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Excess post-exercise oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon following critical speed swimming

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Summary

The present study measured the excess post-exercise oxygen cost (EPOC) following tests at critical swimming speed (U_{crit}) in three stocks of adult, wild, Pacific salmon (*Oncorhynchus* sp.) and used EPOC to estimate the time required to return to their routine level of oxygen consumption (recovery time) and the total oxygen cost of swimming to U_{crit}. Following exhaustion at U_{crit}, recovery time was 42–78 min, depending upon the fish stock. The recovery times are several-fold shorter than previously reported for juvenile, hatchery-raised salmonids. EPOC varied fivefold among the fish stocks, being greatest for Gates Creek sockeye salmon (*O. nerka*), which was the salmon stock that had the longest in-river migration, experienced the warmest temperature and achieved the highest maximum oxygen consumption compared with the other salmon stocks that were studied. EPOC was related to U_{crit}, which in turn was directly influenced by ambient test temperature. The non-aerobic cost of swimming to U_{crit} was estimated to add an additional 21.4–50.5% to the oxygen consumption measured at U_{crit}. While these non-aerobic contributions to swimming did not affect the minimum cost of transport, they were up to three times higher than the value used previously for an energetic model of salmon migration in the Fraser River, BC, Canada. As such, the underestimate of non-aerobic swimming costs may require a reevaluation of the importance of how in-river barriers like rapids and by-pass facilities at dams, and year-to-year changes in river flows and temperatures, affect energy use and hence migration success.

Key words: recovery, exhaustive exercise, salmon, oxygen consumption, non-aerobic swimming, post-exercise oxygen cost (EPOC), fish stock, spawning run.

Introduction

Like all other vertebrates, fish need time to recover after exhaustive activity. Furthermore, a rapid rate of recovery may be beneficial if the activity is important to survival and reproduction. For example, a rapid rate of recovery is needed to keep migratory passage timely when adult salmon use anaerobic swimming to negotiate difficult hydraulic challenges during their spawning migration in the Fraser River, British Columbia (BC), Canada (as revealed by telemetry of electromyographic signals; Rand and Hinch, 1998; Hinch and Bratty, 2000). Of equal importance to these migratory fish is the actual cost of anaerobic swimming because the entire upstream migration is completed using stored energy reserves and without feeding. Therefore, the purpose of the present study was to compare recovery time and the non-aerobic cost of swimming among different stocks of adult, wild Pacific salmon (*Oncorhynchus* spp.). Such comparisons were likely to be revealing because of the conspicuous absence of large changes in the rate of oxygen consumption ($\dot{M}_{O_2}$) near to the critical swimming speed (U_{crit}) for the Gates Creek (GC) stock of sockeye salmon *Oncorhynchus nerka* in our accompanying study (Lee et al., 2003), which suggested a greater anaerobic effort compared with other salmon stocks of adult salmon. The more typical response is that $\dot{M}_{O_2}$ continues to increase up to U_{crit} (see for example, Brett, 1964; Brett and Groves, 1979; Kiceniuk and Jones, 1977; Thorarensen et al., 1993; Gallaugher et al., 2001).

The elevated $\dot{M}_{O_2}$ following exhaustive exercise, termed ‘excess post-exercise oxygen consumption’ (EPOC; Gaesser and Brooks, 1984) can be used to assess both recovery time and the non-aerobic oxygen cost of exercise. EPOC, which replaces the term ‘oxygen debt’ (Hill et al., 1924) to avoid causal implications, reflects the increased quantity of oxygen required to restore tissue and cellular stores of oxygen and high-energy phosphates, biochemical imbalances in metabolites such as lactate and glycogen, and other functions such as ionic and osmotic balance. Measurements of EPOC with salmonids are limited, however, to juvenile, hatchery-raised fish. In fact, the number of studies of EPOC in all ectotherms is quite limited (e.g. Heath and Prichard, 1962; Brett, 1964; Smit, 1965; Smit et al., 1971; Scarabello et al., 1991, 1992; Gleeson, 1991; Reidy et al., 1995; Hancock et al., 2001) compared with mammals (e.g. Bahrm and Maehlum, 1986; Bangsbo et al., 1997; Baker and Gleeson, 1998).

