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Low cardiac and aerobic scope in a coastal population of sockeye salmon *Oncorhynchus nerka* with a short upriver migration

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This study showed that a coastal population (Harrison) of Fraser River sockeye salmon *Oncorhynchus nerka* had a lower aerobic and cardiac scope compared with interior populations with more challenging upriver spawning migrations, providing additional support to the idea that Fraser River *O. nerka* populations have adapted physiologically to their local migratory environment.

Key words: cardiovascular; climate change; exercise; local adaptation; oxygen consumption; Pacific salmon.

Fraser River sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) return to their natal streams with strong fidelity, resulting in genetically and geographically distinct populations (Beacham *et al*., 2005). The relative difficulty of the upriver migration varies widely among populations, depending on spawning ground location and river entry timing (Crossin *et al*., 2004; Eliason *et al*., 2011). The cardiorespiratory needs for this upriver migration are probably under strong selective pressure because *O. nerka* have a single opportunity to spawn (semelparity), and fish that fail to reach their spawning grounds have zero reproductive success. Indeed, Fraser River *O. nerka* populations appear to be locally adapted to their upriver migration environment (Crossin *et al*., 2004; Eliason *et al*., 2011). On the basis of an analysis of just eight of the >100 genetically distinct populations, those with more challenging

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migrations are characterized by a greater aerobic scope, larger relative ventricular mass with an enhanced coronary supply, fewer eggs, a more stream-lined body and more somatic energy stores compared with coastal populations with an easier migration (Lee *et al*., 2003; Crossin *et al*., 2004; Eliason *et al*., 2011). In addition, the optimal thermal range for aerobic scope is maintained across the breadth of temperatures typically encountered during the upstream migration for a given population (Farrell *et al*., 2008; Eliason *et al*., 2011). Of the seven populations with aerobic scope measurements, only one represents a coastal population with a comparatively easy migration (Weaver). Furthermore, cardiovascular performance has never been assessed in a coastal population. Therefore, the objective of this study was to examine thermal tolerance and cardiorespiratory performance in migrating adult Harrison *O. nerka*.

The Harrison *O. nerka* population is of particular interest for several reasons. Foremost, as a coastal population, their spawning area is only 121 km from the ocean with an elevation of just 10 m, which represents a relatively short and easy upriver migration compared with interior populations [distance and elevation can exceed 1000 km and 1100 m, respectively (Eliason *et al*., 2011)]. Second, while most Fraser River *O. nerka* populations migrate directly to their spawning area after entering the Fraser River and spawn immediately, Harrison *O. nerka* typically leave the ocean in September (termed a late run) and spend *c*. 2 months congregating in Harrison River and Harrison Lake before spawning in November (Burgner, 1991). Third, since 1995, several late run populations (*e.g*. Harrison, Weaver, Cultus and Lower Adams) have entered the Fraser River 3–6 weeks earlier than normal, a phenomenon that is poorly understood. As a result of the early river entry, these fish encounter considerably warmer temperatures and *en route* mortality has exceeded 90% in some years (Cooke *et al*., 2004; Hinch *et al*., 2012). Lastly, unlike most populations that typically spend a year as fry in a freshwater nursery lake adjacent to their spawning grounds, Harrison *O. nerka* migrate directly downstream to the Fraser River estuary after they hatch. Given the key role of the heart in supporting aerobic swim performance, cardiac scope and aerobic scope were hypothesized to be positively associated with migration difficulty, with maximum aerobic scope being maintained across the range of temperatures most frequently encountered during their upriver migration.

