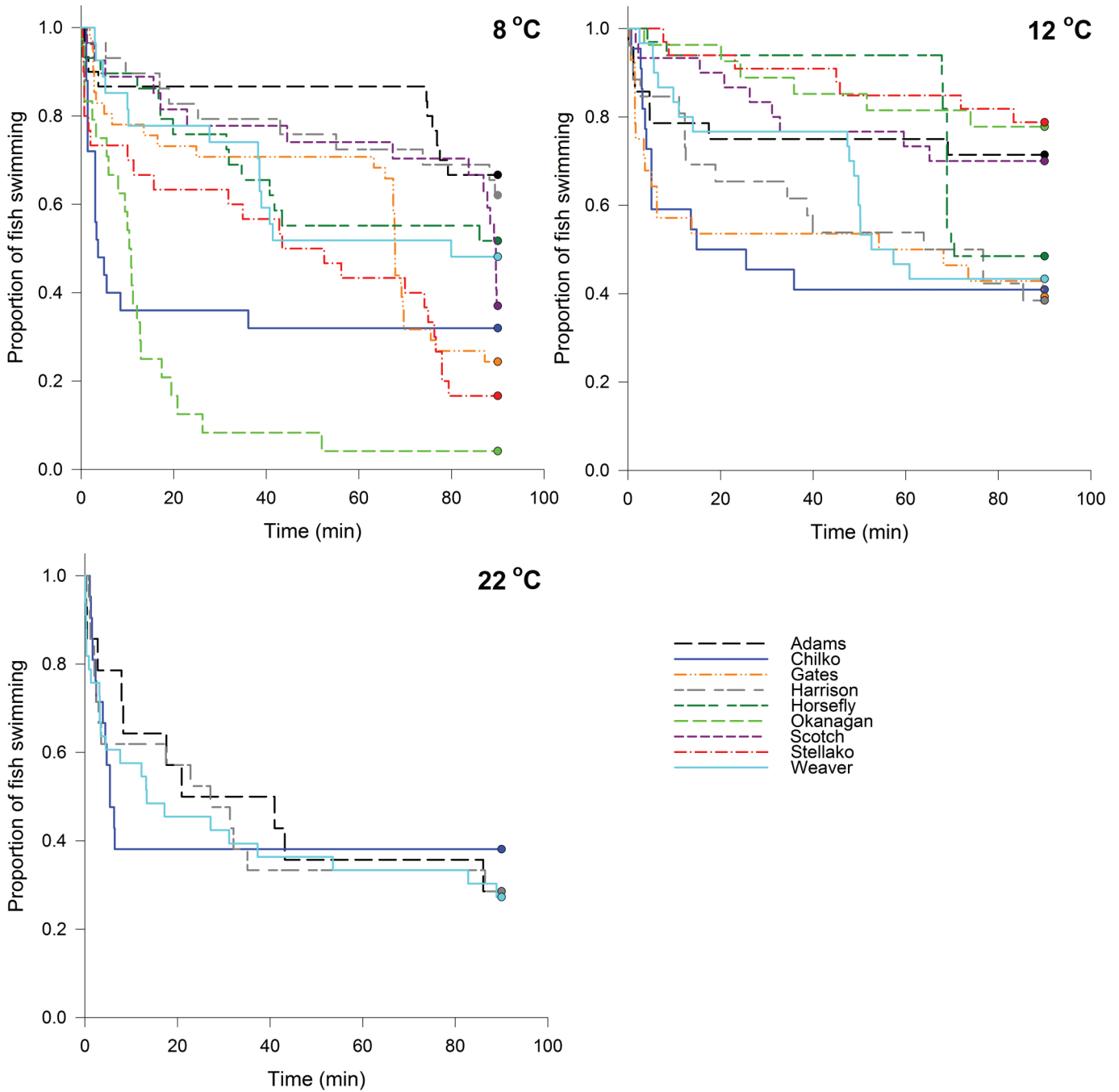


than three times during the ramping period, then it was removed from the flume and not included in the statistical analysis (Winger et al. 1999).

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, Ontario, 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

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



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 ven-

tricle 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 grams (g) and fork length is in centimetres (cm). The actual swim speed for each individual fish was determined as water velocity/fork length. RVM was determined as $RVM = \text{ventricle mass} / \text{body mass} \times 100$.

All statistics were performed using SigmaPlot version 11.0 (Systat Software, Inc., San Jose, California, USA). Failure time analysis, also known as survival analysis, was used to statistically compare endurance swim performance. See Winger et al. (1999) for

Can. J. Zool. Downloaded from www.nrcresearchpress.com by Santa Barbara (UCSB) on 08/15/17
For personal use only.

