RESEARCH ARTICLE

Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate

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SUMMARY

Little is known of the physiological mechanisms underlying the effects of climate change on animals, yet it is clear that some species appear more resilient than others. As pink salmon (*Oncorhynchus gorbuscha*) in British Columbia, Canada, have flourished in the current era of climate warming in contrast to other Pacific salmonids in the same watershed, this study investigated whether the continuing success of pink salmon may be linked with exceptional cardiorespiratory adaptations and thermal tolerance of adult fish during their spawning migration. Sex-specific differences existed in minimum and maximum oxygen consumption rates ($\dot{M}_{O_2,min}$ and $\dot{M}_{O_2,max}$, respectively) across the temperature range of 8 to 28°C, reflected in a higher aerobic scope ($\dot{M}_{O_2,max}-\dot{M}_{O_2,min}$) for males. Nevertheless, the aerobic scope of both sexes was optimal at 21°C (T_{opt}) and was elevated across the entire temperature range in comparison with other Pacific salmonids. As T_{opt} for aerobic scope of this pink salmon population is higher than in other Pacific salmonids, and historic river temperature data reveal that this population rarely encounters temperatures exceeding T_{opt}, these findings offer a physiological explanation for the continuing success of this species throughout the current climate-warming period. Despite this, declining cardiac output was evident above 17°C, and maximum attainable swimming speed was impaired above ~23°C, suggesting negative implications under prolonged thermal exposure. While forecasted summer river temperatures over the next century are likely to negatively impact all Pacific salmonids, we suggest that the cardiorespiratory capacity of pink salmon may confer a selective advantage over other species.

Key words: cardiac output, climate change, energy expenditure, fish, global warming, heart rate, metabolic rate, oxygen consumption rate, sex specific, temperature.

INTRODUCTION

The population structure, distribution and persistence of many fish species are being altered by the changing climate (e.g. O'Brien et al., 2000; Perry et al., 2005; Pörtner and Knust, 2007). While there exist obvious interspecific differences in resilience to climate change (Perry et al., 2005), there is a general consensus among scientists that little is known of the physiological mechanisms underlying these differences (e.g. Wilson et al., 2010).

The complex anadromous life histories of the Pacific salmonids place them under particular pressure from climate change and make them interesting model species, as they must endure both freshwater and marine environments. The Fraser River in British Columbia, Canada, is one of the world's largest salmon-bearing watersheds and is home to five anadromous Pacific salmonid species: pink (*Oncorhynchus gorbuscha*), sockeye (*O. nerka*), coho (*O. kisutch*), chum (*O. keta*) and Chinook (*O. tshawytscha*) salmon (Groot and Margolis, 1991). These species have significant cultural and biological value, and they form the basis of a commercial fishery in British Columbia that can exceed $1 billion annually. However, recent decades have seen a precipitous yet unexplained decline in the abundance of many Pacific salmonid species in the Fraser River watershed (Cooke et al., 2004; Farrell et al., 2008; Welch et al., 2009; Chittenden et al., 2010; Hague et al., 2011).

While Pacific salmonids generally experience water temperatures below 10°C during the marine phase of their lifecycle (Walker et al., 2000; Friedland et al., 2001; Azumaya and Ishida, 2005; Walker et al., 2006; Morita et al., 2010), summer-migrating species can be abruptly exposed to significantly warmer temperatures (>8°C increment in 1 h) as they enter the Fraser River during their once-in-a-lifetime migration to freshwater spawning grounds following cessation of feeding in the ocean [see, for example, fig. 5 of Cooke et al. (Cooke et al., 2008)]. This burden is becoming progressively worse, as the peak summer temperature of the Fraser River has warmed by around 2°C over the last 60 years and it is now more common for summer-migrating species to encounter temperatures exceeding 20°C (Patterson et al., 2007; Farrell et al., 2008). Probably as a result, high river temperatures have been associated with extreme (>70%) *en route* mortality in species such as sockeye salmon that have summer-migrating populations (Crossin et al., 2008; Farrell et al., 2008; Mathes et al., 2010; Martins et al., 2011). While many species are of increasing conservation concern, pink salmon have maintained steady populations despite their migration period including summer months, and there is little evidence of significant *en route* mortality in this species (PSC, 2009) (M. Lapointe, Pacific Salmon Commission, personal communication).

It is unclear what sets the limits of thermal tolerance in migrating adult Pacific salmonids. One leading possibility relates to an inability of the circulatory and ventilatory systems to meet the ever-increasing oxygen requirements of the tissues as they become progressively warmer (termed 'oxygen-limited thermal tolerance')

(Pörtner and Knust, 2007; Wang and Overgaard, 2007; Pörtner and Farrell, 2008). As tissues warm, minimum oxygen consumption rate ($\dot{M}_{O2,min}$) and circulatory oxygen transport increase exponentially until a critical thermal limit (T_{crit}) is reached, beyond which death ensues. The corresponding increases in maximum oxygen consumption rate ($\dot{M}_{O2,max}$) and circulatory oxygen transport during warming generally stop at a temperature below T_{crit}, thereby setting the optimal temperature (T_{opt}) for aerobic scope ($\dot{M}_{O2,max}$–$\dot{M}_{O2,min}$) and limiting the scope for oxygen transport at warmer temperatures. While this concept has received scant attention in adult Pacific salmonids, the limited existing data suggest a narrow, species- and population-specific temperature range over which aerobic scope is maximal (Lee et al., 2003; Farrell et al., 2008; Steinhausen et al., 2008; Eliason et al., 2011).