The pioneering measurements of EPOC following a $U_{\rm crit}$ test with juvenile, hatchery-reared sockeye revealed that $\dot{M}_{\rm O_2}$ returned to a routine level after 4–5 h (Brett, 1964). A similarly protracted recovery time of up to 6 h was reported for juvenile, hatchery-reared rainbow trout *O. mykiss* after vigorous chasing for 3 min followed by an electrical stimulation for a further 2 min (Scarabello et al., 1992). In contrast, recovery time was only 1.5 h in adult Atlantic cod *Gadus morhua*, regardless of whether the fish had been chased to exhaustion, accelerated to exhaustion, or performed a $U_{\rm crit}$ test (Reidy et al., 1995). Furthermore, the protracted recovery times for juvenile salmonids contrasts with their ability either to repeat $U_{\rm crit}$ after as little as a 45 min recovery period (Randall et al., 1987; Peake et al., 1997; Jain et al., 1997; Farrell et al., 1998, 2003), or to repeat burst swimming 60 min after being chased, swum or fished to exhaustion (Stevens and Black, 1966; Farrell et al., 2001b). Although none of these studies measured EPOC along with repeat swimming performance, $\dot{M}_{\rm O_2}$ for adult, wild sockeye salmon did approach routine $\dot{M}_{\rm O_2}$ after only a 45 min recovery period (Farrell et al., 1998). Given the possibility of a difference in recovery times between juvenile and adult salmonids, the present study measured post-exercise $\dot{M}_{\rm O_2}$ for adult, wild salmon during recovery from exhaustion following a $U_{\rm crit}$ test. Because EPOC was measured concurrently with the accompanying assessment of swimming energetics on various salmon stocks (Lee et al., 2003) that encounter different ambient water temperatures and hydraulic challenges while migrating up the Fraser River to different natal streams, we sought additional information on some of the other factors that may modulate EPOC, none of which have been thoroughly studied in fish.

Materials and methods

Methodological details for the present study and the results for the $U_{\rm crit}$ swimming tests are reported in full in the accompanying paper (Lee et al., 2003). The focus here is on the $\dot{M}_{\rm O_2}$ recovery curves that were measured following the $U_{\rm crit}$ tests with two stocks of Fraser River sockeye salmon *Oncorhynchus nerka* Walbaum and one stock of Fraser River coho salmon *O. kisutch* Walbaum. Gates Creek (GC) sockeye salmon (mass, 2.69±0.10 kg; fork length, 64.2±0.7 cm; 10 males and 10 females) were studied at the BC Hydro Seton Dam site near Lillooet, BC, Canada using ambient river water (18.0±0.2°C). As mature adults, GC sockeye salmon migrate in mid-summer to spawning grounds in the interior of the province of BC (~400 km up-river from the ocean) and, in doing so, negotiate particularly demanding hydraulic challenges (Standen et al., 2003). By comparison, Weaver Creek (WVR) sockeye salmon and Chehalis River (CHE) coho salmon spawn in coastal streams and both experience shorter (~100 km) and similar up-river migrations in the fall and experience cooler ambient water temperature compared with GC sockeye salmon. Two groups of WVR sockeye salmon were tested at different temperatures and locations after being intercepted at their natal stream, Weaver Creek. One group (mass, 2.90±0.14 kg; fork length, 62.5±1.7 cm: 5 males and 7 females) were transported to (60 km) and tested at Simon Fraser University (SFU) using a water temperature (16.0±0.2°C) similar to the ambient creek temperature in Weaver Creek at the time of capture. Later in the year, a second group (mass, 3.00±0.11 kg; fork length, 64.0±0.9 cm; 6 males and 6 females) were transported to (5 km) and tested at the Chehalis River Fish Hatchery using a now cooler ambient river temperature (12.2±0.2°C). CHE coho salmon were intercepted at the Chehalis River fish hatchery and were tested on-site on two occasions. Because ambient water temperature was similar on these occasions (8.2±0.4°C and 7.6±0.1°C), the EPOC data were pooled (mass, 2.26±0.19 kg; fork length, 57.7±1.4 cm; 7 males and 6 females).