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 log-rank 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. RVM 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 with 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 versus poor swim performance (Table 4; two-way ANOVA, $p > 0.05$). The overall mean (\pm SE) 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). Numer-

Table 2. Kaplan–Meier log-rank survival analysis of the swimming endurance of nine populations of sockeye salmon (*Oncorhynchus nerka*) at three temperatures with different letters indicating statistically significant difference between test temperatures within a population.

Population	Statistic	df	P	Temperature (°C)		
				8	12	22
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

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

Covariate	Coefficient	SE	χ^2	P
8 °C				
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
12 °C				
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
22 °C				
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/body mass \times 100) for parr from nine populations of sockeye salmon (*Oncorhynchus nerka*).

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

ous 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 because the lakes are complex

environments with high inter- and intra-seasonal variations and because environmental data are 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 (*Oncorhynchus kisutch* (Walbaum, 1792)), steelhead trout (*Oncorhynchus mykiss* (Walbaum, 1792)), Atlantic salmon, 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 that 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 with 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 because 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. As 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 with 8 and 12 °C. In contrast, Chilko fish exhibited equally poor swim performance at all three 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 four 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 were 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%), whereas 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, nongenetic 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 RVM, thus alternative factors should be considered.

Acknowledgements

We thank Fisheries and Oceans Canada Environmental Watch Program and L. Pon for assistance with Table 1 and M. Lawrence for assistance with fish husbandry and endurance swim tests. This research was supported by the Ocean Tracking Network through the Natural Sciences and Engineering Research Council of Canada (NSERC), with additional support from the Canadian Foundation for Innovation and an NSERC Discovery grant (S.G.H.).

References

- Abrahams, M.V., and Kattenfeld, M.G. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. *Behav. Ecol. Sociobiol.* 40(3): 169–174. doi:10.1007/s002650050330.
- Beacham, T.D., and Murray, C.B. 1987a. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. *Can. J. Fish. Aquat. Sci.* 44(2): 244–261. doi:10.1139/f87-034.
- Beacham, T.D., and Murray, C.B. 1987b. Effects of transferring pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon embryos at different developmental stages to a low incubation temperature. *Can. J. Zool.* 65(1): 96–105. doi:10.1139/z87-015.
- Beacham, T.D., and Murray, C.B. 1989. Variation in developmental biology of sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*) in British Columbia. *Can. J. Zool.* 67(9): 2081–2089. doi:10.1139/z89-297.
- Breen, M., Dyson, J., O'Neill, F.G., Jones, E., and Haigh, M. 2004. Swimming endurance of haddock (*Melanogrammus aeglefinus* L.) at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears. *ICES J. Mar. Sci.* 61(7): 1071–1079. doi:10.1016/j.icesjms.2004.06.014.
- Brett, J.R. 1964. The respiratory metabolism and swimming performance of

