

## Corrigendum

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**, 3239-3251.

In both the on-line and printed versions of this paper, some of the equations in the legends to Figs 2–4 were printed incorrectly.

On page 3245, in the legend to Fig. 2, the two equations should read:

$$\dot{M}_{O_2\text{routine}}=2.12+0.09e^{0.18t} \text{ (ambient; broken line) and } \dot{M}_{O_2\text{routine}}=1.39+0.54e^{0.08t} \text{ (adjusted; solid line).}$$

On page 3246, in the legend to Fig. 3, the equations should read as follows:

$$\text{For GC sockeye salmon: } \dot{M}_{O_2\text{max}}=15.26/\{1+[(t-17.13)/8.95]^2\}.$$

$$\text{For WVR sockeye salmon: } \dot{M}_{O_2\text{max}}=-108.18+119.2/\{1+[(t-14.88)/25.52]^2\}.$$

$$\text{For CHE coho salmon: } \dot{M}_{O_2\text{max}}=9.72/\{1+[(t-8.42)/7.31]^2\}.$$

$$\text{For GC sockeye salmon: scope for activity}=11.22/\{1+[(t-16.63)/8.11]^2\}.$$

$$\text{For WVR sockeye salmon: scope for activity}=7.29/\{1+[(t-7.89)/6.03]^2\}.$$

$$\text{For CHE coho salmon: scope for activity}=8.41/\{1+[(t-14.48)/5.10]^2\}.$$

On page 3247, in the legend to Fig. 4, the equations should read as follows:

$$\text{For GC sockeye salmon: } U_{\text{crit}}=2.17/\{1+[(t-16.15)/9.59]^2\}.$$

$$\text{For WVR sockeye salmon: } U_{\text{crit}}=1.60/\{1+[(t-15.18)/8.52]^2\}.$$

The authors apologise for any inconvenience these errors may have caused.

# The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks

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## Summary

Our knowledge of the swimming capabilities and metabolic rates of adult salmon, and particularly the influence of temperature on them, is extremely limited, and yet this information is critical to understanding the remarkable upstream migrations that these fish can make. To remedy this situation, we examined the effects of temperature on swimming performance and metabolic rates of 107 adult fish taken from three stocks of sockeye salmon *Oncorhynchus nerka* and one stock of coho salmon *O. kisutch* at various field and laboratory locations, using large, portable, swim tunnels. The salmon stocks were selected because of differences in their ambient water temperature (ranging from 5°C to 20°C) and the total distance of their in-river migrations (ranging from ~100 km for coastal stocks to ~1100 km for interior stocks). As anticipated, differences in routine metabolic rate observed among salmon stocks were largely explained by an exponential dependence on ambient water temperature. However, the relationship between water temperature and maximum oxygen consumption

( $\dot{M}_{O_2max}$ ), i.e. the  $\dot{M}_{O_2}$  measured at the critical swimming speed ( $U_{crit}$ ), revealed temperature optima for  $\dot{M}_{O_2max}$  that were stock-specific. These temperature optima were very similar to the average ambient water temperatures for the natal stream of a given stock. Furthermore, at a comparable water temperature, the salmon stocks that experienced a long and energetically costly in-river migration were characterized by a higher  $\dot{M}_{O_2max}$ , a higher scope for activity, a higher  $U_{crit}$  and, in some cases, a higher cost of transport, relative to the coastal salmon stocks that experience a short in-river migration. We conclude that high-caliber respirometry can be performed in a field setting and that stock-specific differences in swimming performance of adult salmon may be important for understanding upstream migration energetics and abilities.

Key words: salmon, *Oncorhynchus nerka*, *Oncorhynchus kisutch*, respirometry, energetics, temperature, oxygen consumption, critical swimming speed, fish stock, spawning run.

## Introduction

Temperature has been coined the ‘ecological master factor’ for fish (Brett, 1971), and important physiological functions such as growth, swimming performance and active metabolic rate can have species-specific temperature optima that are near a species-preferred or acclimated temperature (Fry, 1947; Brett, 1971; Dickson and Kramer, 1971; Beamish, 1978; Houston, 1982; Bernatchez and Dodson, 1985; Johnston and Temple, 2002). Thus, when fish are exposed to temperature changes, they can obtain optimal performance by altering either their behaviour (preference/avoidance) or their physiology (adaptation and acclimation), when the temperature change is sufficiently long. Certain short-term variations in temperature may be unavoidable, however, and this is particularly the case for adult migratory salmon that are returning to their natal streams to spawn. For example, water temperatures in one of the world’s greatest salmon-bearing rivers, the Fraser River, BC, Canada, may vary annually on a

given date by as much as 6°C. Furthermore, the river temperatures encountered by the Early Stuart stock of Fraser River sockeye salmon *Oncorhynchus nerka* during its 25-day migration can vary by as much as 10.5°C (Idler and Clemens, 1959) and reach up to 22°C (Rand and Hinch, 1998).

Given the adult salmon’s short migration window and its exposure to a wide variation in temperature, it is possible that acclimation mechanisms that would normally compensate for temperature change may be incomplete. Conversely, Guderley and Blier (1988) suggest that swimming performance and most of its components demonstrate thermal compensation on an evolutionary time scale (i.e. adaptation) such that optimal performance and lowest thermal sensitivity are typically within the temperature range most frequently encountered by the organism. In the case of adult salmon stock, the prediction is that they would retain sufficient physiological flexibility to accommodate the range of temperatures most frequently

encountered during their river migration; otherwise intolerance of non-optimal temperatures in reaching spawning grounds (Macdonald et al., 2000) could hamper spawning success.

While considerable information on the temperature effects on swimming (e.g. critical swimming speed,  $U_{crit}$ ) and oxygen consumption ( $M_{O_2}$ ) exists for juvenile Pacific salmon (*Oncorhynchus* spp.) (e.g. Brett et al., 1958; Brett, 1971; Griffiths and Alderdice, 1972; Beamish, 1978), only four studies have measured  $M_{O_2}$  in adult, wild Pacific salmon (Brett and Glass, 1973; Jain et al., 1998; Farrell et al., 1998, 2003). One of these studies (Brett and Glass, 1973) established a temperature optimum of 15°C for both  $U_{crit}$  and maximum  $M_{O_2}$  ( $M_{O_2max}$ ). All the same, important intraspecific (between stocks) as well as interspecific differences in swimming energetics with respect to temperature are anticipated. Different salmon stocks migrate to different spawning streams in the Fraser River watershed, resulting in dissimilar up-river migration costs due to different water temperatures, coupled to variation in migration timing as well as unequal migration distances in the presence of differing hydraulic impediments. Indeed, juvenile salmonids reared or

held under laboratory conditions can show intraspecific differences among populations and strains (Tsuyuki and Willisroft, 1977; Thomas and Donahoo, 1977; Taylor and McPhail, 1985). Our focus was on whether performance differences exist among adult, wild salmon stocks.

Berst and Simon (1981) suggested that field-based rather than laboratory-based studies are more likely to reveal any differences among species or stocks, because animal transportation is minimized and natal river water can be used. While  $U_{crit}$  has been previously measured in adult salmonids under field conditions (e.g. Jones et al., 1974; Brett, 1982; Williams et al., 1986; Farrell et al., 2003), only two field studies have previously reported active  $M_{O_2}$  for adult salmon (Farrell et al., 2003; C. G. Lee, A. P. Farrell and R. H. Devlin, manuscript submitted for publication). Because no field study has comprehensively examined the effects of temperature on swimming energetics in adult salmon, the present study considered: (1) how the temperature affects swimming energetics of adult salmon from the Fraser River watershed, and (2) whether intraspecific differences in swimming energetics exist with respect to temperature. Assuming that natural selection acts strongly on the physiology associated with up-river migration, we predicted that swimming ability (as measured by  $U_{crit}$  and  $M_{O_2max}$ ) should increase with

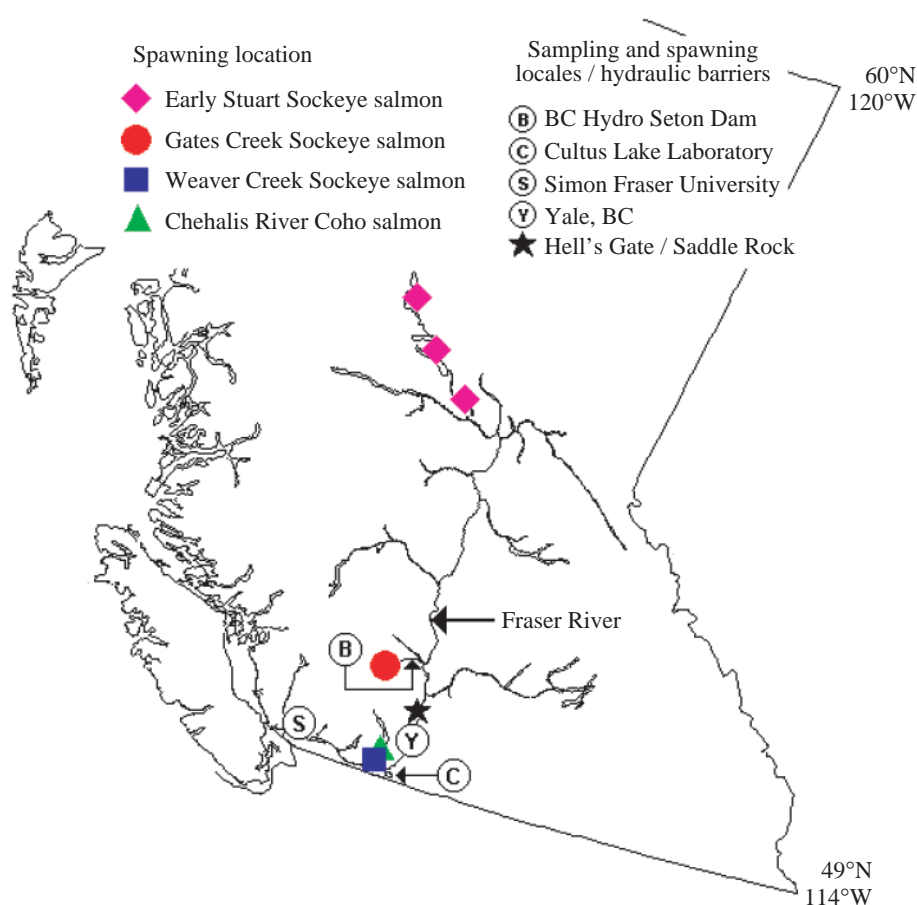


Fig. 1. Map of British Columbia, Canada illustrating the locations of fish sampling, fish spawning and in-river hydraulic challenges to upstream migration.

migration distance and difficulty among stocks of sockeye salmon that were studied, one of which was a coastal (short-distance migrating) stock while the other stocks (long-distance migrating) were from the interior of the province of British Columbia (BC).