Exercise protocols

Prior to an overnight recovery in the swim tunnel at a water speed of 0.30–0.45 body lengths (*BL*) s^{-1}, fish were given a practice swim (Jain et al., 1997) to estimate $U_{\rm crit}$. The following morning, routine $\dot{M}_{\rm O_2}$ ($\dot{M}_{\rm O_2routine}$)was measured over a period of 15–20 min. Then a ramp–$U_{\rm crit}$ test (Jain et al., 1997) was performed using the 471 litre mobile swim tunnel respirometer. Initially, 5 min ramp steps of 0.15 *BL* s^{-1} were used up to 50% of the estimated $U_{\rm crit}$, followed by 20 min steps of 0.15 *BL* s^{-1} until $U_{\rm crit}$. As fish approached their $U_{\rm crit}$, a burst-and-coast swimming gait was used more frequently, and this change in swimming gait was associated with progressive accumulation of lactate in the white skeletal muscle (Burgetz et al., 1998). $\dot{M}_{\rm O_2}$ was measured at every other speed increment, and the $\dot{M}_{\rm O_2}$ measured immediately before $U_{\rm crit}$ was designated maximum $\dot{M}_{\rm O_2}$ ($\dot{M}_{\rm O_2max}$). Fish were considered exhausted when they failed to move off the rear grid after 20 s, at which time water speed was immediately decreased to between 0.30 and 0.45 *BL* s^{-1} for the 45 min recovery period during which EPOC was measured. In most cases, the swim tunnel was closed for the entire recovery period and $\dot{M}_{\rm O_2}$ was estimated at 5 min intervals. Water oxygen concentration would typically decrease by 1.5–2.5 mg O_2 l^{-1} to a final water concentration of approximately 8.0 mg O_2 l^{-1}. In a few instances (large fish at a warm temperature), the water oxygen concentration approached 6.0 mg O_2 l^{-1} and so the swim tunnel was flushed with fresh water for up to 5 min, with the resultant loss of that $\dot{M}_{\rm O_2}$ measurement. When $\dot{M}_{\rm O_2}$ was not being measured, water flow into the swim tunnel was restored. The ramp–$U_{\rm crit}$ protocol was repeated after this recovery period and EPOC was remeasured after the fish fatigued for a second time.

Data analysis and statistics

Values are means ± S.E.M. and $P<0.05$ was used as the level of statistical significance. For reference, $\dot{M}_{\rm O_2routine}$, $\dot{M}_{\rm O_2max}$ and $U_{\rm crit}$ (as reported in Lee et al., 2003) are summarized in Table 1. These values were based on an average value for the first and second swim tests because the two swim tests were not significantly different. EPOC values were treated in the same manner. The present analysis of recovery time and non-

Table 1. *Measurements of routine oxygen consumption ($\dot{M}_{O_2}$), maximum oxygen consumption ($\dot{M}_{O_2max}$) and critical swimming speed (U_{crit}) for three stocks of adult Pacific salmon measured at their ambient temperature*

Species	Stock	Average temperature (°C)	$\dot{M}_{O_2}$ (mg O_2 kg^{-1} min^{-1}) Routine	Max 1	Max 2	U_{crit} (BL s^{-1}) U_{crit1}	U_{crit2}
Sockeye	GC	17.5±0.3	4.35±0.09^{a}	15.07±0.16^{a}	15.14±0.20^{a}	2.08±0.05^{a}	2.08±0.05^{a}
Sockeye	WVR	16.0±0.2	2.94±0.14^{b}	11.89±0.41^{b}	11.98±0.70^{b}	1.73±0.07^{b}	1.76±0.09^{b}
Sockeye	WVR	12.2±0.2	2.80±0.12^{b}	9.91±0.43^{b,c}	9.73±0.52^{b,c}	1.41±0.04^{c}	1.41±0.05^{c}
Coho	CHE	7.9±0.2	2.47±0.12^{b}	9.20±0.27^{c}	9.33±0.26^{c}	1.66±0.03^{b,d}	1.61±0.03^{b,d}

$\dot{M}_{O_2max}$ was taken concurrently with maximal swimming performance (U_{crit}).