This study was conducted in accordance with guidelines of the Canadian Council of Animal Care, as administered by Carleton University (Animal Care #B10-06) and the University of British Columbia (Animal Care #A11-0212). Adult Harrison *O. nerka* (mean ± S.E. mass $= 2{\cdot}73 \pm 0{\cdot}08$ kg) were collected by beach seine from the Harrison River on 26 October 2011 and held for 3–22 days at 10·8–12·9° C in outdoor freshwater tanks at the Cultus Lake Salmon Research Laboratory (Cultus Lake, BC, Canada). Individual fish were assigned to a control ($n = 7$), cardiovascular ($n = 6$) or accelerometry ($n = 9$) group. The control fish were placed directly in a Brett-type swim tunnel (Lee *et al*., 2003; Steinhausen *et al*., 2008) and allowed to recover overnight at a resting velocity of $0{\cdot}15\ \mathrm{m\ s^{-1}}$ at ambient water temperature (*c*. 12° C). The cardiovascular group was anaesthetized with buffered MS-222 ($0{\cdot}1\ \mathrm{g\ l^{-1}}$ MS-222 and $0{\cdot}2\ \mathrm{g\ l^{-1}}$ $NaHCO_3$, Sigma; www.sigmaaldrich.com), transferred to a surgery table and maintained under a lower dose of anaesthetic ($0{\cdot}075\ \mathrm{g\ l^{-1}}$ MS-222 and $0{\cdot}15\ \mathrm{g\ l^{-1}}$ $NaHCO_3$) while a PE-50 cannula was inserted into the dorsal aorta to sample arterial blood (Soivio *et al*., 1973) and a Transonic flowprobe was placed around the ventral aorta to monitor cardiac output (Steffensen & Farrell, 1998), as detailed elsewhere (Steinhausen *et al*., 2008; Eliason *et al*., 2011). Individuals in the accelerometry group were anaesthetized with buffered MS-222 (0·1 g l^{-1} MS-222 and 0·2 g l^{-1} $NaHCO_3$) and received a gastrically inserted accelerometer (VEMCO Model V9A-2H, 69 kHz, 16 mm × 67 mm; www.vemco.com). Cardiovascular and accelerometer fish were similarly placed in a swim tunnel and allowed to recover overnight at a resting velocity of 0·15 m s^{-1} at ambient water temperature (*c*. 12° C). Accelerometry fish were also used to calibrate acoustic accelerometer tags with swim speed, tailbeat frequency and oxygen consumption in a separate study presented elsewhere (Wilson *et al*., 2013).

Resting oxygen consumption (MO_2) and cardiac output (V_b; when applicable) were measured at a water velocity of 0·15 m s^{-1}. Fish then performed a ramp-U_{crit} swim test (Jain *et al*., 1997; Lee *et al*., 2003) in which water velocity was first increased to *c*. 50% of U_{crit} (*c*. 1 bl s^{-1}) over a 15 min period. Thereafter, the water velocity was increased by 0·15 m s^{-1} (*c*. 0·20 bl s^{-1}) every 20 min until the fish ceased swimming and remained on the rear grid for >10 s. Upon fatigue, the water velocity was decreased to 0·15 m s^{-1} and the fish were allowed to recover for 1 h before a second swim test was conducted.

Accelerometer fish were tested at four or six randomly selected temperatures (12, 14, 16, 18, 20 and 22° C) over 2 or 3 days. The water temperature in the swim tunnel was either increased or decreased by 4° C h^{-1} and held at this temperature for 1 h before the swim test was started. Cardiovascular fish were tested at two temperatures over a single day in the same manner (14° C and 21–24° C). Control fish were tested once at 14° C in a single day. In this way fish were made to swim over a range of water temperatures from 12 to 24° C.

Oxygen uptake was measured during the final 10 min of each 20 min velocity interval using an Oxyguard dissolved oxygen meter (Point Four Systems; www.pointfour.com), Windaq box (Dataq instruments; www.dataq.com) and Labview software (National Instruments; www.canada.ni.com). Microbial (background) MO_2 was negligible. V_b was recorded continuously throughout the swim test using a flowmeter (Transonic systems; www.transonic.com) and Biopac hardware with Acknowledge software (Biopac systems; www.biopac.com). V_b was calculated as the mean of at least three 30 s segments from the continuous trace. Aerobic scope and cardiac scope were determined as the difference between resting and maximum values.