## Materials and methods

### Study design

Experiments were conducted in 2000 and 2001 on sockeye salmon *Oncorhynchus nerka* Walbaum and coho salmon *O. kisutch* Walbaum intercepted during their up-river migration in the Fraser River watershed (Fig. 1), which provides considerable variability in the timing, temperature, distance and difficulty of migration among salmon stocks and species as a study system because of its large size, numerous tributaries and hydrological challenges (Gilhousen, 1990; G. T. Crossin, S. G. Hinch, A. P. Farrell, D. A. Higgs, A. G. Lotto, J. D. Oakes, and M. C. Healey, unpublished observations). Experiments were performed at both field (i.e. near the sites of fish capture and using natal stream water) and laboratory (i.e. captured fish returned to Cultus Lake laboratory, Fisheries and Oceans Canada, Chilliwack, BC, Canada, or the home laboratory at Simon Fraser University) locations using mobile

Brett-type respirometer swim tunnels (Farrell et al., 2003). Comparisons were made among three sockeye salmon stocks, hereafter identified by name and relative river migration distance from the mouth of the Fraser River to the spawning stream [Early Stuart (ES), 1100 km; Gates Creek (GC), 400 km; Weaver Creek (WVR), 100 km], and one coho salmon (*O. kisutch*) stock [Chehalis River (CHE), 110 km] (see Table 1). In addition, the ambient water temperatures encountered by these stocks in their natal rivers showed some degree of overlap (Table 1). The sockeye stocks that migrate to the interior of the province (GC and ES) also negotiate particularly demanding hydrological challenges (e.g. Hell's Gate and Saddle Rock) during their upstream migration (Fig. 1) (Hinch and Rand, 1998; Hinch and Bratty 2000). Compared with most sockeye salmon stocks, which migrate during the warmer summer and fall months, Fraser River coho salmon encounter cooler temperatures during their fall and winter migration (Groot and Margolis, 1991). Therefore, while coastal stocks of CHE coho salmon and WVR sockeye salmon experience a comparable migration distance and difficulty, they encounter different river temperatures because of differences in run timing.

Field tests were always performed at ambient natal river water temperature and fish were transferred directly to the swim tunnel from the nearby stream or creek. Laboratory tests at both Simon Fraser University (with dechlorinated municipal water) and the Cultus Lake laboratory (with lake water) were performed either at the ambient temperature of the natal stream or at an adjusted temperature (Table 1). Laboratory-tested fish were transported in a 330 litre insulated tank containing oxygenated water, dilute Marinil anaesthetic (0.02 mg l<sup>-1</sup> metomidate hydrochloride, Syndel International Inc., Vancouver, BC, Canada) to calm the fish, and block ice to chill the water. Fish were held in 1000 litre aquaria, one of which was maintained at the ambient temperature of the fish's natal stream. The water temperature was adjusted (*via* mixing warm surface and cold deep Cultus Lake water) in the other aquaria at a rate of approximately 1°C per day over 5 days to extend the temperature range slightly beyond the ambient temperatures, after which two fish were tested daily in one of two swim tunnels receiving water at the fish's adjusted temperature. A longer temperature acclimation period was not used because some of these mature fish were within weeks of spawning. For all tests, fish were given a practice swim after 1 h and then allowed to recover in the swim tunnel overnight. Water delivery was at a rate of 30 l min<sup>-1</sup> *via* a submersible sump pump to ensure that dissolved oxygen was normally >90% of air saturation.

*Gates Creek sockeye salmon: Seton Hydro dam and Cultus Lake laboratory*

Experiments were conducted on ten male and ten female adult GC sockeye salmon at the BC Hydro Seton Dam near Lillooet, BC (Fig. 1) in mid-August 2000. Fish were dip-netted on-site at the top of a fish ladder and immediately placed into a swim-tunnel. Fish, which were ripe and within 1–2 weeks of

Table 1. Details of experimental groupings of adult salmon, including date of experiments, species, stock, migration distance, sample size, physical parameters and experimental temperature

Date	Species	Stock	Migration distance (km)	N	Mass (kg)	Fork length (cm)	Area (cm <sup>2</sup> )	Temperature (°C)		
								Ambient mean	Ambient range	Adjusted range
Aug-00	Sockeye	GC – field	400	20	2.69±0.10	64.2±0.7	58.0±1.6	18.0±0.2	13.6–19.8	10.9–22.7
Aug-01	Sockeye	GC – adjusted (lab)	400	17	2.67±0.15	63.7±1.0	52.2±2.6		14.8–16.9	
Jun-00	Sockeye	ES – lab	1100	6	2.02±0.14	57.9±1.6	46.0±1.6	13.0±0.2	12.1–14.4	
Sep-00	Sockeye	WVR – lab	100	12	2.90±0.26	62.4±1.6	59.9±3.7	15.9±0.2	14.8–17.1	
Oct-00	Sockeye	WVR – field	100	12	3.00±0.11	64.0±0.9	61.5±1.3	12.2±0.2	10.6–13.7	
Oct-01	Sockeye	WVR – adjusted (lab)	100	8	2.56±0.14	61.4±1.0	54.0±2.5	8.2±0.4	13.0–14.0	13.0–19.5
Nov-00	Coho	CHE – field	110	13	2.26±0.19	57.7±1.4	49.0±2.9	7.6±0.1	4.6–10.9	
Jan-01	Coho	CHE – field	110	12	2.34±0.14	61.1±0.9	50.9±2.7		5.9–8.5	
Nov-01	Coho	CHE – adjusted (lab)	110	7	2.60±0.29	60.7±2.4	59.5±3.4		9.1–9.5	9.1–12.5

GC, Gates Creek stock; ES, Early Stuart stock; WVR, Weaver Creek stock; CHE, Chehalis River stock.

Migration distance refers to the approximate in-river distance a salmon stock would migrate to reach its natal spawning ground.

Mass, fork length and cross-sectional area of fish are presented as means ± S.E.M.

Most fish were tested at their ambient water temperature and this information is presented as both a mean value ± S.E.M. and a range. Fish were also tested at an adjusted temperature and these temperatures are presented as a range because they were both higher and lower than the ambient temperature.

spawning, were not killed after the experiments to comply with the sampling permit and so gonad mass was not measured. In early August 2001, six male and eleven female GC sockeye salmon were again collected at the Seton Dam site, but were transported (1.5 h) to the Cultus Lake laboratory. Three fish were tested at the ambient temperature of the Seton River at that time ( $15.0 \pm 1.0^\circ\text{C}$ ), while six fish were tested at a colder and eight fish at a warmer temperature.

*Weaver Creek sockeye salmon: Chehalis River, and SFU and Cultus Lake laboratories*

Experiments were performed in October 2000 on six male and six female WVR sockeye salmon at the Chehalis River Fish Hatchery, which is situated <5 km from Weaver Creek, their natal stream. Fish were dip-netted at the spawning creek, transported to the hatchery and immediately placed in the swim tunnel for overnight recovery. Experiments were also conducted at Simon Fraser University (SFU) on five male and seven female WVR sockeye salmon, captured by beach seine from the Harrison River, BC, Canada (Fig. 1) in September 2000. Transportation to SFU took 1 h, where fish were held at  $13.0 \pm 0.2^\circ\text{C}$  for a minimum of 3 days before testing commenced. An additional five male and three female WVR sockeye salmon were collected from Weaver Creek *via* dip-net and transported (0.5 h) to the Cultus Lake laboratory in October 2001. Two fish were tested at the ambient water temperature at Weaver Creek ( $12^\circ\text{C}$ ), while five fish were tested at a warmer temperature.

*Early Stuart sockeye salmon: SFU laboratory*

A small number of ES sockeye salmon were dip-netted from the Fraser River near Yale, BC, Canada (Fig. 1) in early July 2000, and transported (1.5 h) to SFU, where they were held for a minimum of 3 days before testing commenced. These fish were 4–5 weeks from spawning and were beginning to exhibit secondary sexual characteristics.

*Chehalis coho salmon: Chehalis River and Cultus Lake laboratory*

Experiments were conducted in November 2000 on seven male and six female CHE coho salmon that were captured with a knotless cotton dip-net from the stream entering at the Chehalis River Fish Hatchery. Fish were immediately placed into a swim tunnel for overnight recovery. Additional experiments were conducted at the Chehalis River Fish Hatchery on six male and six female CHE coho salmon in January 2001. Experiments were also conducted in November 2001 on four male and three female CHE coho salmon after transportation (0.5 h) to Cultus Lake laboratory. Two fish were at the ambient temperature of the Chehalis River ( $9^\circ\text{C}$ ), while five fish were tested at a warmer temperature.

*Swim tunnel*

The 272 litre and 471 litre swim tunnels (after Gehrke et al., 1990), described in Farrell et al. (2003; [www.sfu.ca/biology/faculty/farrell/swimtunnel/swimtunnel](http://www.sfu.ca/biology/faculty/farrell/swimtunnel/swimtunnel)).

html) were mounted on trailers to facilitate transportation to the field locations. The 124.3 cm long transparent swim chamber had an internal diameter of 20.3 cm for the small tunnel and 25.4 cm for the large swim tunnel. A 'shocking' grid (2–10 V; 0.4–2.0 W), made of graphite rods and mounted at the rear of the swim chamber, was utilized briefly at higher water velocities to promote swimming in some fish. Water flow in the swim tunnels was driven by a 29 cm diameter fiberglass centrifugal impeller pump and a 7.5 hp three-phase motor, controlled by a Siemens Midimaster Vector frequency drive (PLAD, Coquitlam, BC, Canada). Water velocity was calibrated against the motor frequency (Farrell et al., 2003). Throughout the course of an experiment, water temperature in the swim tunnel did not fluctuate by more than  $0.5^\circ\text{C}$ .