- young sockeye salmon. *J. Fish. Res. Board Can.* **21**(5): 1183–1226. doi:10.1139/f64-103.
- Brett, J.R. 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Board Can.* **24**(8): 1731–1741. doi:10.1139/f67-142.
- Chen, Z., Anttila, K., Wu, J., Whitney, C.K., Hinch, S.G., and Farrell, A.P. 2013. Optimum and maximum temperatures of sockeye salmon (*Oncorhynchus nerka*) populations hatched at different temperatures. *Can. J. Zool.* **91**(5): 265–274. doi:10.1139/cjz-2012-0300.
- Claireaux, G., McKenzie, D.J., Genge, A.G., Chatelier, A., Aubin, J., and Farrell, A.P. 2005. Linking swimming performance, cardiac pumping ability and cardiac anatomy in rainbow trout. *J. Exp. Biol.* **208**(10): 1775–1784. doi:10.1242/jeb.01587. PMID:15879059.
- Cotterell, S.P., and Wardle, C.S. 2004. Endurance swimming of diploid and triploid Atlantic salmon. *J. Fish Biol.* **65**: 55–68. doi:10.1111/j.0022-1112.2004.00552.x.
- Cox, D. 1972. Regression models and life-tables. *J. R. Stat. Soc. Ser. B Methodol.* **34**(2): 187–220.
- Cox, D.R., and Oakes, D. 1984. Analysis of survival data. CRC Press, London.
- Crossin, G.T., Hinch, S.G., Farrell, A.P., Higgs, D.A., Lotto, A.G., Oakes, J.D., and Healey, M.C. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *J. Fish Biol.* **65**(3): 788–810. doi:10.1111/j.0022-1112.2004.00486.x.
- Drinan, T.J., McGinnity, P., Coughlan, J.P., Cross, T.F., and Harrison, S.S.C. 2012. Morphological variability of Atlantic salmon *Salmo salar* and brown trout *Salmo trutta* in different river environments. *Ecol. Freshw. Fish.* **21**(3): 420–432. doi:10.1111/j.1600-0633.2012.00561.x.
- Eliason, E.J., Clark, T.D., Hagu, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., and Farrell, A.P. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science*, **332**(6025): 109–112. doi:10.1126/science.1199158. PMID:21454790.
- Eliason, E.J., Wilson, S.M., Farrell, A.P., Cooke, S.J., and Hinch, S.G. 2013. Low cardiac and aerobic scope in a coastal population of sockeye salmon *Oncorhynchus nerka* with a short upriver migration. *J. Fish Biol.* **82**(6): 2104–2112. doi:10.1111/jfb.12120. PMID:23731155.
- Farrell, A.P. 1996. Features heightening cardiovascular performance in fishes, with special reference to tunas. *Comp. Biochem. Physiol. Part A Physiol.* **113**: 61–67. doi:10.1016/0300-9629(95)02058-6.
- Fraser, D., Weir, L., Bernatchez, L., Hansen, M., and Taylor, E. 2011. Extent and scale of local adaptation in salmonid fishes: review and meta-analysis. *Heredity*, **106**: 404–420. doi:10.1038/hdy.2010.167. PMID:21224881.
- Gamperl, A.K., and Farrell, A.P. 2004. Cardiac plasticity in fishes: environmental influences and intraspecific differences. *J. Exp. Biol.* **207**(15): 2539–2550. doi:10.1242/jeb.01057. PMID:15201287.
- Goodlad, J.C., Gjernes, T.W., and Brannon, E.L. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. *J. Fish. Res. Board Can.* **31**(5): 871–892. doi:10.1139/f74-106.
- Gregory, R.S. 1993. Effect of turbidity on the predator avoidance behaviour of juvenile Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **50**(2): 241–246. doi:10.1139/f93-027.
- Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific salmon. *Trans. Am. Fish. Soc.* **127**(2): 275–285. doi:10.1577/1548-8659(1998)127<0275:TRPOM>2.0.CO;2.
- Groot, C., and Margolis, L. 1991. Pacific salmon life histories. UBC Press, Vancouver, B.C.
- Gustafson, R.G., Wainwright, T.C., Winans, G.A., Waknitz, F.W., Parker, L.T., and Waples, R.S. 1997. Status review of sockeye salmon from Washington and Oregon. U.S. Dept. Commer. NOAA Tech. Memo. NMFS-NWFSC-33.
- Hume, J.M., Shortreed, K.S., and Morton, K.F. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. *Can. J. Fish. Aquat. Sci.* **53**(4): 719–733. doi:10.1139/f95-237.
- Hyatt, K., McQueen, D., Rankin, D., Stockwell, M., Wright, H., Lawrence, S., Stevens, A., Mathieu, C., and Weins, L. 2015. Methods and summary data for limnology and food web structure in Osoyoos Lake, BC (2005–2013). *Can. Data Rep. Fish. Aquat. Sci.* No. 1258. pp. 1–71.
- Janhunen, M., Peuhkuri, N., and Piironen, J. 2009. Morphological variability among three geographically distinct Arctic charr (*Salvelinus alpinus* L.) populations reared in a common hatchery environment. *Ecol. Freshw. Fish.* **18**(1): 106–116. doi:10.1111/j.1600-0633.2008.00329.x.
- Kawecki, T.J., and Ebert, D. 2004. Conceptual issues in local adaptation. *Ecol. Lett.* **7**(12): 1225–1241. doi:10.1111/j.1461-0248.2004.00684.x.
- Keeley, E.R., Parkinson, E.A., and Taylor, E.B. 2005. Ecotypic differentiation of native rainbow trout (*Oncorhynchus mykiss*) populations from British Columbia. *Can. J. Fish. Aquat. Sci.* **62**(7): 1523–1539. doi:10.1139/f05-062.
- Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. *Evolution*, **55**(8): 1656–1667. doi:10.1111/j.0014-3820.2001.tb00685.x. PMID:11580025.