In view of this concept, the objectives of the present study were to (1) determine whether cardiorespiratory adaptations may enhance resilience of adult pink salmon to warm river temperatures, and (2) predict the effects of continued climate warming on this species in comparison with other Pacific salmonids. While it is noteworthy that thermal acclimation can alter the oxygen-limited thermal tolerance of a species (Wang and Overgaard, 2007), this is not considered to be ecologically relevant for adult pink salmon because they abruptly depart the ocean and experience broad and rapid temperature fluctuations throughout their 1–3 week freshwater migration before they reproduce and die.

MATERIALS AND METHODS
Animal collection and holding conditions

Wild pink salmon [*O. gorbuscha* (Walbaum 1792); body mass 1.6±0.1 kg, fork length (FL) 51±1 cm] were beach seined from the Harrison River, British Columbia, Canada, which is a tributary of the Fraser River approximately 130 km upstream of the Fraser River mouth (Fig. 1). Fish were caught over 4 days in the period of 10–24 September 2009, during which time the Harrison River water temperature ranged from 13 to 16°C. The fish were immediately transported 45 min by road in ~12°C water to the Fisheries and Oceans Canada Cultus Lake Laboratory. Upon arrival, fish were individually dip-netted from the transport truck and temporarily (<2 min) held in a water-filled trough to be injected with an identifying passive integrated transponder (PIT) tag into the ventral muscle tissue ~3 cm anterior of the vent. Fish were then placed into 5000 l holding tanks (diameter ~2.5 m, depth ~1 m) that were continuously flushed with filtered and UV-sterilised freshwater from nearby Cultus Lake (8–9°C), and given at least 24 h to recover from handling before use in experiments. This research was conducted with the approval of the Animal Ethics Committees of the University of British Columbia and the Department of Fisheries and Oceans, in accordance with the Canadian Council on Animal Care.

$\dot{M}_{O2,min}$

Intermittent flow-through respirometry was used to measure $\dot{M}_{O2,min}$ of 20 fish (10 males, 10 females). Fish were placed individually into three custom-built respirometers (each 138 l), which were submerged side by side within a 2000 l tank. Typically three fish were used for each trial, but occasionally one respirometer was left empty for measurement of background respiration rates, which were found to be negligible in all cases. The respirometers were automatically flushed with aerated freshwater for 45 min every hour, and oxygen consumption rates were determined from the slope of the decline in water oxygen saturation during each 15 min period between the flushes, as measured with Clark-type oxygen electrodes interfaced with data collection equipment (Loligo Systems, Tjele, Denmark).
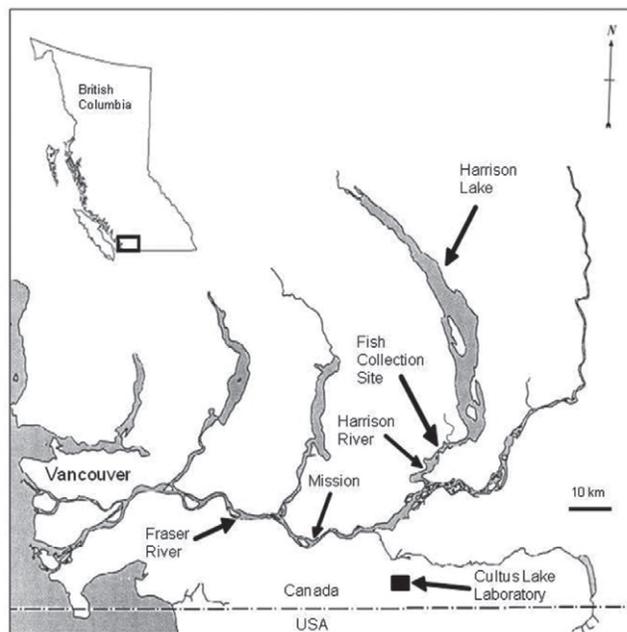

Fig. 1. Map of south-western British Columbia, Canada, illustrating the migration route of the pink salmon (*Oncorhynchus gorbuscha*) used in the present study. Generally throughout 15 August to 30 September every odd year, the Harrison population of pink salmon migrates up the Fraser River, past Mission, and spawns in the Harrison River watershed in late September through to mid-October.

Fish were placed into the respirometers in the evening when the water temperature was set at 8°C, and then allowed to recover from handling overnight while $\dot{M}_{O2}$ was continually measured. The fish were then exposed to a stepwise temperature increase to obtain $\dot{M}_{O2}$ measurements at four additional temperatures (typically 13, 17, 20 and 24°C). New temperatures were achieved by increasing water temperature at a rate of ~2°C h^{-1} by regulating a heating system, and fish were held at each new temperature for 4–10 h to ensure low and stable values of $\dot{M}_{O2}$. This duration may mimic resting phases of upriver migrating pink salmon. $\dot{M}_{O2,min}$ for each fish was taken as the lowest $\dot{M}_{O2}$ value recorded at each temperature.