The temperature distributions [Fig. 1(b)] for the typical Harrison *O. nerka* river migration from 1995 to 2008 were simulated from daily river and lake temperatures during the active period of the spawning migration (*i.e*. did not include lake or river holding) (Farrell *et al*., 2008; Eliason *et al*., 2011). These were used to create temperature frequency histograms for both the historical run timing (prior to 1995 with a peak river entry on 27 September) and the current early entry phenomenon (with a peak river entry on 27 August).

Data are presented as mean ± S.E., unless otherwise indicated. An exponential equation was fitted to individual resting MO_2 data in relation to temperature. A polynomial quadratic equation was fitted to individual maximum MO_2 and to individual aerobic scope in relation to temperature. The optimal temperature (T_{opt}) was defined as the temperature corresponding to the peak of the polynomial regression between aerobic scope and temperature. The upper and lower pejus temperatures (T_p) were defined as the temperatures corresponding to 90% of aerobic scope and

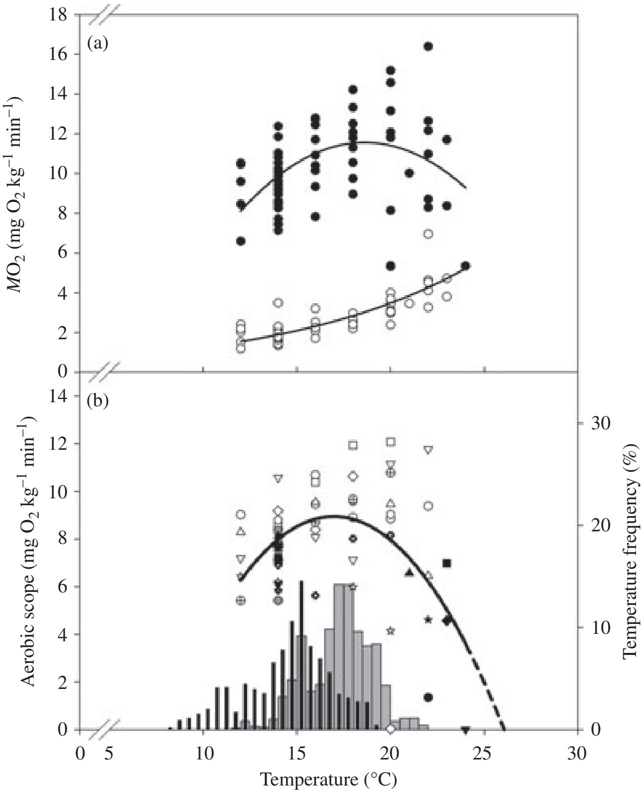

FIG. 1. (a) Resting (○) and maximum (●) oxygen consumption rates (MO_2) in relation to water temperature for individual Harrison *Oncorhynchus nerka*. (b) Aerobic scope, the difference between maximum and resting MO_2, for individual fish from (a). Open symbols correspond to individual fish with accelerometers, black symbols correspond to individuals that underwent surgery for cardiovascular measurements and grey symbols correspond to individual control fish. The frequency histogram shows simulated distributions of average river temperatures encountered by individual modelled fish during their upriver migration from 1995 to 2008 for both historical river entry (■) and the current early entry phenomenon (▨). (a) An exponential equation was fitted to resting MO_2 ($y = 0{\cdot}5\mathrm{e}^{0{\cdot}1x}$; $r^2 = 0{\cdot}699$, $P < 0{\cdot}001$) and a polynomial quadratic equation was fitted to maximum MO_2 ($y = -15{\cdot}7 + 2{\cdot}9x + -0{\cdot}1x^2$; $r^2 = 0{\cdot}188$, $P < 0{\cdot}01$) and (b) aerobic scope data ($y = -22{\cdot}2 + 3{\cdot}7x + -0{\cdot}1x^2$; $r^2 = 0{\cdot}206$, $P < 0{\cdot}01$).