*Swim test protocol*

The practice swim involved water velocity increments of 0.15 body lengths ( $BL$ )  $s^{-1}$  every 2 min until failure and was used to familiarize naïve fish to the swim tunnel and also provide an estimate of the  $U_{crit}$  (Jain et al., 1997). The following day, each salmon was tested with a ramp- $U_{crit}$  protocol (Jain et al., 1997), in which the water velocity was ramped up in 5 min increments of  $0.15 BL s^{-1}$  up to approximately 50% of the fish's maximum speed attained in the practice swim. Water velocity increments of  $0.15 BL s^{-1}$  then followed every 20 min until the fish ceased swimming. Testing was terminated when the fish failed to move off the rear grid for 20 s. Water velocity was then reduced to  $0.30$ – $0.45 BL s^{-1}$  for a 45 min recovery period, after which the a second ramp- $U_{crit}$  protocol was performed. Approximately half the fish swam intermittently as they recovered, while the remainder rested on the bottom of the swim chamber for the entire recovery period.  $U_{crit}$  values were calculated as in Brett (1965):  $U_{crit} = U_f + (t_f/t_i)U_i$ , where  $U_f$  is the water velocity of the last fully completed increment;  $t_f$  is the time spent on the last water velocity increment;  $t_i$  is the time period for each completed water velocity increment (20 min); and  $U_i$  is the water velocity increment ( $0.15 BL s^{-1}$ ).  $U_{crit}$  was corrected for the solid blocking effect as outlined by Bell and Terhune (1970). A streamline shape factor was used in the correction equation  $U_F = U_T(1 + \epsilon_s)$ , where  $U_F$  is the corrected flow speed,  $U_T$  is the speed in the tunnel without a fish in the swim chamber and  $\epsilon_s$  is the fractional error due to solid blocking.  $\epsilon_s$  is defined for each fish by  $\epsilon_s = \tau \lambda (A_o/A_T)^{1.5}$ , where  $\tau$  is a dimensionless factor depending on swim chamber cross section (equivalent to 0.8 in this study),  $\lambda$  is the shape factor for the fish ( $\lambda = 0.5$  body length/body thickness),  $A_o$  is the cross sectional area of the fish, and  $A_T$  is the cross sectional area for the swimming chamber. The  $U_{crit}$  correction averaged  $16.2 \pm 0.1\%$ . The second  $U_{crit}$  test examined the ability of fish to recover and re-perform. A recovery ratio (RR) expressed the ratio of the two swimming performance tests:  $RR = U_{crit2}/U_{crit1}$ . Thus, when  $RR = 1$ , the  $U_{crit}$  performance was identical for both swim tests.



### Oxygen consumption measurements

A Mark IV Oxyguard probe (Point Four Systems, Richmond, BC, Canada), housed outside the swim tunnel in a flow-through, cylindrical housing (600 ml), was used to measure oxygen concentration to  $0.01 \text{ mg O}_2 \text{ l}^{-1}$  in water delivered from the swim tunnel at a rate of  $30 \text{ ml s}^{-1}$  using a peristaltic pump (Masterflex, Cole Palmer, Vernon Hills, IL, USA). The oxygen probe was air-calibrated daily and had automatic temperature compensation. Early experiments used a stopwatch to time the decrease in oxygen concentration, but subsequently signals were acquired by an in-house computer program (Labview 6.0, National Instruments, Austin, Texas, USA) at a sampling frequency of 0.2 Hz. Measurements of oxygen consumption lasted 5–20 min, depending on the fish's size and swimming speed, which was long enough to record a change of  $0.3\text{--}1.0 \text{ mg O}_2 \text{ l}^{-1}$ , but without decreasing the dissolved oxygen concentration below 75% saturation during any  $\dot{M}_{\text{O}_2}$  measurement. The swim tunnel was thoroughly flushed and bleached between experiments. Biweekly assessments of background oxygen consumption without a fish in the tunnel revealed no changes in the water oxygen concentration during a 20 min recording period. The rate of oxygen consumption ( $\text{mg O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ) was calculated as:

$$\dot{M}_{\text{O}_2} = \Delta[\text{O}_2]v/mt,$$

where oxygen concentration  $[\text{O}_2]$  is measured in  $\text{mg O}_2 \text{ l}^{-1}$ ,  $v$  is swim tunnel water volume (the total volume of the swim tunnel less the fish's volume, assuming  $1 \text{ kg}=1 \text{ l}$ ), and time  $t$  is in min.

### Terminology and data analysis

The oxygen consumption measured immediately prior to the initial  $U_{\text{crit}}$  swim test was assigned as routine  $\dot{M}_{\text{O}_2}$  ( $\dot{M}_{\text{O}_2\text{routine}}$ ). We did not attempt to estimate standard metabolic rate either by eliminating data for fish that were active, as others have done (see Brett and Groves, 1979), or by extrapolating to zero velocity, because of concerns regarding this method of extrapolation (see Thorarensen et al., 1993; Farrell et al., 2003). Oxygen consumption rates during swimming were measured for every other water velocity increment during both swim tests. The  $\dot{M}_{\text{O}_2}$  measured at  $U_{\text{crit}}$  was designated maximum  $\dot{M}_{\text{O}_2}$  ( $\dot{M}_{\text{O}_2\text{max}}$ ). We distinguish  $\dot{M}_{\text{O}_2\text{max}}$  from active metabolic rate, which is defined as the  $\dot{M}_{\text{O}_2}$  during maximum sustained activity (i.e. steady state swimming for >200 min; Brett and Groves, 1979). The designation of  $\dot{M}_{\text{O}_2\text{max}}$  during swimming at  $U_{\text{crit}}$  in salmonids was rationalized because both cardiac output and venous oxygen partial pressure can plateau before  $U_{\text{crit}}$  is reached, and arterial oxygen partial pressure can decrease (Thorarensen et al., 1993; Gallaughier et al., 1995; Farrell and Clutterham, 2003). In addition, some fish can show a plateau in  $\dot{M}_{\text{O}_2}$  measurements before  $U_{\text{crit}}$  is reached (see data for GC sockeye). We did not calculate metabolic scope (defined as active metabolic rate – standard metabolic rate; Brett and Groves, 1979). Instead, we calculated scope for activity (from  $\dot{M}_{\text{O}_2\text{max}} - \dot{M}_{\text{O}_2\text{routine}}$ ). Cost of transport, COT, was calculated from  $\dot{M}_{\text{O}_2}/U$  for each swimming speed,  $U$ , and net

cost of transport,  $\text{COT}_{\text{net}}$ , was calculated from  $(\dot{M}_{\text{O}_2} - \dot{M}_{\text{O}_2\text{routine}})/U$ . The minimum costs of transport were interpolated from the curves fitted to these data.  $\dot{M}_{\text{O}_2}$  measured immediately prior to the second  $U_{\text{crit}}$  test was termed  $\dot{M}_{\text{O}_2\text{recovery}}$ , and was compared with  $\dot{M}_{\text{O}_2\text{routine}}$  to determine the degree of recovery from the first swim test.

### Statistical analysis

Values are means  $\pm$  S.E.M. and  $P < 0.05$  was used as the level of statistical significance. Intraspecific statistical comparisons between the first and second swim trial and between the laboratory-based and field-based measurements were performed with paired and unpaired students  $t$ -tests, respectively. Statistical comparisons among all fish stocks were accomplished using a parametric analysis of variance (ANOVA). In cases where the ANOVA reported significant differences, a pairwise *post-hoc* Tukey test was used to determine specifically which groups were different. For the relationship between swimming speed  $U$  and  $\dot{M}_{\text{O}_2}$ , regression analysis used exponential equations, based on previous findings (e.g. Webb, 1971), although preliminary analysis indicated that power functions (e.g. a 4-parameter Lorentzian regression) also produced similar  $r^2$  values (to within 10%). For the relationships with water temperature, exponential regressions were used for  $\dot{M}_{\text{O}_2\text{routine}}$  and bell-shaped regression for  $\dot{M}_{\text{O}_2\text{max}}$  and  $U_{\text{crit}}$ , based on previous findings (Brett and Groves, 1979).

## Results

### Swimming performance

$U_{\text{crit}}$  values for adult salmon tested at ambient water temperature are presented in Table 2. Overall, fish swam just as well on the second test because no significant differences were observed between  $U_{\text{crit}1}$  and  $U_{\text{crit}2}$  (first and second swim tests, respectively) for any of the salmon stocks. In fact, the first and second  $U_{\text{crit}}$  values rarely differed by more than 5% and, as a result, the recovery ratios (RR) for all groups of salmon were not significantly different from unity (Table 3). Similarly, the  $\dot{M}_{\text{O}_2\text{max}}$  and scope for activity for the two swims did not differ (Table 2). Interestingly, swimming performance was repeatable without  $\dot{M}_{\text{O}_2}$  being restored to within 5% of  $\dot{M}_{\text{O}_2\text{routine}}$  in 77 out of the 107 tests (35 out of 37 tests for GC sockeye salmon, 6 out of 6 tests for ES sockeye salmon, 21 out of 32 tests for WVR sockeye salmon, and 14 out of 32 tests for CHE coho salmon). Because fish performed equally well on their first and second swim tests, averaged  $U_{\text{crit}}$  and  $\dot{M}_{\text{O}_2\text{max}}$  values for the two tests were used to analyze the effects of temperature.

ES sockeye salmon had a significantly higher  $U_{\text{crit}}$  ( $P < 0.05$ ) than either GC or WVR sockeye salmon stocks but at a comparable ambient water temperature (Table 3). Conversely, CHE coho salmon swam as well as WVR sockeye ( $P > 0.05$ ), but at a lower ambient temperature (Table 3). Therefore, stock-specific differences existed independent of temperature differences.

Table 2. Measurements of routine oxygen consumption ( $\dot{M}_{O_2}$ ), oxygen consumption taken at critical swimming speed ( $\dot{M}_{O_{2max}}$ ), recovery  $\dot{M}_{O_2}$  and metabolic scope for three adult sockeye salmon stocks and one adult coho salmon stock at their ambient temperatures

Group (date)	$\dot{M}_{O_2}$ values (mg O <sub>2</sub> kg <sup>-1</sup> min <sup>-1</sup> )				Metabolic scope (mg O <sub>2</sub> kg <sup>-1</sup> min <sup>-1</sup> )	
	Routine	45-min recovery	Max 1	Max 2	1	2
GC (Aug-00)	4.35±0.09 <sup>a</sup>	8.83±0.28 <sup>a</sup>	15.07±0.16 <sup>a</sup> (15.10±0.12)	15.14±0.20 <sup>a</sup>	10.72±0.14 <sup>a</sup> (10.76±0.13)	10.81±0.19 <sup>a</sup>
ES (Jun-00)	3.35±0.15 <sup>b</sup>	–	13.53±0.51 <sup>b</sup> (13.64±0.30)	13.75±0.36 <sup>b</sup>	10.18±0.61 <sup>a</sup> (10.29±0.40)	10.40±0.47 <sup>a</sup>
WVR (Sep-00)	2.94±0.14 <sup>b</sup>	4.26±0.31 <sup>b</sup>	11.81±0.49 <sup>c</sup> (11.89±0.41)	11.98±0.61 <sup>c</sup>	8.87±0.40 <sup>b</sup> (8.94±0.36)	9.02±0.53 <sup>b</sup>
WVR (Oct-00)	2.80±0.10 <sup>b</sup>	3.87±0.39 <sup>b</sup>	9.91±0.43 <sup>d</sup> (9.82±0.33)	9.73±0.52 <sup>d</sup>	7.11±0.43 <sup>c</sup> (7.22±0.38)	6.93±0.48 <sup>c</sup>
CHE (Nov-00)	2.70±0.19 <sup>c</sup>	3.10±0.31 <sup>c</sup>	8.60±0.45 <sup>e</sup> (8.77±0.31)	8.94±0.44 <sup>e</sup>	5.90±0.40 <sup>d</sup> (6.07±0.28)	6.24±0.39 <sup>c</sup>
CHE (Jan-01)	2.23±0.09 <sup>c</sup>	2.44±0.14 <sup>c</sup>	9.85±0.13 <sup>d</sup> (9.80±0.12)	9.75±0.21 <sup>d</sup>	7.62±0.17 <sup>c</sup> (7.57±0.13)	7.52±0.20 <sup>c</sup>

GC, Gates Creek stock; ES, Early Stuart stock; WVR, Weaver Creek stock; CHE, Chehalis River stock.