Once measurements of $\dot{M}_{O2,min}$ were complete, water temperature was decreased to 8°C (at 4°C h^{-1}) for >2 h before the fish were removed. Fish from one or two respirometers were transferred to swim tunnel respirometers for determination of $\dot{M}_{O2,max}$ (see below), while fish from the remaining respirometer(s) were killed by cerebral concussion, weighed and measured (FL, straight body width and depth – taken immediately anterior to the dorsal fin). The ventricle was removed from each of these fish, blotted and then weighed to obtain relative ventricular mass (RVM).

$\dot{M}_{O2,max}$

$\dot{M}_{O2,max}$ was determined in two large swim tunnel respirometers that have been described previously (Farrell et al., 2003; Steinhausen et al., 2008). Clark-type oxygen electrodes (Point Four Systems, Richmond, Canada) monitored water oxygen levels in the respirometers at all times, and the voltage output from each electrode was interfaced with a PowerLab data acquisition system and associated LabChart software (ADInstruments, Sydney, Australia). Fish (7 males, 8 females) were introduced at 8°C and given >2 h to recover from handling at a low water speed (U; ~0.3 FL s^{-1}) before being

exercised maximally. Water speeds were corrected for the solid blocking effect of each individual using methods described previously (Jones et al., 1974). Maximal exercise was achieved by ramping water speed at a rate of ~0.5 FL min^{-1} until visual observations of the swimming gait (e.g. early stages of burst and glide swimming) suggested that the fish was approaching its maximum aerobic swimming speed. At this point, the swim tunnel was sealed from incoming freshwater and $\dot{M}_{O_2}$ measurements commenced. Water speed was typically increased further at this point (usually to ~3 FL s^{-1}), but modulated dynamically to ensure the fish was maximally challenged without constantly being pushed to the grid at the rear of the swim tunnel. An electric 'shocking' grid at the rear of the swim tunnel was used when necessary to promote maximal exercise. Water speed was decreased to ~0.3 FL s^{-1} after ~20 min or once the fish showed signs of exhaustion (e.g. failing to maintain position in the swim tunnel), and $\dot{M}_{O_2,max}$ was taken as the highest value (i.e. steepest slope of water oxygen saturation vs time) obtained for any 5 min period during the swim. Freshwater was flushed through the swim tunnel during a 1 h recovery period prior to warming the water to the next test temperature (typically a 3–5°C increment at 2°C h^{-1}). Once the new temperature was reached, the fish was given >1 h to adjust before it was challenged with the same swimming protocol as described above. $\dot{M}_{O_2,max}$ was determined at 4–6 temperatures for each fish, and then the fish was removed from the swim tunnel, killed by cerebral concussion, sampled for blood from the caudal vasculature (2 ml into a heparinised vacutainer), weighed, measured and the ventricle removed as described above.

Cardiovascular measurements

To determine the cardiovascular adjustments governing the increase in $\dot{M}_{O_2}$ with exercise across the entire temperature range, 13 additional fish (6 males, 7 females) were individually instrumented with temperature-calibrated blood flow probes (Transonic Systems, Ithaca, NY, USA) around the ventral aorta. Methods for attaching the flow probes were identical to those described previously (Clark et al., 2008b). Surgeries were conducted in the evening, and the fish were placed into the swim tunnels to recover overnight at ~0.3 FL s^{-1} and 8°C. The swimming protocol to determine $\dot{M}_{O_2,max}$ began the following morning and was identical to that described above, including the post-exercise blood and ventricle sampling. Cardiac output ($\dot{V}_b$) data from the flow probes were collected at 200 Hz using the same PowerLab and LabChart software described above. Heart rate (f_H) was determined from the pulsatile blood flow trace, and cardiac stroke volume (V_S) was calculated as $V_S = \dot{V}_b/f_H$. Maximum values for the three cardiovascular variables (denoted by subscript 'max') were taken as the mean of a 4–5 min period when f_H was maximal during the $\dot{M}_{O_2,max}$ measurement.

For four male fish, following five swim challenges at progressively incrementing temperatures up to 25–26°C, the temperature of the swim tunnel was decreased to 18 or 12°C (at ~4°C h^{-1}) to determine whether the fish could achieve the same level of performance as for their previous swim at the respective temperature. On all occasions, the fish on their second swim performed equally as well as on their first swim for each of swim speed (within +10% of the first swim), $\dot{V}_{b,max}$ (within +24%), $f_{H,max}$ (within −7%), $V_{S,max}$ (within +23%) and $\dot{M}_{O_2,max}$ (within +1%) (positive signs indicate higher values on the second swim, negative signs indicate lower values on the second swim). Thus, data from the first swim were used and the data for these fish are pooled with those of all other fish herein.

Data analyses and statistics

Haematocrit (Hct) of blood samples was determined using micro-capillary tubes spun at 10,000 g for 7 min, haemoglobin concentration ([Hb]) was determined using a handheld haemoglobin analyser calibrated for fish blood (HemoCue 201+) (Clark et al., 2008a), and mean cell haemoglobin concentration (MCHC) was calculated as [Hb]/(Hct/100).

To calculate the aerobic scope of individual fish (i.e. $\dot{M}_{O_2,max}-\dot{M}_{O_2,min}$), the overall $\dot{M}_{O_2,min}$ regression line for each sex was used to determine values of $\dot{M}_{O_2,min}$ that corresponded with the same temperatures for which $\dot{M}_{O_2,max}$ was measured in each individual. Gross cost of transport at maximum exercise (GCOT$_{exer}$; i.e. the mass-specific amount of oxygen consumed per metre travelled at maximum exercise) was calculated as $\dot{M}_{O_2,max}/U_{max}$ (where U_{max} is maximum swimming speed), following conversion of U_{max} to m min^{-1}. Net cost of transport at maximum exercise (NCOT$_{exer}$) was calculated as $(\dot{M}_{O_2,max}-\dot{M}_{O_2,min})/U_{max}$.