GC, Gates Creek sockeye salmon; WVR, Weaver Creek sockeye salmon; CHE, Chehalis River coho salmon.

Data adapted from Lee et al. (2003).

Each fish performed two consecutive U_{crit} swims, designated by the subscripts 1 and 2, separated by a 45 min recovery period.

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

aerobic cost of swimming was based on the relationship between mean $\dot{M}_{O_2}$ and time during the U_{crit} swim test and recovery period (as presented in Fig. 1). For regression analysis of mean $\dot{M}_{O_2}$ values *versus* time after exhaustion (SigmaPlot 6.0, SPSS, Chicago, IL, USA), it was assumed that $\dot{M}_{O_2}$ decayed exponentially during recovery (Brett and Groves, 1979; Scarabello et al., 1991). Total EPOC (mg O_2 kg^{-1}) was obtained by integrating (Maple 8.00, Waterloo Maple Inc., Waterloo, ON, Canada) the area bounded between the recovery curve and $\dot{M}_{O_2routine}$ value, and between the time when the fish exhausted and the time the recovery curve reached $\dot{M}_{O_2routine}$ (Fig. 2). Similarly, the cost of transport through water increases exponentially with swimming speed (Brett, 1964; Webb, 1975), so it was assumed that mean $\dot{M}_{O_2}$ increased exponentially with time during the U_{crit} test because swimming speed was increased in an incremental fashion. The 5 min steps were adjusted to 20 min steps to ensure a constant relationship between time and swimming speed throughout the U_{crit} test.

Statistical comparisons of EPOC for the first and second swims were compared with a paired Student's t-test. 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.

Results

Modeling recovery time and EPOC

$\dot{M}_{O_2}$ for the GC sockeye did not recover to a routine level during the recovery period, whereas recovery was nearly completed for the other three salmon groups (Fig. 1). The $\dot{M}_{O_2}$ recovery curves were adequately modeled for each group of salmon (P<0.05) by an exponential regression equation (r^2>0.975) (Fig. 2A–D). These regression equations predicted that $\dot{M}_{O_2routine}$ would be reached after recovery times of 78 min ($t_{1/2}$=35 min), 42 min ($t_{1/2}$=13 min), 65 min ($t_{1/2}$=14 min) and 63 min ($t_{1/2}$=14 min) for GC sockeye salmon, CHE coho salmon, and WVR sockeye salmon tested at 16°C and 12°C, respectively.

Using the regression curves, total EPOC was estimated as between 60.9 and 289.8 mg O_2 kg^{-1}, depending on the fish stock (Table 2). The empirical data from the 45 min recovery period, which ranged from 61.6 to 254.2 mg O_2 kg^{-1} (Table 2), confirmed the model estimates of total EPOC because the values agreed to within 2–12%. This close agreement between modeled and measured EPOC values reflected that fact that $\dot{M}_{O_2}$ was at or near $\dot{M}_{O_2routine}$ following the 45 min recovery period.