the T_{opt} window was defined as the range of temperatures between the upper and lower T_{p} (Eliason *et al*., 2011). The upper critical temperature (T_{crit}) was estimated by extrapolating the polynomial equation to the upper temperature when aerobic scope reached zero. The upper temperature experienced by the 90th percentile of each population ($T_{90\%}$) was estimated from the temperature frequency distributions and the percent aerobic scope available at $T_{90\%}$ was determined. Aerobic scope at T_{opt} was determined as the mean ± S.E. of the individual data points within the T_{opt} window (14–20° C for Harrison *O. nerka*). Cardiac scope at T_{opt} was determined as the mean ± S.E. of the individual data points at 14° C.

Aerobic scope and cardiac scope were compared with existing data on Fraser River *O. nerka* populations (Eliason *et al*., 2011) using one-way ANOVA and a *post hoc* Holm-Sidak test. Pearson correlation compared aerobic scope at T_{opt} (from eight

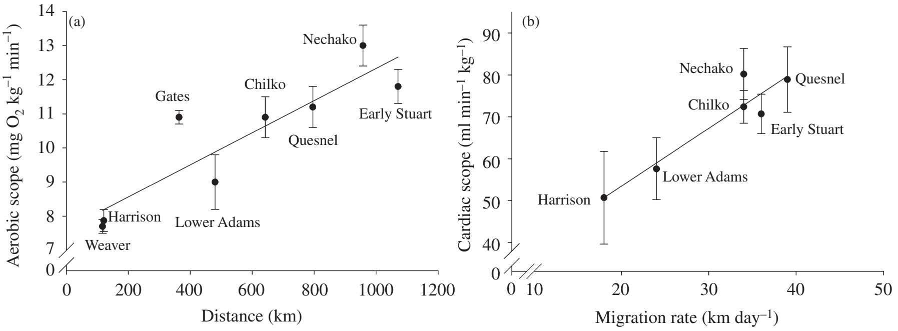

FIG. 2. Linear regressions between the migration difficulty index with the strongest Pearson correlation coefficient (Table I) and (a) aerobic scope and (b) cardiac scope for populations of Fraser River *Oncorhynchus nerka*. Data for Early Stuart, Nechako, Quesnel, Chilko, Lower Adams, Gates and Weaver populations are from Eliason *et al*., 2011. Population means ± S.E. are presented. The curves were fitted by (a) $y = 7{\cdot}619 + 0{\cdot}00471x$ ($r^2 = 0{\cdot}80$, $P < 0{\cdot}01$) and (b) $y = 25{\cdot}832 + 1{\cdot}381x$ ($r^2 = 0{\cdot}88$, $P < 0{\cdot}01$).

populations) and cardiac scope at T_{opt} (from six populations) with eight different migration difficulty indices: migration distance, elevation gain, migration rate, duration, work (distance × elevation), river slope (elevation/distance), migration effort (distance × river flow) and accumulated thermal units (ATU; Eliason *et al*., 2011). Linear regression was used to relate aerobic scope and cardiac scope to the migration difficulty index with the highest correlation coefficient and strongest P-value from the Pearson correlation matrix. All statistics were performed using SigmaPlot 11.0 (www.systat.com).

U_{crit}, $M\text{O}_{2\text{rest}}$, $M\text{O}_{2\text{max}}$ and aerobic scope did not significantly differ between male and female fish in the accelerometry group (Wilson *et al*., 2013). When compared at a common temperature of 14° C, $M\text{O}_{2\text{rest}}$, $M\text{O}_{2\text{max}}$ and aerobic scope did not significantly differ among the three groups (control, cardiovascular and accelerometry; one-way ANOVA, $P > 0{\cdot}05$). $M\text{O}_{2\text{rest}}$, $M\text{O}_{2\text{max}}$ and aerobic scope for all three groups are included in Figs 1 and 2.