All statistical analyses were conducted in SigmaStat (Build 3.01.0, Systat Software Inc., www.systat.com) and SPSS (Build 16.0, SPSS Inc., Chicage, IL, USA). Linear mixed models were used to test the effects of temperature (covariate) and sex (fixed factor) (including a temperature × sex interaction) on all dependent variables (i.e. U_{max}, $\dot{M}_{O_2,min}$, $\dot{M}_{O_2,max}$, aerobic scope, GCOT$_{exer}$, NCOT$_{exer}$, $\dot{V}_{b,max}$, $f_{H,max}$, $V_{S,max}$), where individual fish identity was treated as a random factor. Model selection was accomplished using Akaike information criterion (AIC), and the model with the lowest AIC was considered to be the most parsimonious. The temperature × sex interaction was not significant in any model and was subsequently removed. Significance was considered at $P<0.05$. Data are discussed herein with regards to the model-derived regressions.

RESULTS

$\dot{M}_{O_2,min}$ and $\dot{M}_{O_2,max}$

The duration of 4 h+ at each temperature in the respirometer was sufficient to ensure low, stable measurements characterised as $\dot{M}_{O_2,min}$. $\dot{M}_{O_2,min}$ was significantly elevated in male fish compared with female fish and increased with water temperature by the same absolute amount in the two sexes (Fig. 2A). The temperature coefficient (Q_{10}) for $\dot{M}_{O_2,min}$ was 2.6±0.3 for males and 2.7±0.2 for females across the temperature range 8–24°C.

Maximum swimming speed (U_{max}) during the exercise trials generally ranged between 2.5 and 4 FL s^{-1}, and was dependent on temperature and sex (females on average 5% higher than males; Fig. 2D). $\dot{M}_{O_2,max}$ increased with water temperature in both sexes until reaching a plateau after ~21°C (Fig. 2A). Despite a marginally lower swimming speed across the temperature range, male fish achieved significantly higher $\dot{M}_{O_2,max}$ than females (23 vs 20 mg min^{-1} kg^{-1}, respectively), in excess of the sex-specific difference in $\dot{M}_{O_2,min}$ discussed above (Fig. 2A). This finding was not attributable to sex-specific differences in any of the measured variables relating to blood oxygen carrying capacity, as Hct, [Hb] and MCHC did not differ between sexes (e.g. MCHC: males 241±7 g l^{-1}; females 255±7 g l^{-1}; ANOVA, $P=0.158$). Consequently, GCOT$_{exer}$ and NCOT$_{exer}$ were elevated in male fish at all temperatures, indicating less efficient locomotion at maximal exercise (Fig. 2B,C). A laterally compressed body shape of males [greater ratio of body depth:width in males (2.19±0.05) vs females (1.80±0.04); ANOVA, $P<0.001$] may have played some role in this finding by increasing drag.

Reflecting the temperature- and sex-specific patterns in $\dot{M}_{O_2,min}$ and $\dot{M}_{O_2,max}$, T_{opt} for aerobic scope was ~21°C for both sexes, but
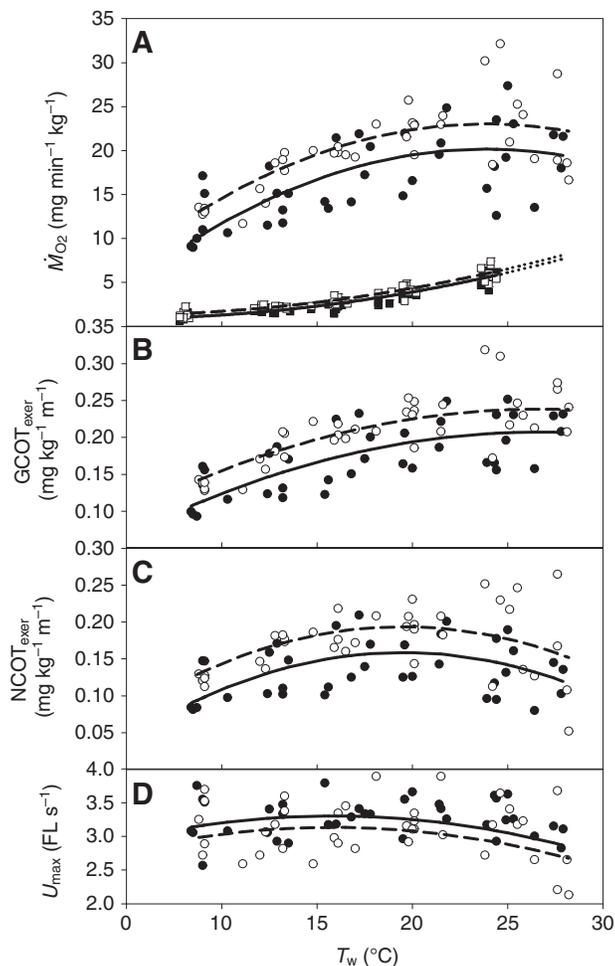
Fig. 2. Effects of water temperature (T_W) on (A) minimum (squares) and maximum (circles) oxygen consumption rate ($\dot{M}_{O2,min}$ and $\dot{M}_{O2,max}$, respectively), (B) gross cost of transport during exercise ($GCOT_{exer}$), (C) net cost of transport during exercise ($NCOT_{exer}$) and (D) maximum swimming speed (U_{max}) of male (open symbols, dashed regression lines) and female (filled symbols, solid regression lines) uninstrumented pink salmon (*O. gorbuscha*). Regression lines (s.e.m. in parentheses) are described by: (A) $\dot{M}_{O2,min}=1.496(0.447)–0.425(0.105)\times sex–0.098(0.060)\times T_W+0.012(0.002)\times T_W^2$ ($P<0.0001$); $\dot{M}_{O2,max}=–2.014(3.592)–2.860(0.768)\times sex+2.099(0.423)\times T_W–0.044(0.012)\times T_W^2$ ($P<0.0001$); (B) $GCOT_{exer}=0.025(0.033)–0.031(0.007)\times sex+0.016(0.004)\times T_W–0.0003(0.0001)\times T_W^2$ ($P<0.0001$); (C) $NCOT_{exer}=–0.018(0.040)–0.035(0.009)\times sex+0.022(0.005)\times T_W–0.0006(0.0001)\times T_W^2$ ($P<0.0001$); (D) $U_{max}=2.380(0.377)+0.171(0.081)\times sex+0.095(0.044)\times T_W–0.003(0.001)\times T_W^2$ ($P<0.0001$). The term 'sex' has a value of 0 for males and 1 for females. Dotted lines in A are extrapolations of $\dot{M}_{O2,min}$ regression lines.