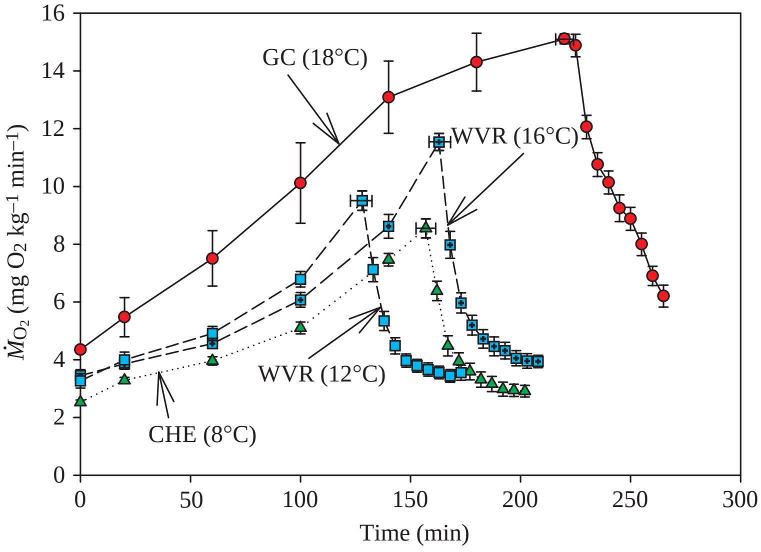

Fig. 1. Relationships between rate of oxygen consumption ($\dot{M}_{O_2}$) and duration (min) of a ramp–U_{crit} swim test followed by a 45 min recovery period for Gates Creek (GC) sockeye salmon (solid line), Weaver Creek (WVR) sockeye salmon (measured at two temperatures; broken lines) and Chehalis (CHE) coho salmon (dotted line). $\dot{M}_{O_2}$ data during swimming were adapted from fig. 5A in Lee et al. (2003).