$M\text{O}_{2\text{rest}}$ increased exponentially with increasing temperature (Fig. 1). $M\text{O}_{2\text{max}}$ also increased with increasing temperature but became more variable and started to decline at the highest test temperatures. Aerobic scope was optimal (T_{opt}) at 17·0° C and the lower and upper T_{p} were 14·1 and 19·9° C, respectively, with a T_{opt} window of 5·8° C. The predicted T_{crit} was 26·1° C (Fig. 1). The aerobic scope curve varied in parallel with the temperature frequency histograms (Fig. 1). Harrison *O. nerka* had 100 and 94% of aerobic scope available at historical (17·1° C) and current (19·1° C) $T_{90\%}$, respectively. Aerobic scope at T_{opt} was $7{\cdot}9 \pm 0{\cdot}3$ mg O$_2$ kg^{-1} min^{-1} and cardiac scope at T_{opt} was $50{\cdot}7 \pm 11{\cdot}1$ ml min^{-1} kg^{-1}.

Beyond the novel information of the cardiorespiratory responses of a coastal population of *O. nerka*, it is possible to integrate these data with those for other populations and strengthen support for the idea that Fraser River *O. nerka* populations have adapted physiologically to their local upriver migration conditions (Crossin *et al*., 2004; Eliason *et al*., 2011). For example, aerobic scope significantly differed among populations (one-way ANOVA, $P < 0{\cdot}001$) and population-specific aerobic scope was positively associated with several different migration difficulty indices (Table I). Consistent with previous findings (Eliason *et al*., 2011), aerobic

TABLE I. Pearson correlation matrix relating aerobic scope and cardiac scope from eight and six *Oncorhynchus nerka* populations, respectively, to eight migration difficulty variables (Eliason *et al*., 2011). Bold font indicates the migration difficulty variable with the highest correlation coefficient and strongest P-value. Three critical values are indicated: $P < 0.05$ (*, no correction for multiple comparisons), $P < 0.018$ [**, Benjamini and Yekutieli False Discovery Rate (Benjamini & Yekutieli, 2001; Narum, 2006)] and $P < 0.006$ [***, Bonferroni correction (Holm, 1979; Rice, 1989)]

	Aerobic scope	Cardiac scope
Migration distance (D_M)	**0·889*****	0·847*
Migration elevation (E_M)	0·737*	0·787
Work ($0.0001 E_M D_M$)	0·826**	0·891**
River slope ($500(E_M D_M^{-1})$)	0·513	0·531
Migration effort ($0.0001 D_M F_M$)	0·774*	0·618
Migration duration	0·826**	0·736
Migration rate	0·885***	**0·941*****
Historical ATU	0·867***	0·795
Aerobic scope		0·937***

ATU, accumulated thermal units using historical migration conditions; F_M, Fraser River discharge.

scope had the highest Pearson correlation coefficient with migration distance (Table I and Fig. 2). By adding Harrison to the population comparisons between aerobic scope and migration difficulty, every Pearson correlation coefficient increased (see Table I and Eliason *et al*., 2011). In addition, the r^2 value increased (0·73–0·80) and P-value decreased (<0.05 to <0.01) for linear regression between aerobic scope and migration distance (see Fig. 2 and Eliason *et al*., 2011).

Furthermore, cardiac scope is compared for the first time across *O. nerka* populations with widely varying migration difficulty, revealing that cardiac scope differed significantly among populations (one-way ANOVA, $P < 0.05$) and population-specific cardiac scope was positively associated with several different migration difficulty indices (Table I). Cardiac scope had the highest Pearson correlation coefficient with migration rate (Table I and Fig. 2). Furthermore, Harrison *O. nerka* had the lowest cardiac scope among the populations examined to date. In addition, aerobic scope and cardiac scope were strongly correlated (Table I), supporting the idea that cardiac capacity is tightly linked with aerobic scope (Farrell, 2009; Eliason *et al*., 2011). Indeed, cardiac morphometry, such as relative ventricular mass, percentage compact myocardium (the proportion of the ventricle that is supported by coronary circulation) and relative compact mass, have previously been shown to vary among populations according to migration difficulty (Eliason *et al*., 2011).