For details of each group, see Table 1.

Subscripts 1 and 2 refer to the first and second swim tests and values in parentheses represent the averaged value for the first and second swim tests, since there was no significant difference between them.

$\dot{M}_{O_{2max}}$  was taken concurrently with the  $U_{crit}$  shown in Table 3.

Significant differences ( $P < 0.05$ ) between groups within a column are denoted by superscript letters following each value.

Table 3. Measurements of swimming performance ( $U_{crit}$ ) and the recovery ratio (RR) in three adult sockeye salmon stocks and one adult coho salmon stock at their ambient temperature

Group	$U_{crit}$ (BL s <sup>-1</sup> )		$U_{crit}$ (cm s <sup>-1</sup> )		RR
	$U_{crit1}$	$U_{crit2}$	$U_{crit1}$	$U_{crit2}$	
GC (Aug-00)	2.08±0.05 <sup>b</sup> (2.08±0.05)	2.08±0.05 <sup>b</sup>	133.0±2.4 <sup>b</sup> (132.9±1.7)	132.8±2.5 <sup>b</sup>	1.00±0.01
ES (Jun-00)	2.36±0.04 <sup>a</sup> (2.36±0.06)	2.36±0.07 <sup>a</sup>	136.6±3.9 <sup>a</sup> (136.8±3.4)	137.0±5.9 <sup>a</sup>	1.00±0.03
WVR (Sep-00)	1.73±0.07 <sup>c</sup> (1.74±0.05)	1.76±0.07 <sup>c</sup>	108.6±3.9 <sup>c</sup> (110.4±2.7)	112.8±4.2 <sup>c</sup>	1.02±0.05
WVR (Oct-00)	1.41±0.07 <sup>d</sup> (1.41±0.03)	1.41±0.05 <sup>d</sup>	89.9±2.5 <sup>d</sup> (89.8±1.7)	89.7±2.5 <sup>d</sup>	1.00±0.01
CHE (Nov-00)	1.68±0.05 <sup>c</sup> (1.68±0.05)	1.68±0.05 <sup>c</sup>	96.6±2.8 <sup>c</sup> (96.5±1.9)	96.4±2.7 <sup>c</sup>	1.00±0.01
CHE (Jan-01)	1.64±0.03 <sup>c</sup> (1.61±0.02)	1.54±0.04 <sup>c</sup>	100.1±2.1 <sup>c</sup> (98.2±1.8)	94.5±3.3 <sup>c</sup>	0.94±0.02

GC, Gates Creek stock; ES, Early Stuart stock; WVR, Weaver Creek stock; CHE, Chehalis River stock.

For details of each group, see Table 1.

Recovery ratio RR =  $U_{crit2}/U_{crit1}$ .

The subscripts 1 and 2 refer to the first and second swim tests and values in parentheses represent the averaged value for the first and second swim tests, since there was no significant difference between them.

Significant differences ( $P < 0.05$ ) between groups within a column are denoted by superscript letters following each value.

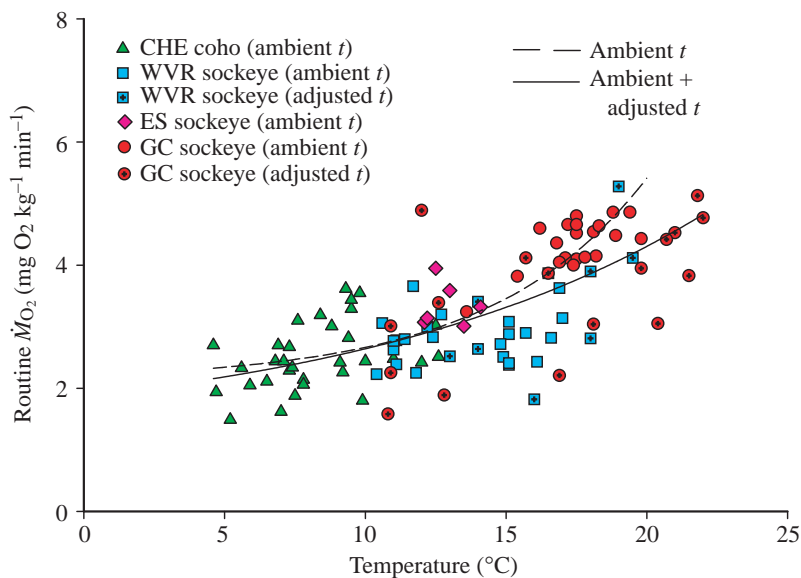
## Field versus laboratory testing

The swimming performance of some stocks did not vary between field and laboratory tests (Tables 1–3). In addition, preliminary laboratory experiments conducted with CHE coho salmon ( $N=4$ ) showed that routine  $\dot{M}_{O_2}$ ,  $U_{crit}$  and  $\dot{M}_{O_2max}$  ( $2.59 \pm 0.14$  mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>;  $1.72 \pm 0.12$  BL s<sup>-1</sup>;  $9.19 \pm 0.61$  mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>, respectively) were not statistically different compared with field tests (Tables 1–3). Similarly, preliminary laboratory experiments with GC sockeye salmon ( $N=4$ ) showed that  $U_{crit}$  and  $\dot{M}_{O_2max}$  ( $2.15 \pm 0.11$  BL s<sup>-1</sup>;  $14.71 \pm 0.69$  mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>) were not statistically different compared with field tests (Tables 2, 3), although  $\dot{M}_{O_2routine}$  ( $3.31 \pm 0.43$  mg O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>) was significantly ( $P < 0.05$ ) lower than field tests (Table 2).

The two sets of field measurements for CHE coho salmon were pooled for subsequent analyses because there were no significant differences (Tables 1–3). In contrast, WVR sockeye salmon tested at the SFU laboratory had a significantly higher  $U_{crit}$  (23%),  $\dot{M}_{O_2max}$  (19%) and scope for activity (25%) compared with the same stock tested in the field when the fish were in a slightly more mature state and also at a temperature 4°C colder (Tables 1–3). Consequently, the two data sets for WVR sockeye salmon were treated separately for subsequent analyses.

The effect of temperature on  $\dot{M}_{O_2routine}$ 

$\dot{M}_{O_2routine}$  measured at ambient temperature could vary significantly, but not always among stocks, between years and between species (Table 2). To investigate the influence of ambient water temperature on  $\dot{M}_{O_2routine}$ , all stocks were pooled and a statistically significant ( $P < 0.05$ ) exponential relationship existed between  $\dot{M}_{O_2routine}$  and ambient water temperature that accounted for 65% of the variation in the individual data (Fig. 2). Addition of temperature-adjusted fish to this pooled data set slightly weakened the relationship ( $r^2 = 0.52$ ;  $P < 0.05$ ) (Fig. 2).

The effect of temperature on  $\dot{M}_{O_2max}$ , scope for activity and  $U_{crit}$ 

Regression analysis was performed for three salmon stocks (GC, WVR and CHE), revealing significant ( $P < 0.05$ ) bell-shaped relationships between  $\dot{M}_{O_2max}$  and temperature (Fig. 3A) when data from temperature-adjusted fish were included. Temperature optima for  $\dot{M}_{O_2max}$  were interpolated from the regression equations (GC=17.5°C; WVR=15.0°C; CHE=8.5°C) and were found to correspond closely to the ambient water temperature for each stock (Table 1; Fig. 3A). Furthermore, when individual  $\dot{M}_{O_2max}$  values were compared among sockeye stocks and at common ambient temperatures, there were clear differences between stocks (Fig. 3A). These results suggest that important stock-specific differences existed for  $\dot{M}_{O_2max}$  and its thermal sensitivity. Similarly, significant ( $P < 0.05$ ) bell-shaped regressions were found between scope for activity and temperature for each salmon stock (Fig. 3B). The temperature optimum for scope for activity was either similar to that for  $\dot{M}_{O_2max}$  (CHE stock), or 1°C lower (WVR and GC stocks) (Fig. 3B), reflecting the important contribution of temperature on  $\dot{M}_{O_2routine}$ .

For GC and WVR sockeye salmon stocks, there were significant ( $P < 0.05$ ) bell-shaped regressions between  $U_{crit}$  and temperature, with  $U_{crit}$  falling off at temperatures  $> 19^\circ\text{C}$  and  $> 16^\circ\text{C}$ , respectively (Fig. 4). For CHE coho salmon, the regression between  $U_{crit}$  and temperature was not significant ( $P = 0.71$ ) (Fig. 4).

## Oxygen cost of transport

The increase in  $\dot{M}_{O_2}$  with swimming speed is illustrated for three salmon stocks from the various test locations (Fig. 5A). As expected,  $\dot{M}_{O_2}$  varied exponentially ( $r^2 = 0.99$ ) with swimming speed for WVR sockeye salmon and CHE coho salmon. However, for GC sockeye, the data were not satisfactorily fitted by an exponential relationship and a sigmoidal regression ( $r^2 = 0.99$ ) was required to account for the plateau in  $\dot{M}_{O_2}$  prior to  $U_{crit}$ . Only  $\dot{M}_{O_2routine}$  and  $\dot{M}_{O_2max}$  were measured for ES sockeye salmon and these values are included in Fig. 5A–C.