- Langerhans, R.B. 2008. Predictability of phenotypic differentiation across flow regimes in fishes. *Integr. Comp. Biol.* **48**(6): 750–768. doi:10.1093/icb/092. PMID:21669830.
- Lee, C.G., Farrell, A.P., Lotto, A., MacNutt, M.J., Hinch, S.G., and Healey, M.C. 2003. The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *J. Exp. Biol.* **206**(18): 3239–3251. PMID:12909705.
- Martínez, M., Guderley, H., Dutil, J.-D., Winger, P.D., He, P., and Walsh, S.J. 2003. Condition, prolonged swimming performance and muscle metabolic capacities of cod *Gadus morhua*. *J. Exp. Biol.* **206**(3): 503–511. doi:10.1242/jeb.00098. PMID:12502771.
- Nelson, J.A., Gotwalt, P.S., and Snodgrass, J.W. 2003. Swimming performance of blacknose dace (*Rhinichthys atratulus*) mirrors home-stream current velocity. *Can. J. Fish. Aquat. Sci.* **60**(3): 301–308. doi:10.1139/f03-023.
- Patterson, D.A., Guderley, H., Bouchard, P., Macdonald, J.S., and Farrell, A.P. 2004. Maternal influence and population differences in activities of mitochondrial and glycolytic enzymes in emergent sockeye salmon (*Oncorhynchus nerka*) fry. *Can. J. Fish. Aquat. Sci.* **61**(7): 1225–1234. doi:10.1139/f04-076.
- Pavey, S.A., Nielsen, J.L., MacKas, R.H., Hamon, T.R., and Breden, F. 2010. Contrasting ecology shapes juvenile lake-type and riverine sockeye salmon. *Trans. Am. Fish. Soc.* **139**(5): 1584–1594. doi:10.1577/T09-182.1.
- Pon, L.B., Hinch, S.G., Wagner, G.N., Lotto, A.G., and Cooke, S.J. 2007. Swimming performance and morphology of juvenile sockeye salmon, *Oncorhynchus nerka*: comparison of inlet and outlet fry populations. *Environ. Biol. Fishes.* **78**(3): 257–269. doi:10.1007/s10641-006-9094-4.
- Riddell, B.E., Leggett, W.C., and Saunders, R.L. 1981. Evidence of adaptive polygenic variation between two populations of Atlantic salmon (*Salmo salar*) native to tributaries of the S.W. Miramichi River, N.B. *Can. J. Fish. Aquat. Sci.* **38**(3): 321–333. doi:10.1139/f81-043.
- Shortreed, K., Hume, J.M., and Morton, K.F. 1996. Trophic status and rearing capacity of Francois and Fraser lakes. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2151. pp. 1–58.
- Shortreed, K., Morton, K., Malange, K., and Hume, J. 2001. Factors limiting juvenile sockeye production and enhancement potential for selected BC nursery lakes. Canadian Science Advisory Secretariat Research Document No. 2001/098.
- Sopinka, N.M., Hinch, S.G., Lotto, A.G., Whitney, C.K., and Patterson, D.A. 2013. Does among-population variation in burst swimming performance of sockeye salmon *Oncorhynchus nerka* fry reflect early life migrations? *J. Fish Biol.* **83**(5): 1416–1424. doi:10.1111/jfb.12225. PMID:24117961.
- Stockner, J.G., and Shortreed, K.S. 1983. A comparative limnological survey of 19 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Fraser River system, British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 1190. pp. 1–62.
- Stockner, J.G., and Shortreed, K. 1991. Autotrophic picoplankton: community composition, abundance and distribution across a gradient of oligotrophic British Columbia and Yukon Territory lakes. *Int. Rev. Hydrobiol.* **76**(4): 581–601. doi:10.1002/iroh.19910760410.
- Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture*, **98**(1–3): 185–207. doi:10.1016/0044-8486(91)90383-1.
- Taylor, E.B., and McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**(12): 2029–2033. doi:10.1139/f85-250.
- Tsuyuki, H., and Willisroft, S.N. 1977. Swimming stamina differences between genotypically distinct forms of rainbow (*Salmo gairdneri*) and steelhead trout. *J. Fish Res. Board Can.* **34**(7): 996–1003. doi:10.1139/f77-152.
- Whitney, C.K., Hinch, S.G., and Patterson, D.A. 2013. Provenance matters: thermal reaction norms for embryo survival among sockeye salmon *Oncorhynchus nerka* populations. *J. Fish Biol.* **82**(4): 1159–1176. doi:10.1111/jfb.12055. PMID:23557297.
- Whitney, C.K., Hinch, S.G., and Patterson, D.A. 2014. Population origin and water temperature affect development timing in embryonic sockeye salmon. *Trans. Am. Fish. Soc.* **143**(5): 1316–1329. doi:10.1080/00028487.2014.935481.
- Winger, P.D., He, P., and Walsh, S.J. 1999. Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. *ICES J. Mar. Sci.* **56**(3): 252–265. doi:10.1006/jmsc.1999.0441.
- Winger, P.D., He, P., and Walsh, S.J. 2000. Factors affecting the swimming endurance and catchability of Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **57**(6): 1200–1207. doi:10.1139/f00-049.
- Zeng, L.-Q., Cao, Z.-D., Fu, S.-J., Peng, J.-L., and Wang, Y.-X. 2009. Effect of temperature on swimming performance in juvenile southern catfish (*Silurus meridionalis*). *Comp. Biochem. Physiol. Part A Mol. Integr. Physiol.* **153**(2): 125–130. doi:10.1016/j.cbpa.2009.01.013.