Harrison and Weaver *O. nerka* migrate up the Fraser River at the same time and share a similar, short and relatively easy migration. Harrison and Weaver *O. nerka*, however, differ in their optimal thermal range. Harrison *O. nerka* have a higher T_{opt} and a higher thermal tolerance compared to co-migrating Weaver *O. nerka* (T_{opt}: 17·0 and 14·5° C, respectively; upper T_p: 19·9 and 16·4° C, respectively). Notably, measurements were made in Weaver *O. nerka* in 2000 (Lee *et al*., 2003), only 5 years after the early entry migration behaviour began (or *c*. one generation because Weaver *O. nerka* life cycle is typically 4 years). Harrison *O. nerka* were measured in 2011 or 16 years after the early entry phenomenon began (four to five generations because Harrison *O. nerka* life cycle is typically 3–4 years), during which time peak summer migration temperatures have continued to increase and late run populations have continued to enter the Fraser River 3–6 weeks earlier than normal. This leaves the question: have Harrison *O. nerka* adapted to tolerate elevated river temperatures associated with early river entry? A repeat measurement for Weaver *O. nerka* would help answer this question. Nevertheless, Harrison *O. nerka* had 100% (historical) and 94% (current) of aerobic scope available at the 90th percentile of encountered temperatures, demonstrating that they could theoretically maintain swimming performance across the majority of the river temperatures that they encounter (both historically and currently). This finding adds support to previous findings for six other Fraser River *O. nerka* populations (Farrell *et al*., 2008; Eliason *et al*., 2011), Weaver *O. nerka* being an exception for recent years. Harrison *O. nerka* have a T_{opt} window (5·8° C) that is intermediate compared to the other six populations [ranging from 3·9° C for Weaver up to 7·8° C for Chilko *O. nerka* (Eliason *et al*., 2011)].

Peak summer temperature in the Fraser River has warmed by *c*. 2° C since the 1950s and is expected to continue along the same trajectory (Morrison *et al*., 2002; Ferrari *et al*., 2007). High river temperatures have been correlated with elevated *en route* mortality in *O. nerka* (Crossin *et al*., 2008; Farrell *et al*., 2008; Mathes *et al*., 2010; Martins *et al*., 2011). Current peak Fraser River temperatures (*c*. 21·5° C) already exceed the upper T_{p} for every population examined to date (present study and Eliason *et al*., 2011). As a result, populations are already experiencing temperatures that exceed their upper limit, and some individuals may be dying *en route* as a result of insufficient aerobic scope. The results presented here and elsewhere (Farrell *et al*., 2008; Eliason *et al*., 2011; Hinch & Martins, 2011) suggest that there will be population-specific responses to further increases in summer river temperatures, raising conservation concerns for biodiversity. Between 1996 and 2008, Weaver, Harrison and Chilko *O. nerka* experienced >50% *en route* mortality in 12, 6 and 0 years, respectively (Hinch & Martins, 2011). These differences in *en route* mortality may be, at least in part, a reflection of the different thermal tolerances among these populations.

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References

Beacham, T. D., Candy, J. R., McIntosh, B., MacConnachie, C., Tabata, A., Kaukinen, K., Deng, L., Miller, K. M., Withler, R. E. & Varnavskaya, N. (2005). Estimation of stock composition and individual identification of sockeye salmon on a Pacific Rim basis using microsatellite and major histocompatibility complex variation. *Transactions of the American Fisheries Society* **134,** 1124–1146.

Benjamini, Y. & Yekutieli, D. (2001). The control of the false discovery rate in multple testing under dependency. *The Annals of Statistics* **29,** 1165–1188.

Burgner, R. L. (1991). Life history of sockeye salmon *(Oncorhynchus nerka)*. In *Pacific Salmon Life Histories* (Groot, C. & Margolis, L., eds), pp. 1–118. Vancouver, BC: UBC Press.