$\dot{M}_{O_2}$  differed significantly ( $P < 0.05$ ) among the salmon stocks at intermediate swimming velocities, with GC sockeye salmon having the highest  $\dot{M}_{O_2}$  values and CHE coho salmon the lowest values for

Fig. 2. Individual routine oxygen consumption ( $\dot{M}_{O_2routine}$ ) values as a function of ambient and adjusted temperature  $t$  for Gates Creek (GC) and Weaver Creek (WVR) sockeye salmon and Chehalis River (CHE) coho salmon. Individual  $\dot{M}_{O_2routine}$  increased exponentially for all stocks tested at ambient  $t$  (broken line):  $\dot{M}_{O_2routine} = 2.12 + 0.09 \times 10^{0.18t}$  ( $P < 0.05$ ;  $r^2 = 0.65$ ). Inclusion of adjusted temperature data for two stocks (solid line) changed the regression equation to:  $\dot{M}_{O_2routine} = 1.39 + 0.54 \times 10^{0.08t}$  ( $P < 0.05$ ;  $r^2 = 0.52$ ).



a given swimming velocity. The cost of transport showed typical U-shaped curves with the exception of GC sockeye salmon (Fig. 5B), because GC sockeye salmon were tested at

the highest temperature and  $\dot{M}_{O_2\text{routine}}$  increased exponentially with temperature. GC sockeye salmon were the least economical swimmers. The difference among stocks could simply reflect a higher  $\dot{M}_{O_2\text{routine}}$ . However, this was found not to be the case because the net cost of transport was also elevated for GC sockeye salmon (Fig. 5C). In contrast, because WVR sockeye salmon and CHE coho salmon had a similar net cost of transport, the small differences in the cost of transport between these two stocks were likely a result of temperature effects on  $\dot{M}_{O_2\text{routine}}$ . The minimum cost of transport occurred at around  $1 \text{ BL s}^{-1}$  for all three salmon stocks (Fig. 5B).

**Discussion**

This study is the first to extensively examine the role of temperature on swimming energetics within and among different stocks of adult Pacific salmon under field and laboratory settings. With a total of 107 adult

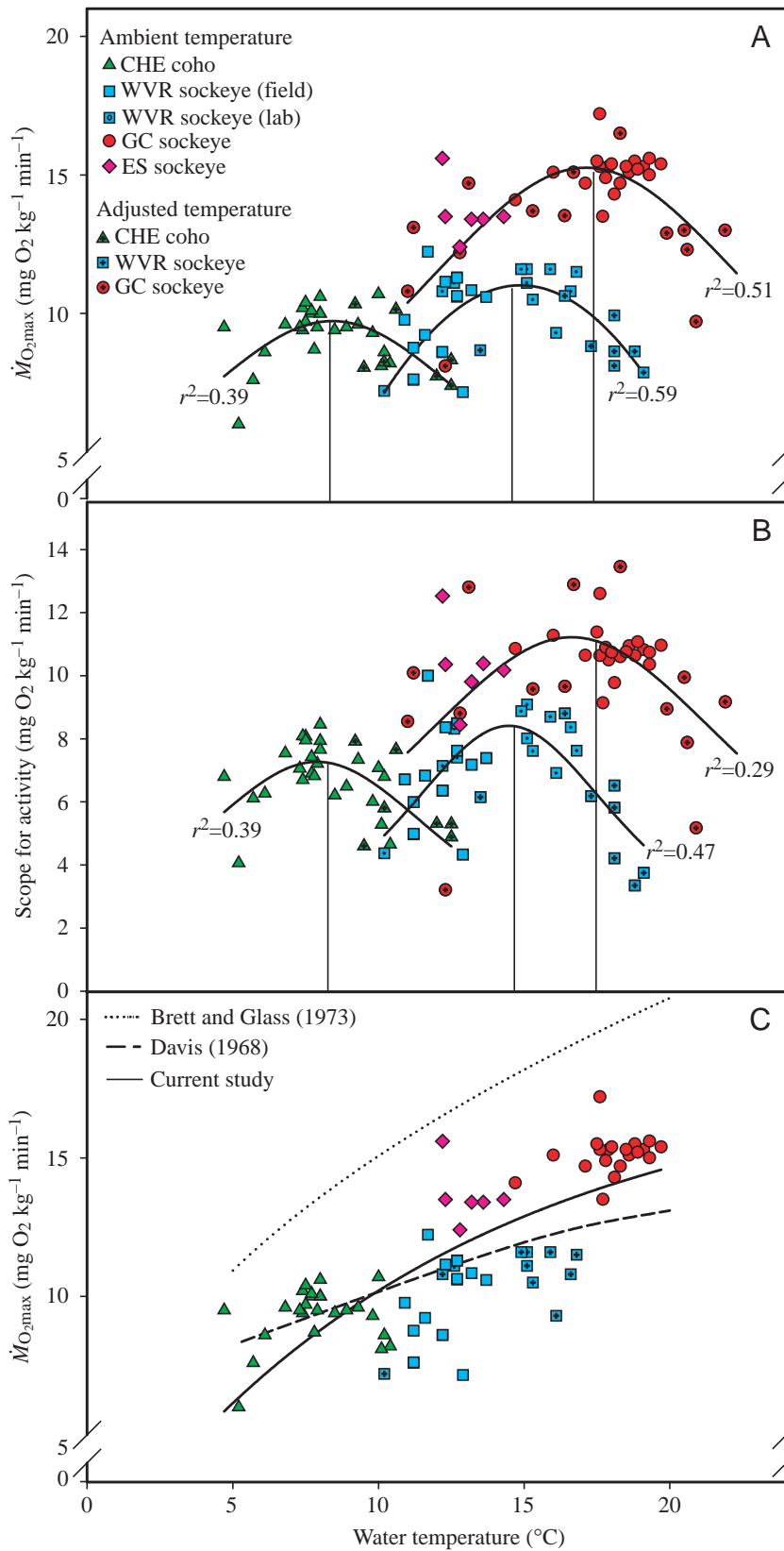


Fig. 3. (A) Stock-specific relationships between oxygen consumption at  $U_{crit}$  ( $\dot{M}_{O_2\text{max}}$ ) and water temperature  $t$  from different fish stocks (GC, Gates Creek stock; WVR, Weaver Creek stock; CHE, Chehalis River stock; ES, Early Stuart stock). Fish were tested at either ambient temperature (symbols without a cross) or an adjusted temperature (symbols with a cross). The vertical lines indicate the average ambient water temperature for each stock, which corresponded closely with the peak  $\dot{M}_{O_2\text{max}}$  for that stock. For GC sockeye salmon:  $\dot{M}_{O_2\text{max}}=15.26/1+[(t-17.13)/8.95]^2$  ( $P<0.05$ ;  $r^2=0.51$ ). For WVR sockeye salmon:  $\dot{M}_{O_2\text{max}}=-100.82+119.2/1+[(t-14.88)/25.52]^2$  ( $P<0.05$ ;  $r^2=0.59$ ). For CHE coho salmon:  $\dot{M}_{O_2\text{max}}=9.72/1+[(t-8.42)/7.31]^2$  ( $P<0.05$ ;  $r^2=0.39$ ). (B) Stock-specific relationships between scope for activity ( $\dot{M}_{O_2\text{max}}-\dot{M}_{O_2\text{routine}}$ ) and water temperature from different fish stocks. The vertical lines indicate the average ambient water temperature for each stock, which corresponded closely with the peak  $\dot{M}_{O_2\text{max}}$  for that stock. For GC sockeye salmon: scope for activity= $11.22/1+[(t-16.63)/8.11]^2$  ( $P<0.05$ ;  $r^2=0.29$ ). For WVR sockeye salmon: scope for activity= $7.29/1+[(t-7.89)/6.03]^2$  ( $P<0.05$ ;  $r^2=0.47$ ). For CHE coho salmon: scope for activity= $8.41/1+[(t-14.48)/5.10]^2$  ( $P<0.05$ ;  $r^2=0.39$ ). (C) Relationship between  $\dot{M}_{O_2\text{max}}$  and ambient water temperature among individual fish from different stocks of sockeye and coho salmon. The regression equation for the relationship (solid line,  $P<0.05$ ;  $r^2=0.63$ ) is compared with earlier studies of adult sockeye salmon (broken line, Davis 1966; dotted line, Brett and Glass, 1973).

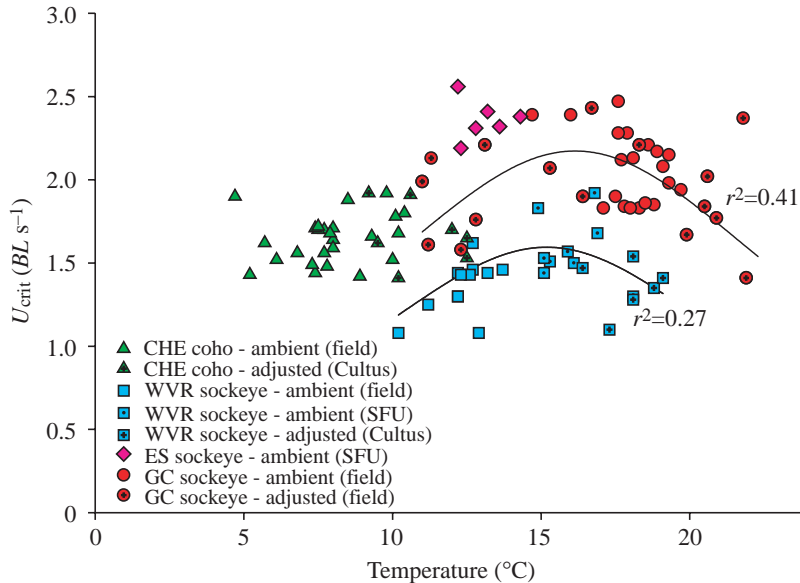


Fig. 4. Stock-specific relationships between critical swimming speed ( $U_{crit}$ ) and water temperature  $t$  among individual fish from different fish stocks. For Gates Creek (GC) sockeye salmon:  $U_{crit}=2.17/1+[(t-16.15)/9.59]^2$  ( $P<0.05$ ;  $r^2=0.41$ ). For Weaver Creek (WVR) sockeye salmon:  $U_{crit}=1.60/1+[(t-15.18)/8.52]^2$  ( $P<0.05$ ;  $r^2=0.27$ ). The relationship for Chehalis (CHE) coho salmon was not statistically significant over the temperature range examined. Results for Early Stuart (ES) sockeye salmon are included for reference.

salmon tested, it is also the most comprehensive study of adult salmon swimming performance to date.