Fig. 3. Aerobic scope of uninstrumented pink salmon (*O. gorbuscha*) over a range of water temperatures (T_W). Symbols are individual data points for male (open circles, black dashed regression line) and female (filled circles, black solid regression line) fish. Regression lines (s.e.m. in parentheses) are described by: Aerobic scope=19.623(12.314)–2.043(0.855)$\times$sex–2.432(2.313)$\times T_W$+0.224(0.135)$\times T_W^2$–0.0053(0.0025)$\times T_W^3$ ($P<0.0001$). The term 'sex' has a value of 0 for males and 1 for females. The vertical bar plots represent histograms of historic river temperatures from 15 August to 15 October, which is the period throughout which Harrison River pink salmon undergo their upriver migration and spawning. T_W measurements are from the Harrison River from 1997 to 2005 (white bars), the Fraser River (at Mission) from 1959 to 1996 (grey bars), and the Fraser River (at Mission) from 1997 to 2006 (black bars). Temperatures are binned as 10–10.9°C, 11–11.9°C, etc. Also presented are previously published aerobic scope curves for representative Pacific salmonids: Chehalis River coho salmon (CHE, green line); Weaver Creek sockeye salmon (WVR, blue line); Nechako metapopulation of sockeye salmon (NCH, yellow line); and Chilko metapopulation of sockeye salmon (CHK, red line). Data for CHE and WVR from Lee et al. (Lee et al., 2003), and data from NCH and CHK from Eliason et al. (Eliason et al., 2011).

aerobic scope was significantly elevated in male fish compared with female fish (18.3 *vs* 16.2 mg min^{-1} kg^{-1}, respectively, at 21°C; Fig. 3). Overlaying historic river temperature data on the aerobic scope curves revealed that Harrison River pink salmon most frequently encounter temperatures of 15–19°C during their freshwater migration and rarely experience temperatures exceeding T_{opt} for aerobic scope (Fig. 3). Factorial aerobic scope increased with temperature from 8 to 11°C, where it reached a maximum of 8.5 for males and 7.1 for females, before declining almost linearly with temperature to reach values of 2.7 and 2.4 at 28°C for males and females, respectively.
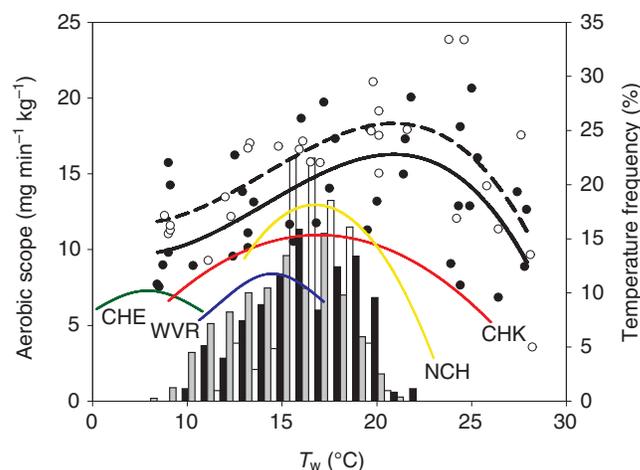
Cardiorespiratory physiology at maximum exercise

Fish instrumented with blood flow probes around the ventral aorta did not achieve the same swimming speed or $\dot{M}_{O2,max}$ as uninstrumented fish, and the sex-specific difference in $\dot{M}_{O2,max}$ no longer existed (Fig. 4A). Nevertheless, the qualitative trends in $\dot{M}_{O2,max}$ (i.e. increasing until ~21°C and generally plateauing thereafter) were the same as in uninstrumented fish.