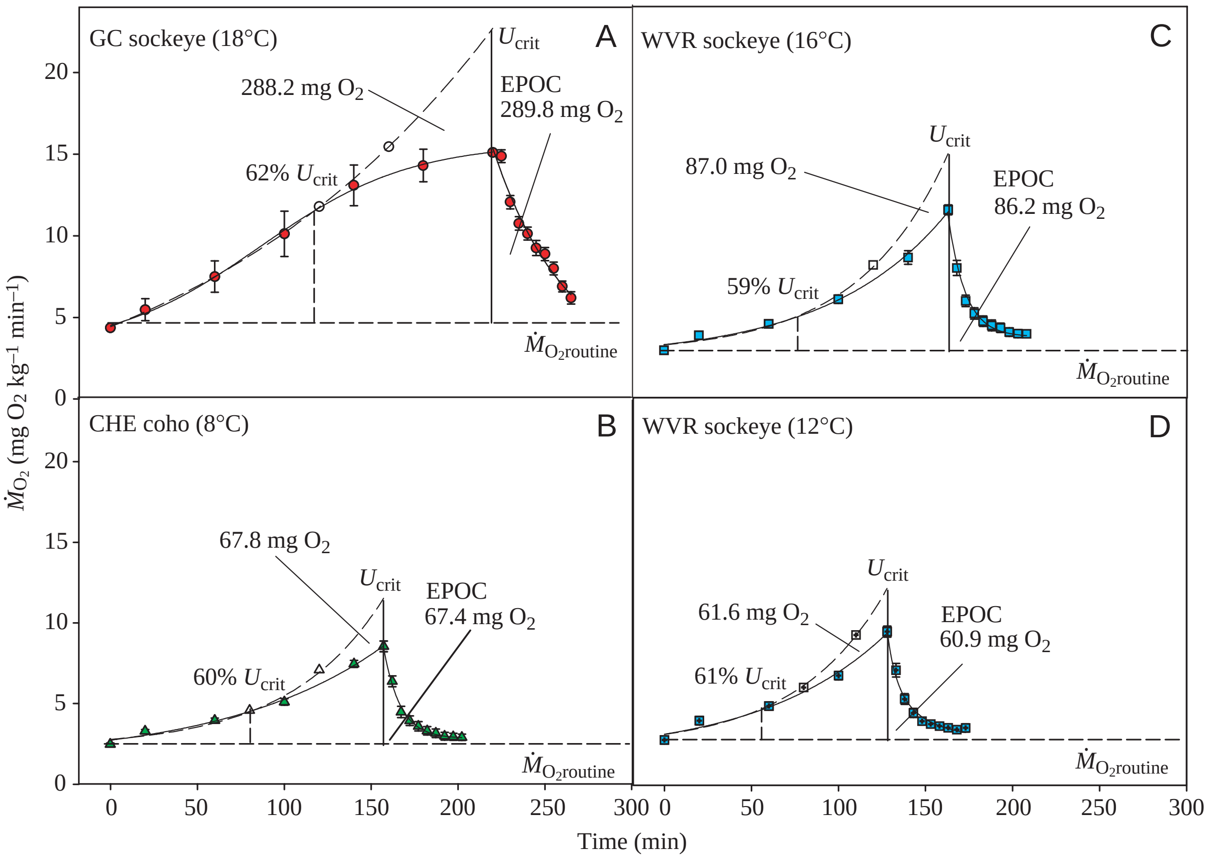

Fig. 2. Modeling of the oxygen cost of swimming to U_{crit} and recovering from exhaustion (solid lines fitted to data points) for adult Pacific salmon stocks. The broken vertical line represents the point in time t when the fish exhausted and the critical swimming speed (U_{crit}) is indicated for each stock. The horizontal broken line represents the $\dot{M}_{O_2routine}$ that was used to estimate total post exercise oxygen cost (EPOC; (the area bound by the vertical and horizontal broken lines and the $\dot{M}_{O_2}$ recovery curve). EPOC was then used in the derivation of the curve (broken curve) that estimated the total oxygen cost of swimming to U_{crit} (i.e. aerobic oxygen cost + EPOC; see text for details). The solid vertical line indicates the transition time during the swim test (and the interpolated swimming speed) when non-aerobic swimming costs began to accrue. (See Fig. 1 for abbreviations.) The aerobic curve, total oxygen cost curve and $\dot{M}_{O_2}$ recovery curves for each stock were as follows: (A) GC sockeye salmon: $\dot{M}_{O_2}$=3.00+12.68/(1e$^{-(t-86.10/43.21)}$) (P<0.05, r^2=0.994); $\dot{M}_{O_2}$=–3.67+8.10e$^{0.0054t}$ (P<0.05, r^2=0.999) and $\dot{M}_{O_2}$=1.53+2.30×10^^{3}e$^{-0.023t}$ (P<0.05, r^2=0.976). (B) CHE coho salmon: $\dot{M}_{O_2}$=1.47+1.26e$^{0.011t}$ (P<0.05, r^2=0.995); $\dot{M}_{O_2}$=2.28+0.50e$^{0.019t}$ (P<0.05, r^2=0.970) and $\dot{M}_{O_2}$=2.84+8.14×10^^{7}e$^{-0.11t}$ (P<0.05, r^2=0.994). (C) WVR sockeye salmon tested at 16°C: $\dot{M}_{O_2}$=2.45+0.83e$^{0.015t}$ (P<0.05, r^2=0.995); $\dot{M}_{O_2}$=2.77+0.51e$^{0.020t}$ (P<0.05, r^2=0.980) and $\dot{M}_{O_2}$=3.76+1.14×10^^{8}e$^{-0.10t}$ (P<0.05, r^2=0.990). (D) WVR sockeye salmon tested at 12°C: $\dot{M}_{O_2}$=1.84+1.32e$^{0.014t}$ (P<0.05, r^2=0.987); $\dot{M}_{O_2}$=2.37+0.79e$^{0.020t}$ (P<0.05, r^2=0.985) and $\dot{M}_{O_2}$=2.26e$^{22.09/(t-112.70)}$ (P<0.05, r^2=0.989).