Although the blocking effect for a few of the fish was high, the  $U_{crit}$  and  $\dot{M}_{O_2max}$  data obtained here for sockeye salmon are entirely consistent with earlier laboratory and field studies involving adult Pacific salmon (e.g. Brett and Glass, 1973; Jones et al., 1974; Williams et al., 1986). For example,  $U_{crit}$  ( $2.41 BL s^{-1}$ ,  $N=8$ ) reported for smaller ( $1.65\pm 0.07$  kg) adult sockeye salmon (Brett and Glass, 1973) lies in the upper end of our  $U_{crit}$  range, while our  $\dot{M}_{O_2max}$  data tend to be higher than theirs at corresponding temperatures (Fig. 3C).  $\dot{M}_{O_2max}$  ( $13.83 mg O_2 kg^{-1} min^{-1}$ ) and  $U_{crit}$  ( $2.33 BL s^{-1}$ ) for pink salmon (Williams et al., 1986) are comparable to the present study. The exponential relationships between  $\dot{M}_{O_2max}$  and temperature reported earlier for adult sockeye salmon either lie below (Davis, 1966) or above (Brett and Glass, 1973) a significant exponential relationship ( $r^2=0.63$ ; Fig. 3C) that could be fitted to our  $\dot{M}_{O_2max}$  data. (Note: this exponential regression tended to over-represent WVR sockeye salmon and under-represent both ES and GC sockeye salmon, i.e. there was a poor fit for any of the individual salmon stocks.) The high quality of the present data was also illustrated by the repeatability of the swim tests, because RR decreases significantly (Jain et al., 1998; Tierney, 2000) when rainbow trout *Oncorhynchus mykiss* and sockeye salmon are either sick or have been challenged by toxicants.

#### Temperature effects

The final temperature preferendum paradigm, proposed by Fry (1947), embodied three principal inferences: a species-specificity to the final temperature preferendum; a relationship between the final temperature preferendum and field distribution; and a relationship between final temperature preferendum and the temperature at which centrally important processes take place at maximum efficiency. Indeed, the concept of temperature optima for physiological processes

related to swimming is well documented (see reviews by Beamish, 1978; Houston, 1982; Guderley and Blier, 1988; Hammer, 1995; Kelsch, 1996; Johnston and Ball, 1997; Kieffer, 2000). Furthermore, there is emerging evidence that maximum cardiac performance and the oxygen supplying the cardiac tissue may be 'centrally important processes' (Farrell, 1997, 2002), though other processes are likely to be important (Pörtner, 2002). The present results therefore extend the idea of temperature optima to include the possibility of stock-specific temperature optima, in addition to confirming an important temperature effect on the physiological processes that determine  $\dot{M}_{O_2max}$ , scope for activity and  $U_{crit}$ . Three stocks of adult salmon demonstrated distinct temperature optima for  $\dot{M}_{O_2max}$  and scope for activity, while GC and WVR sockeye salmon also exhibited temperature optima for  $U_{crit}$ . In contrast,  $U_{crit}$  for CHE coho salmon displayed low temperature sensitivity. Temperature optima around  $15^\circ C$  have been reported previously for  $\dot{M}_{O_2}$ , metabolic scope and sustained cruising speed with juvenile and adult sockeye salmon (Brett and Glass, 1973). While this temperature is very close to the temperature optima reported here for GC sockeye salmon, there were clear differences in the temperature optima for WVR sockeye salmon (Fig. 3). Furthermore, the temperature optima adult CHE coho salmon are considerably lower than that reported earlier for juvenile coho salmon (approx.  $20^\circ C$ ; Brett et al., 1958), a difference that could reflect either a stock-specific effect or developmental effect.

Although temperature optima were clearly established for the salmon stocks, a measure of temperature insensitivity for peak swimming capability is likely to be critical for these salmon stocks because they routinely face varying water temperatures. To gauge temperature insensitivity we used the regression equations to arbitrarily estimate the temperature range over which a salmon stock could reach at least 90% of its peak  $\dot{M}_{O_2max}$ . These temperature ranges were:  $14.7\text{--}20.3^\circ C$  for GC sockeye salmon,  $12.7\text{--}17.3^\circ C$  for WVR sockeye salmon and  $5.0\text{--}11.4^\circ C$  for CHE coho salmon. Using a similar analysis for scope for activity, the temperature ranges for the three stocks were similar to those for  $\dot{M}_{O_2max}$ , but marginally cooler and/or narrower ( $13.9\text{--}19.3^\circ C$  for GC sockeye salmon,  $12.8\text{--}16.2^\circ C$  for WVR sockeye salmon and  $6.6\text{--}8.9^\circ C$  for CHE

coho salmon). This analysis clearly shows that these three salmon stocks can approach their respective peak aerobic activity over a temperature range spanning as much as 5°C. Such physiological flexibility may be adaptive (see Guderley and Blier, 1998) because the water temperature in the Fraser River may vary annually on a given date by as much as 6°C, perhaps even providing sufficient flexibility to handle all but the most extreme temperature conditions encountered in the

Fraser River during a particular migration window. This does not mean that extreme temperature and/or hydrological conditions (known to occur in certain years) would not impose difficulties for migration (e.g. ES sockeye have faced water temperatures reaching 22°C and flows of 9000 m<sup>3</sup> s<sup>-1</sup>; Macdonald et al., 2000). But it does mean that physiological information provided here could be useful in predicting which river conditions are more likely to impair passage and reduce spawning success.

An equally important discovery was that these temperature optima correlated very closely with the ambient water temperature of the natal river for individual salmon stocks. This meant that the lowest