Possibly as a result of greater RVM (males 0.166±0.003%, females 0.152±0.004%; ANOVA, $P=0.008$), males achieved a significantly higher $\dot{V}_{b,max}$ compared with females (154 *vs* 129 ml min^{-1} kg^{-1} at ~17°C; Fig. 4B), although neither $f_{H,max}$ nor $V_{S,max}$ reached statistical significance between sexes (Fig. 4C,D). $V_{S,max}$ declined linearly in both sexes as temperature increased beyond 8°C. $f_{H,max}$ initially increased more rapidly than the decrease in $V_{S,max}$, but the rate of increase slowed after ~17°C and $f_{H,max}$ plateaued at temperatures higher than ~21°C. Consequently, $\dot{V}_{b,max}$ of both sexes increased with temperature up to ~17°C and declined thereafter (Fig. 4B). The fact that $\dot{M}_{O2,max}$ did not suffer the same decrease as $\dot{V}_{b,max}$ at high temperatures points to an increase in tissue oxygen extraction (i.e. arteriovenous oxygen content difference).

The patterns in cardiovascular variables (instrumented fish) and $\dot{M}_{O2,max}$ (instrumented and uninstrumented fish) at high temperatures were not artefacts of fish becoming progressively fatigued following multiple swim challenges, as fish were able to repeat their
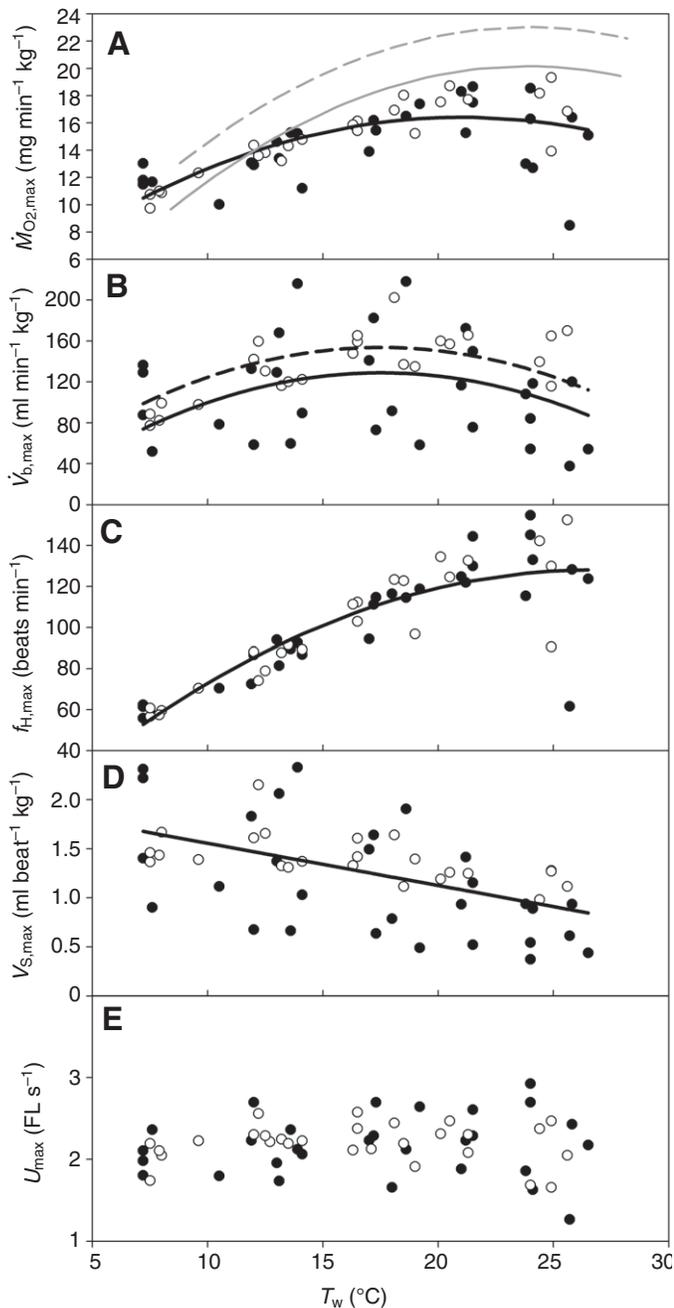
Fig. 4. Effects of water temperature (T_W) on maximum values of (A) oxygen consumption rate ($\dot{M}_{O_2,max}$), (B) cardiac output ($\dot{V}_{b,max}$), (C) heart rate ($f_{H,max}$), (D) cardiac stroke volume ($V_{S,max}$) and (E) swimming speed (U_{max}) of male (open circles) and female (filled circles) instrumented pink salmon (*O. gorbuscha*). Separate regression lines are presented for males (dashed lines) and females (solid lines) where statistically significant sex-specific differences exist. A single solid regression line on any panel indicates that sexes have been combined. Grey regression lines in A are those given in Fig. 2A for uninstrumented male (dashed line) and female (solid line) fish. Swimming speed was not dependent on sex or T_W. Regression lines (s.e.m. in parentheses) are described by: (A) $\dot{M}_{O_2,max}=2.705(2.066)+1.304(0.270)\times T_W-0.031(0.008)\times T_W^2$ ($P<0.0001$); (B) $\dot{V}_{b,max}=-4.429(43.370)-24.753(10.852)\times$ sex$+18.047(5.585)\times T_W-0.515(0.167)\times T_W^2$ ($P=0.003$); (C) $f_{H,max}=-13.290(15.978)+10.608(2.082)\times T_W-0.199(0.062)\times T_W^2$ ($P<0.0001$); (D) $V_{S,max}=1.986(0.169)-0.043(0.010)\times T_W$ ($P<0.0001$). The term 'sex' has a value of 0 for males and 1 for females.

performance at 12 and 18°C following five maximum swim challenges at temperatures ranging from 8 to 26°C (see Materials and methods).