Cooke, S. J., Hinch, S. G., Farrell, A. P., Lapointe, M. F., Jones, S. R. M., Macdonald, J. S., Patterson, D. A., Healey, M. C. & Van Der Kraak, G. (2004). Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries* **29,** 22–33.

Crossin, G. T., Hinch, S. G., Farrell, A. P., Higgs, D. A., Lotto, A. G., Oakes, J. D. & Healey, M. C. (2004). Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology* **65,** 788–810.

Crossin, G. T., Hinch, S. G., Cooke, S. J., Welch, D. W., Patterson, D. A., Jones, S. R. M., Lotto, A., Leggatt, R. A., Mathes, M. T., Shrimpton, J. M., Van Der Kraak, G. & Farrell, A. (2008). Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Canadian Journal of Zoology* **86,** 127–140.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G. & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science* **332,** 109–112.

Farrell, A. P. (2009). Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *Journal of Experimental Biology* **212,** 3771–3780.

Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M. & Mathes, M. T. (2008). Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology* **81,** 697–709.

Ferrari, M. R., Miller, J. R. & Russell, G. L. (2007). Modeling changes in summer temperature of the Fraser River during the next century. *Journal of Hydrology* **342,** 336–346.

Hinch, S. G., Cooke, S. J., Farrell, A. P., Miller, K. M., Lapointe, M. & Patterson, D. A. (2012). Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. *Journal of Fish Biology* **81,** 576–599.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6,** 65.

Jain, K. E., Hamilton, J. C. & Farrell, A. P. (1997). Use of a ramp velocity test to measure critical swimming speed in rainbow trout (*Oncorhynchus mykiss*). *Comparative Biochemistry and Physiology A* **117,** 441–444.

Lee, C. G., Farrell, A. P., Lotto, A., MacNutt, M. J., Hinch, S. G. & 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. *Journal of Experimental Biology* **206,** 3239–3251.

Martins, E. G., Hinch, S. G., Patterson, D. A., Hague, M. J., Cooke, S. J., Miller, K. M., Lapointe, M. F., English, K. K. & Farrell, A. P. (2011). Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*). *Global Change Biology* **17,** 99–114.

Mathes, M. T., Hinch, S. G., Cooke, S. J., Crossin, G. T., Patterson, D. A., Lotto, A. G. & Farrell, A. P. (2010). Effect of water temperature, timing, physiological condition, and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **67,** 70–84.

Morrison, J., Quick, M. C. & Foreman, M. G. G. (2002). Climate change in the Fraser River watershed: flow and temperature projections. *Journal of Hydrology* **263,** 230–244.

Narum, S. (2006). Beyond Bonferroni: Less conservative analyses for conservation genetics. *Conservation Genetics* **7,** 783.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution* **43,** 223–225.

Soivio, A., Nynolm, K. & Westman, K. (1973). Technique for repeated sampling of blood of individual resting fish. *Journal of Experimental Biology* **63,** 207–217.

Steffensen, J. F. & Farrell, A. P. (1998). Swimming performance, venous oxygen tension and cardiac performance of coronary-ligated rainbow trout, *Oncorhynchus mykiss*, exposed to progressive hypoxia. *Comparative Biochemistry and Physiology* **119A,** 585–592.

Steinhausen, M. F., Sandblom, E., Eliason, E. J., Verhille, C. & Farrell, A. P. (2008). The effect of acute temperature increases on the cardiorespiratory performance of resting and swimming sockeye salmon (*Oncorhynchus nerka*). *Journal of Experimental Biology* **211,** 3915–3926.

Wilson, S. M., Hinch, S. G., Eliason, E. J., Farrell, A. P. & Cooke, S. J. (2013). Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon. *Comparative Biochemistry and Physiology A* **164,** 491–498.

Electronic Reference

Hinch, S. G. & Martins, E. G. (2011). A review of potential climate change effects on survival of Fraser River sockeye salmon and an analysis of interannual trends in en route loss and pre-spawn mortality. *Cohen Commission Technical Report* **9**. Available at www.cohencommission.ca