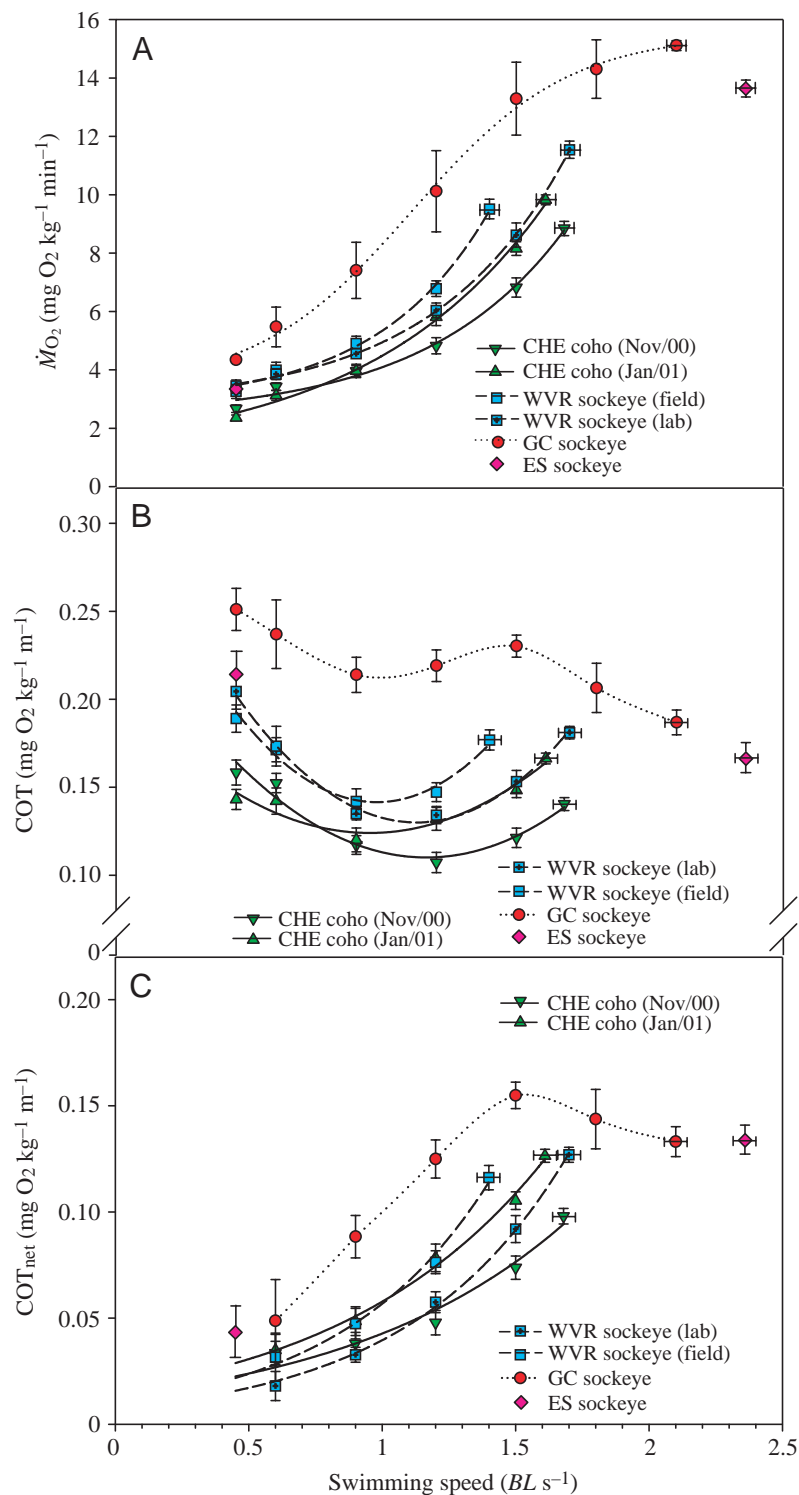


Fig. 5 (A) Relationships between oxygen consumption and swimming speed for Gates Creek (GC) and Weaver Creek (WVR) sockeye salmon and Chehalis (CHE) coho salmon. At comparable intermediate velocities, active  $\dot{M}_{O_2}$  for GC sockeye salmon was significantly higher ( $P < 0.05$ ) than that for other stocks. Active  $\dot{M}_{O_2}$  varied sigmoidally with swimming speed  $U$  for the GC sockeye salmon:  $\dot{M}_{O_2} = -54.44 + 68.85 / [1 + e^{-(U-1.58)/0.087}]^{0.013}$  ( $P < 0.05$ ;  $r^2 = 0.997$ ). Active  $\dot{M}_{O_2}$  varied exponentially for WVR sockeye salmon tested in either the laboratory or field according to the equations:  $\dot{M}_{O_2} = 2.78 + 0.24e^{2.38U}$  ( $P < 0.05$ ;  $r^2 = 0.999$ ) and  $\dot{M}_{O_2} = 2.80 + 0.29e^{2.00U}$  ( $P < 0.05$ ;  $r^2 = 0.995$ ), respectively. Active  $\dot{M}_{O_2}$  varied exponentially for CHE coho salmon tested in either November 2000 or January 2001 according to the equations:  $\dot{M}_{O_2} = 2.37 + 0.25e^{1.93U}$  ( $P < 0.05$ ;  $r^2 = 0.993$ ) and  $\dot{M}_{O_2} = 0.97 + 0.80e^{1.48U}$  ( $P < 0.05$ ;  $r^2 = 0.997$ ), respectively.  $\dot{M}_{O_2, routine}$  and  $\dot{M}_{O_2, max}$  values for Early Stuart (ES) sockeye salmon are included for reference. (B) Relationships between cost of transport (COT) and  $U$  for sockeye and coho salmon. COT varied with  $U$  for WVR sockeye salmon tested in the laboratory and field according to the equations:  $COT = 3.31e^{-1} - 5.71e^{-3}U + 4.06e^{-5}U^2$  ( $P < 0.05$ ;  $r^2 = 0.991$ ) and  $COT = 3.18e^{-1} - 5.65e^{-3}U + 4.52e^{-5}U^2$  ( $P < 0.05$ ;  $r^2 = 0.961$ ), respectively. For CHE coho salmon tested in either November 2000 or January, 2001 COT varied with swimming speed according to the equations:  $COT = 2.54e^{-1} - 3.97e^{-3}U + 2.73e^{-5}U^2$  ( $P < 0.05$ ;  $r^2 = 0.941$ ) and  $COT = 2.07e^{-1} - 2.85e^{-3}U + 2.45e^{-5}U^2$  ( $P < 0.05$ ;  $r^2 = 0.921$ ), respectively. (All  $r^2$  values  $> 0.95$ .) The relationship for GC sockeye salmon was not defined. (C) Relationships between net cost of transport ( $COT_{net}$ ) and  $U$  for sockeye and coho salmon stocks.  $COT_{net}$  varied exponentially for WVR sockeye salmon tested in the laboratory and field according to the equations:  $COT_{net} = -1.07e^{-2} + 1.22e^{-2}e^{0.023U}$  ( $P < 0.05$ ;  $r^2 = 0.999$ ) and  $COT_{net} = 2.01e^{-2} + 2.53e^{-4}e^{0.041U}$  ( $P < 0.05$ ;  $r^2 = 0.999$ ), respectively. For CHE coho salmon tested in either November 2000 or January 2001,  $COT_{net}$  varied exponentially according to the equations:  $COT_{net} = 2.88e^{-3} + 9.10e^{-4}e^{0.041U}$  ( $P < 0.05$ ;  $r^2 = 0.999$ ) and  $COT_{net} = -5.73e^{-3} + 1.98e^{-2}e^{0.019U}$  ( $P < 0.05$ ;  $r^2 = 0.994$ ), respectively. The relationship for GC sockeye salmon was not exponential.

thermal sensitivity of peak aerobic performance occurred around the ambient temperature of the natal stream. While environmental variability can differentially influence the ability of organisms to survive and reproduce, tailoring populations to their respective environmental niches (Cooke et al., 2001), and the 'stock concept' suggests adaptation to local conditions (Berst and Simon, 1981), migratory salmon spend most of their life away from the natal streams. Whether the present correlation between temperature optima and natal stream temperature is a reflection of adult salmon being pre-adapted to water temperatures likely to be encountered during river migrations, or is coincidental with the temperature preferendum of the species (e.g. for sockeye salmon 14.5°C, Brett, 1952; 10.6–12.8°C, Horak and Tanner, 1964), will require further study. Further work will also need to tackle the possibility of rather rapid thermal compensation during the actual in-river migration. For some sockeye salmon stocks, the timing of migration seems to have been far too restrictive for thermal compensatory processes to take full effect. For example, ES sockeye move from seawater in the Georgia Strait, where they encounter temperatures likely to be no warmer than 13°C, into river water as high as 18°C, and then within 4 days face one of their most difficult in-river swimming challenges, Hell's Gate.

Although the majority of tests were performed at ambient water temperature, small temperature adjustments were used to extend the ambient temperature range. Acclimations to these temperatures were necessarily short (5 days) because fully ripe salmon have compromised swimming ability (Williams et al., 1986). While the short acclimation period is a concern, the extent of the temperature change (<6°C) was not unusual compared with changes naturally encountered, because ES and Chilko stocks of adult sockeye salmon routinely face temperature changes of 1°C daily and as much as 7°C over 1 day during their migrations (Idler and Clemens, 1959). In addition, individual fish tested at either their ambient temperature or an adjusted temperature showed a reasonable overlap of  $\dot{M}_{O_{2max}}$  values (Fig. 3A). A second concern is that we did not consider sex differences in swimming energetics. This concern is offset by the fact that we used equal numbers of male and female fish in many test groups. Furthermore, physiological telemetry studies of migrating ES sockeye salmon and Seton River pink salmon have revealed little difference between sexes in terms of the overall cost of transport to the spawning site, although males were less efficient at migrating through hydraulic obstacles (Hinch and Rand, 1998; Standen et al., 2002). The present study could be used as a framework for future studies of sexual dichotomy in swimming capabilities.

The finding that  $\dot{M}_{O_{2routine}}$  increased exponentially with temperature is consistent with previous studies showing exponential relationships for both  $\dot{M}_{O_{2routine}}$  and standard metabolic rate (rainbow trout; Dickson and Kramer, 1971), brown trout *Salmo trutta*; Butler et al., 1992), sockeye salmon (Brett and Glass, 1973), tilapia *Sarotherodon mossambicus*; Caulton, 1978) and largemouth bass *Micropterus salmoides*;

Cooke et al., 2001). As expected, our  $\dot{M}_{O_{2routine}}$  values for adult sockeye salmon were higher than the standard metabolic rate previously reported (Brett and Glass, 1973). Some of this difference could be attributed to the on-going gonadal development in the mature fish used in the present study. It is also possible that the overnight recovery is insufficient (see Farrell et al., 2003) and adult salmon are more restless than less mature fish. Williams et al. (1986) noted that adult pink salmon were more restless than sockeye salmon in swim tunnels.

#### *Intraspecific differences in relation to migration distance and difficulty*

The intraspecific differences in migration capacity were sometimes correlated with in-river migration distance and difficulty. For example, ES sockeye salmon, the furthest migrating stock of any of the Fraser River salmon, attained a significantly higher  $U_{crit}$  at a 5°C cooler temperature and were more efficient swimmers at  $U_{crit}$  because of a lower  $\dot{M}_{O_{2max}}$  compared with GC sockeye salmon. These attributes of ES sockeye salmon may be advantageous because they migrate almost three times the distance up the Fraser River compared with GC sockeye salmon (Table 1). Similarly, both ES and GC sockeye salmon migrate much longer distances and negotiate more severe hydraulic challenges compared with the coastal WVR sockeye salmon and correspondingly had a larger scope for activity at comparable water temperatures. Moreover, almost all of the GC and ES fish repeated their swimming performance without recovering  $\dot{M}_{O_2}$  to within 5% of  $\dot{M}_{O_{2routine}}$ . The differences in swimming energetics found between CHE coho salmon and WVR sockeye also probably reflect species-specific adaptations. Yet, because these two salmon stocks face almost identical in-river migration distances and conditions, other factors must be involved in these adaptations. Thus, the suggestion that distance and/or difficulty of migration are powerful selective factors acting on salmonids (Bernatchez and Dodson, 1985; G. T. Crossin, S. G. Hinch, A. P. Farrell, D. A. Higgs, A. G. Lotto, J. D. Oakes and M. C. Healey, unpublished observations) is supported by the present study.

Intraspecific adaptation of maximum swimming ability has been previously established for juvenile salmonids either held or reared in a laboratory, but to our knowledge not for adult, wild salmon. For example, juvenile Pacific coho salmon from an interior river had an inheritable trait that resulted in a lower initial acceleration for a fast start, but a longer time-to-fatigue at a constant swimming speed compared with coho salmon from a coastal river (Taylor and McPhail, 1985). Similarly, Pacific steelhead trout *O. mykiss* from an interior river also had a greater time-to-fatigue for an incremental swimming speed test and allelic differences in the lactate dehydrogenases compared with a coastal stock (Tsuyuki and Willisroft, 1977). Nevertheless, because Bams (1967) found that rearing conditions could alter swimming performance of sockeye salmon fry, phenotypic rather than genotypic expression could have contributed to the differences we observed.

Paradoxically, GC sockeye salmon were less efficient



swimmers than either WVR sockeye salmon or CHE coho salmon, and why this is so is unclear. GC sockeye salmon were unusual in another regard, the plateau in  $\dot{M}O_2$  as the fish neared  $U_{crit}$ . In fish,  $\dot{M}O_2$  typically increases exponentially with swimming speed (see Beamish, 1978) to overcome drag, which is exponentially related to water velocity (Webb, 1975). Rarely is a plateau observed in  $\dot{M}O_2$  even though fish progressively increase the anaerobic contribution to swimming at 75%  $U_{crit}$  (Brett and Groves, 1979; Burgetz et al., 1998). Consequently, the plateaus for both  $\dot{M}O_2$  and the cost of transport curve near  $U_{crit}$  for GC sockeye salmon point to an unusually high contribution of anaerobically fueled locomotion. This possibility is further explored in the accompanying paper (Lee et al., 2003b), in which excess post-exercise oxygen consumption is examined as a measure of the anaerobic swimming activity.

In summary, we conclude that variation in  $\dot{M}O_{2,routine}$  among adult salmon stocks was primarily due to differences in water temperature. In contrast, distinct temperature optima for  $\dot{M}O_{2,max}$  were evident among salmon stocks, which when combined with differences in scope for activity and  $U_{crit}$ , suggest stock-specific as well as species-specific differences in the temperature sensitivity of the physiological mechanisms that underpin oxygen delivery during swimming in adult Pacific salmon.