DISCUSSION
Cardiorespiratory adaptations

This study presents the first cardiorespiratory measurements of adult pink salmon and documents an elite level of athleticism in comparison with other salmonids. Additionally, this may be the first study to document sex-specific differences in cardiorespiratory performance of swimming salmonids. The metabolic data presented for uninstrumented pink salmon are likely to represent free-roaming individuals and thus they provide a powerful tool for modelling the effects of future climate change on the metabolic capacity of this species. The finding of a lower $\dot{M}_{O_2,max}$ in instrumented fish emphasises the need to include an uninstrumented control group when studying cardiorespiratory responses of swimming fish using standard techniques that require tethering of the fish to recording equipment. Indeed, technology has not yet reached a point where the same measurements can be made from untethered and free-roaming fish. Although the cardiovascular data presented here, and in other studies using similarly instrumented salmonids, should be applied with caution to free-roaming fish, they provide insight into the cardiovascular mechanisms associated with oxygen transport. Direct comparisons with studies of other Pacific salmonids that have used the same cardiovascular instrumentation reveal that pink salmon can achieve exceptional cardiovascular performance. Indeed, the maximum values of $\dot{V}_{b,max}$, $f_{H,max}$ and $V_{S,max}$ measured for pink salmon in the present study are, respectively, 84–135%, 20–100% and 63–150% higher than the maximum values documented for other Pacific salmonids (Gallaugher et al., 2001; Clark et al., 2008b; Steinhausen et al., 2008; Clark et al., 2010).

Moreover, peak $\dot{M}_{O_2,max}$ (at 23°C) of male and female pink salmon is, respectively, 47–156% and 29–124% higher than peak measurements from other adult Pacific salmonids (Williams et al., 1986; Lee et al., 2003; Steinhausen et al., 2008; Eliason et al., 2011). It is noteworthy that a concurrent study of the same population of pink salmon examined the effects of an ecologically relevant thermal acclimation (5 days at either 8 or 19°C) on U_{max} and $\dot{M}_{O_2,max}$ and found no differences compared with the values obtained at the respective temperatures in the present study (T.D.C., unpublished data). This may not be surprising as adult pink salmon routinely experience rapid and broad temperature fluctuations during their 1–3 week river migration prior to reproduction and death, and so their capacity to thermally acclimate in the natural environment may be limited.

The finding of a greater aerobic scope for pink salmon in comparison with previously studied Pacific salmonids (Fig. 3) may result partly from better efforts to ensure low, stable measurements of $\dot{M}_{O_2,min}$, and from the design of the swimming protocol to ensure maximum attainable $\dot{M}_{O_2}$. However, these methodological improvements are unlikely to fully account for the difference in the amplitude of the aerobic scope between pink salmon and other salmonids, and they do not explain why pink salmon maintain an impressive aerobic scope over such a broad temperature range. Using >80% of maximum aerobic scope as a point of comparison, it is evident that both sexes of pink salmon can maintain a high proportion of maximum aerobic scope over a broader temperature window (spanning 12°C; ~14–26°C) than other adult Pacific salmonids (spanning 8±1°C) (Lee et al., 2003; Steinhausen et al., 2008; Eliason et al., 2011). The Chilko population of sockeye salmon has recently been reported to maintain >80% of maximum aerobic

scope over a temperature window more similar to pink salmon (spanning 11°C; ~11–22°C) (Eliason et al., 2011), although the amplitude of aerobic scope is lower than that for pink salmon throughout the temperature range (Fig. 3).

Aside from the magnitude of the aerobic scope of pink salmon, the T_{opt} of 21°C is higher than that reported for other Pacific salmonids and therefore prompts a discussion of the ecological significance of T_{opt} of wild salmon. By definition, T_{opt} signifies the temperature at which a fish can achieve (typically through exercise) the maximum scope between $\dot{M}_{O2,min}$ and $\dot{M}_{O2,max}$. T_{opt} for many fish species corresponds with the most frequently encountered environmental temperature (Asbury and Angilletta, 2010) and is often close to (or slightly higher than) the temperature that permits optimal growth rates (Brett, 1971; Elliott, 1976; Elliott, 1981; Jobling, 1997). This is clearly not the case for pink salmon, which migrate to the ocean shortly after hatching and thus spend the majority of their lifecycle and growth phase in the marine environment at temperatures below ~10°C (Walker et al., 2000; Friedland et al., 2001; Azumaya and Ishida, 2005; Walker et al., 2006; Morita et al., 2010). Indeed, if the temperature-dependent pattern in aerobic scope is similar in saltwater to that in freshwater, it can be estimated that pink salmon spend the marine phase of their adult life restricted to <68% of maximal aerobic scope, where the absolute aerobic scope would be <12.4 mg min^{-1} kg^{-1}. If the same concept is applied to other Pacific salmonids for which data exist (e.g. Fig. 3), it is clear that most species and populations spend the marine phase of their lifecycle with relatively low aerobic scope in comparison with pink salmon and in comparison with the population-specific aerobic scope achievable at higher temperatures. This is an interesting concept in light of the fact that salmon must maintain sufficient aerobic capacity in the marine environment to satisfy essential and often simultaneous aerobic processes such as prey capture, digestion and growth. While there is some evidence for salmonids that both $\dot{M}_{O2,min}$ and $\dot{M}_{O2,max}$ are lower in freshwater than in seawater (Maxime et al., 1990; Wagner et al., 2006), which should not greatly influence aerobic scope, there is a clear need to further investigate these concepts using temperature-controlled, ocean- and river-based experiments. Additionally, developmental changes in T_{opt} and aerobic scope should be further explored.

It has been proposed for sockeye and coho salmon that T_{opt} for aerobic scope is adaptive and is generally matched to the modal historic river temperature experienced by adult fish during their upriver spawning migration (Lee et al., 2003; Farrell et al., 2008; Eliason et al., 2011). The data for Harrison River pink salmon do not agree with this concept, as the historic river temperature distributions are left-shifted in relation to the T_{opt} for aerobic scope, and there are few historic occurrences where river temperatures exceed T_{opt} (Fig. 3). Indeed, it seems for pink salmon that T_{opt} represents the historic maximum rather than modal river temperature encountered during the migration. This may imply that this population has a 'buffer' between current peak summer Fraser River temperatures (~22°C) and the upper critical temperature likely to cause *en route* migration mortality. However, the present study highlights signs of impaired cardiovascular function around 17–21°C in the form of a plateau or decline in $f_{H,max}$ and $\dot{V}_{b,max}$, and so the high temperature tolerance reported here for acutely exposed pink salmon may not persist with longer thermal exposures. Anecdotal reports of pink salmon migrating through rivers associated with hot springs (>30°C) around Kleklane Inlet in northern British Columbia, Canada (A. Whitney and I. Whitney, personal communication), support our finding that pink salmon have the capacity to briefly exercise at exceptionally high temperatures. Conversely, sustained elevations in river water temperature above 17°C have been reported to increase pre-spawn mortality in an Alaskan population of pink salmon (Taylor, 2008). The extent to which population-specific thermal tolerance exists is not yet clear, but this is possible in light of some reported patterns of genetic structure across pink salmon populations from different watersheds (Beacham et al., 1985).

Implications in a warming climate

Our results allow a prediction of the effects of future climate warming on the success of the upriver migration of adult Harrison River pink salmon. With a further increase of 2–4°C estimated for the Fraser River by the end of this century (Morrison et al., 2002; Hague et al., 2011; Martins et al., 2011), many Pacific salmonids may begin to encounter brief periods of summer water temperatures exceeding 24°C during their upriver migration to spawning grounds. While most other Fraser River salmon species will likely have to modify migration timing to avoid peak summer temperatures, adapt to the warmer conditions, or perish, the present data indicate that both sexes of Harrison River pink salmon will retain >92% of maximal aerobic scope and >83% of maximal cardiac scope at 24°C and therefore may hold an advantage over other salmonids with future river warming.

Pink salmon are considered 'colonisers' and do not display the same spawning site fidelity as most other Pacific salmonid species, which consequently precludes genetic differentiation of distinct Fraser River populations using DNA microsatellite loci (K. M. Miller, personal communication) (Beacham et al., 1985). Corroborating previous studies (Williams et al., 1986; MacNutt et al., 2006), the results presented here dispel the historic contention that pink salmon are poor swimmers in comparison with other Pacific salmonids (Heard, 1991). Thus, Harrison River pink salmon should possess the swimming capacity to migrate to more distant freshwater spawning grounds than the Harrison River, including past Hell's Gate, a major hydraulic barrier ~200 km upriver of the Fraser River mouth (Hinch and Bratty, 2000). Indeed, current populations of pink salmon that migrate past Hell's Gate (e.g. Seton and Thompson River populations) are thought to have originated from short-migrating populations such as the Harrison River population used in this study.

Despite the capacity and resilience of pink salmon, the present study highlights the negative cardiorespiratory consequences of high temperature exposure and quantifies the thermal conditions that are likely to impair physiological performance with future climate warming. An additional concern is that the rate of disease progression increases with temperature (Fagerlund et al., 1995; Wagner et al., 2005; Crossin et al., 2008), particularly as Pacific salmonids progressively lose immune function and undergo rapid senescence during the upriver spawning migration (Miller et al., 2009). The sex-specific differences documented here for pink salmon corroborate previous suggestions for sockeye salmon that females have less capacity to tolerate environmental perturbations (Sandblom et al., 2009), and so it may be necessary to incorporate these sex-specific effects into future conservation efforts.

Clearly, further work is required to decipher the adaptive significance and ecological implications of T_{opt}, and quantify how aerobic scope is partitioned across activities and modulated throughout development in the freshwater and marine phases of the lifecycle. The concepts raised here must be investigated in free-roaming populations of Pacific salmonids exposed to the annual range of migration conditions, and biologging and biotelemetry

technologies may play key roles in such future endeavours (e.g. Clark et al., 2010). In any event, the findings of the present study suggest that pink salmon may continue to prove more resilient than other salmonids to increases in river water temperature, and they have the swimming capacity to expand their range to fill niches left by intolerant species and populations.

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