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## References

- Bams, R. A.** (1967). Differences in performance of naturally and artificially propagated sockeye salmon migrant fry as measured with swimming and predation tests. *J. Fish. Res. Bd. Can.* **24**, 1117-1153.
- Beamish, F. W. H.** (1978). Swimming capacity. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 101-187. London: Academic Press.
- Bell, W. H. and Terhune, L. D. B.** (1970). Water tunnel design for fisheries research. *Fish. Res. Bd. Can. Tech. Rep.* **195**, 1-69.
- Bernatchez, L. and Dodson, J. J.** (1985). Influence of temperature and current speed on the swimming capacity of lake whitefish (*Coregonus clupeaformis*) and cisco (*C. artedii*). *Can. J. Fish. Aquat. Sci.* **42**, 1522-1529.
- Berst, A. and Simon, R.** (1981). Proceedings of the International Stock Concept Symposium. *Can. J. Fish. Aquat. Sci.* **38**, 1457-1914.
- Brett, J. R.** (1952). Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *J. Fish. Res. Bd. Can.* **9**, 265-323.
- Brett, J. R.** (1965). The relation of size to rate of oxygen consumption and sustained swimming speed of sockeye salmon (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Can.* **22**, 1491-1501.
- Brett, J. R.** (1971). Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* **11**, 99-113.
- Brett, J. R.** (1982). The swimming speed of adult pink salmon (*Oncorhynchus gorbuscha*) at 20°C and a comparison with sockeye salmon (*O. nerka*). *Can. Tech. Rep. Fish. Aquat. Sci.* **1143**, 33.
- Brett, J. R. and Glass, N. R.** (1973). Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd. Can.* **30**, 379-387.
- Brett, J. R. and Groves, T. D. D.** (1979). Physiological energetics. In *Fish Physiology*, vol. 7 (ed. W. S. Hoar and D. J. Randall), pp. 279-352. London: Academic Press.
- Brett, J. R., Hollands, M. and Alderdice, D. F.** (1958). The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Can.* **15**, 587-605.
- Burgetz, I. J., Rojas-Vargas, A., Hinch, S. G. and Randall, D. J.** (1998). Initial recruitment of anaerobic metabolism during submaximal swimming in rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **201**, 2711-2721.
- Butler, P. J., Day, N. and Namba, K.** (1992). Interactive effects of seasonal temperature and low pH on resting oxygen uptake and swimming performance of adult brown trout, *Salmo trutta*. *J. Exp. Biol.* **165**, 195-212.
- Caulton, M. S.** (1978). The effect of temperature and mass on routine metabolism in *Sarotherodon (Tilapia) mossambicus* (Peters). *J. Fish Biol.* **13**, 195-201.
- Cooke, S. J., Kassler, T. W. and Philipp, D. P.** (2001). Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management. *J. Fish Biol.* **59**, 248-268.
- Davis, J. C.** (1966). The influence of temperature and activity on certain cardiovascular and respiratory parameters in adult sockeye salmon. MSc thesis, University of Victoria, Canada.
- Dickson, I. W. and Kramer, R. H.** (1971). Factors influencing scope for activity and active and standard metabolism of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Can.* **28**, 587-596.
- Farrell, A. P.** (1997). Effects of temperature on cardiovascular performance. In *Global Warming Implications for Freshwater and Marine Fish* (ed. C. M. Wood and D. G. McDonald), pp. 135-158. Cambridge: Cambridge University Press.
- Farrell, A. P.** (2002). Cardiorespiratory performance in salmonids during exercise at high temperature: Insights into cardiovascular design limitations in fishes. *Comp. Biochem. Physiol.* **132A**, 797-810.
- Farrell, A. P. and Clutterham, S. M.** (2003). On-line venous oxygen tensions in rainbow trout during graded exercise at two acclimation temperatures. *J. Exp. Biol.* **206**, 487-496.
- Farrell, A. P., Gamperl, A. K. and Birtwell, I. K.** (1998). Prolonged swimming, recovery and repeat swimming performance of mature sockeye salmon *Oncorhynchus nerka* exposed to moderate hypoxia and pentachlorophenol. *J. Exp. Biol.* **201**, 2183-2193.
- Farrell, A. P., Lee, C. G., Tierney, K., Hodaly, A., Clutterham, S., Healey, M. C., Hinch, S. G. and Lotto, A.** (2003). Field-based measurements of oxygen uptake and swimming performance with adult Pacific salmon (*Oncorhynchus* sp.) using a mobile respirometer swim tunnel. *J. Fish Biol.* **62**, 64-84.
- Fry, F. E. J.** (1947). Effects of the environment on animal activity. *Univ. Toronto Student Biol. Series* **55**, 1-62.
- Gallagher, P., Thorarensen, H. and Farrell, A. P.** (1995). Hematocrit in oxygen transport and swimming in rainbow trout, *Oncorhynchus mykiss*. *Respir. Physiol.* **102**, 279-292.
- Gehrke, P. C., Fidler, L. E., Mense, D. C. and Randall, D. J.** (1990). A respirometer with controlled water quality and computerized data acquisition for experiments for swimming fish. *Fish Physiol. and Biochem.* **8**, 61-67.
- Gilhausen, P.** (1990). Prespawning mortality of sockeye salmon in the Fraser River system and possible causal factors. *Inter. Pacific Salmon Fish. Comm. Bull.* **26**, 1-58.
- Griffiths, J. S. and Alderdice, D. F.** (1972). Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. *J. Fish. Res. Bd. Can.* **29**, 251-264.
- Groot, C. and Margolis, L.** (1991). *Pacific Salmon Life Histories*. Vancouver BC: UBC Press. 564p.
- Guderley, H. and Blier, P.** (1988). Thermal acclimation in fish: conservative and labile properties of swimming muscle. *Can. J. Zool.* **60**, 3153-3164.
- Hammer, C.** (1995). Review: fatigue and exercise tests with fish. *Comp. Biochem. Physiol.* **112A**, 1-20.
- Horak, D. L. and Tanner, H. A.** (1964). The use of vertical gill nets in studying fish depth distribution, Horsetooth Reservoir, Colorado. *Trans. Am. Fish. Soc.* **93**, 137-145.

- Hinch, S. G. and Rand, P. S. (1998). Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Can. J. Fish. Aquat. Sci.* **55**, 1821-1831.
- Hinch, S. G. and Bratty, J. M. (2000). Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Trans. Am. Fish. Soc.* **129**, 604-612.
- Houston, A. H. (1982). *Thermal Effects Upon Fishes*. National Research Council Canada Publication # NRCC 18566, pp. 1-200.
- Idler, D. R. and Clemens, W. A. (1959). The energy expenditure of Fraser River sockeye salmon during the spawning migration to Chilko and Stuart lakes. New Westminster, BC: International Pacific Salmon Fisheries Commission Progress Report.
- Jain, K. E., Birtwell, I. K. and Farrell, A. P. (1998). Repeat swimming performance of mature sockeye salmon following brief recovery period: a proposed measure of fish health and water quality. *Can. J. Zool.* **76**, 1488-1496.
- Jain, K. E., Hamilton, J. C. and Farrell, A. P. (1997). Use of a ramp velocity test to measure critical swimming speed in rainbow trout, *Oncorhynchus mykiss*. *Comp. Biochem. Physiol.* **117A**, 441-444.
- Johnston, I. A. and Ball, D. (1997). Thermal stress and muscle function in fish. In *Global Warming: Implications for freshwater and marine fish* (ed. C. M. Wood and D. G. McDonald), pp. 79-104. Cambridge, UK: Cambridge University Press.
- Johnston, I. A. and Temple, G. K. (2002). Review: thermal plasticity of skeletal muscle phenotype in ectothermic vertebrates and its significance for locomotory behaviour. *J. Exp. Biol.* **205**, 2305-2322.
- Jones, D. R., Kiceniuk, J. W. and Bamford, O. S. (1974). Evaluation of the swimming performance of several fish species from the Mackenzie River. *J. Fish. Res. Bd. Can.* **31**, 1641-1647.
- Kelsch, S. W. (1996). Temperature selection and performance by bluegills: evidence for selection in response to available power. *Trans. Am. Fish. Soc.* **125**, 948-955.
- Kieffer, J. D. (2000). Limits to exhaustive exercise in fish. *Comp. Biochem. Physiol.* **126A**, 161-179.
- Lee, C. G., Devlin, R. H. and Farrell, A. P. (2003a). Swimming performance, oxygen consumption and excess post-exercise oxygen consumption in adult transgenic and ocean-ranched coho salmon (*Oncorhynchus kisutch*, Walbaum). *J. Fish Biol.* **62**, 753-766.
- Lee, C. G., Farrell, A. P., Lotto, A., Hinch, S. G. and Healey, M. C. (2003b). Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming. *J. Exp. Biol.* **206**, 3253-3260.
- Macdonald, J. S., Foreman, M. G. G., Farrell, A. P., Williams, I. V., Grout, J., Cass, A., Woodey, J. C., Enzenhofer, H., Clarke, W. C., Houtman, R., Donaldson, E. M. and Barnes, D. (2000). The influence of extreme water temperatures on migrating Fraser River sockeye salmon during the 1998 spawning season. *Can. Tech Rep. Fish. Aquat. Sci.* **2326**, 117.
- Pörtner, H. O. (2002). Climate change and temperature dependent biogeography: systematic to molecular hierarchy of thermal tolerance in animals. *Comp. Biochem. Physiol.* **132A**, 739-761.
- Rand, P. S. and Hinch, S. G. (1998). Swim speeds and energy use of upriver migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing risk of energy depletion. *Can. J. Fish. Aquat. Sci.* **55**, 1832-1841.
- Standen, E. M., Hinch, S. G., Healey, M. C. and Farrell, A. P. (2003). Energetic costs of migration through the Fraser River canyon, British Columbia in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry. *Can. J. Fish. Aquatic Sci.* **59**, 1809-1818.
- 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**, 2029-2033.
- Thomas, A. E. and Donahoo, M. J. (1977). Differences in swimming performance among strains of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Can.* **34**, 304-307.
- Thorarensen, H., Gallagher, P. E., Kessling, A. K. and Farrell, A. P. (1993). Intestinal blood flow in swimming Chinook salmon *Oncorhynchus tshawytscha* and the effects of hematocrit on blood flow distribution. *J. Exp. Biol.* **179**, 115-129.
- Tierney, K. B. (2000). The repeated swimming performance of sockeye, coho, and rainbow trout in varying environmental and physiological conditions. MSc thesis, Simon Fraser University, Canada.
- Tsuyuki, H. and Willisroft, S. N. (1977). Swimming stamina differences between genotypically distinct forms of rainbow (*Salmo gairdneri*) and steelhead trout. *J. Fish. Res. Bd. Can.* **34**, 996-1003.
- Webb, P. W. (1971). The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. *J. Exp. Biol.* **55**, 521-540.
- Webb, P. W. (1975). Acceleration performance of rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **63**, 451-465.
- Williams, I. V., Brett, J. R., Bell, G. R., Traxler, G. S., Bagshaw, J., McBride, J. R., Fagerlund, U. H. M., Dye, H. M., Sumpter, J. P., Donaldson, E. M. et al. (1986). The 1983 early run Fraser and Thompson River pink salmon; morphology, energetics and fish health. *International Pacific Salmon Fisheries Commission, Bulletin XXIII*, pp. 1-55.