Modeling the total oxygen cost of swimming to U$_{crit}$

Regression curves were fitted to the $\dot{M}_{O_2}$ measurements made during the U_{crit} swim test (solid curves in Fig. 2A–D). While exponential curves satisfactorily fitted the data for WVR sockeye salmon and CHE coho salmon (P<0.05; r^2>0.987), a sigmoid relationship was needed for GC sockeye salmon (P<0.05; r^2>0.995). The area bounded by this curve and $\dot{M}_{O_2routine}$, and by the time zero and the end of the U_{crit} test, represented the measured aerobic cost of swimming to U_{crit} (Table 2). The total oxygen cost of swimming to U_{crit} could then be calculated by adding EPOC to the measured aerobic oxygen, and assuming the non-aerobic oxygen cost of swimming to U_{crit} was equal to EPOC (see Brett, 1964). However, because total oxygen cost of swimming to U_{crit} is always relative to the duration of the U_{crit} test, we modeled the total oxygen cost of swimming by making the further assumption that it would increase exponentially with swimming speed (and therefore time, as shown by the broken curves in Fig. 2A–D). The exponential curves that modeled (P<0.05) the total oxygen cost of swimming to U_{crit} were derived by iterations (r^2>0.970) until the total oxygen cost of swimming to U_{crit} matched the measured aerobic oxygen such that EPOC and the non-aerobic oxygen cost differed by no more than 1.5% (Table 2). The curve for the total cost of swimming to U_{crit} could then be compared with the aerobic oxygen cost curve to derive the additional non-aerobic costs of swimming at a given speed. For example, the non-aerobic costs added an additional 24.1–50.5% to the $\dot{M}_{O_2max}$ measured at U_{crit} [GC=50.5%, CHE=24.5%, WVR (16°C)=26.0%, WVR (12°C)=24.1%].

Table 2. *Measurements and estimates of excess post-exercise oxygen consumption (EPOC) following a critical swim speed (*U_{crit}*) test for three stocks of adult Pacific salmon*

			Oxygen consumption (mg O_2 kg^{-1})			
			Measured		Modeled	
Species	Stock	Temperature (°C)	45 min EPOC*	Total aerobic cost of swimming to U_{crit}	EPOC†	Non-aerobic cost of swimming to U_{crit}
Sockeye	GC	17.5±0.3	254.2	1354.8	289.8	288.2 (0.6%)
Sockeye	WVR	16.0±0.2	104.6	401.8	86.2	87.0 (0.9%)
Sockeye	WVR	12.2±0.2	61.6	280.9	60.9	61.6 (1.1%)
Coho	CHE	7.9±0.6	66.7	364.5	67.4	66.4 (1.5%)

See text for details of analysis.

WVR, Weaver Creek sockeye salmon; CHE, Chehalis River coho salmon.

*EPOC measured during the 45 min recovery period.

†Total EPOC estimated by modeling the oxygen consumption recovery curve during the 45 min recovery period and extrapolating this curve when necessary to intersect the routine oxygen consumption.

Percentage values in parentheses represent the difference between the modeled estimate of EPOC and the total non-aerobic swimming cost of swimming to U_{crit}, derived from the total cost of swimming equation (see text for explanation).

The regression curves for both the total oxygen cost of swimming to U_{crit} and the measured aerobic oxygen cost shared the same data points below 50% U_{crit}, because Burgetz et al. (1998) suggested that rainbow trout can reach 70% U_{crit} without anaerobic swimming. These two curves, however, diverged from each other between 55 and 120 min into the U_{crit} test (Fig. 2), and these times corresponded to swimming speeds of between 0.86 BL s^{-1} and 1.30 BL s^{-1}, depending on the salmon stock. This transition to non-aerobic swimming occurred at between 59% and 62% U_{crit}. As a result, the non-aerobic cost of swimming increased the cost of transport (COT: Fig. 3A) and net cost of transport (COT$_{net}$: Fig. 3B) only at speeds above those associated with minimum cost of transport.

Effect of temperature on EPOC

The longest recovery time was associated with GC sockeye salmon, the salmon stock tested at the highest ambient water temperature and which reached the highest U_{crit} and $\dot{M}_{O_2max}$. EPOC varied exponentially with ambient water temperature (Fig. 4A) and U_{crit} (Fig. 4B) among the salmon stocks.

Discussion

This study is the first to measure EPOC and to estimate the total cost of swimming to U_{crit} among different stocks of adult, wild fish. A primary finding was that $\dot{M}_{O_2routine}$ was restored within approximately 1 h (ranging from 42 to 78 min) of adult salmon being exhausted at U_{crit}. Equally important is the finding that individual recovery performance of these adult, wild salmon was repeatable. These recovery times contrast with the much longer ones (3–6 h) reported for juvenile salmonids exhausted by either U_{crit} swimming or

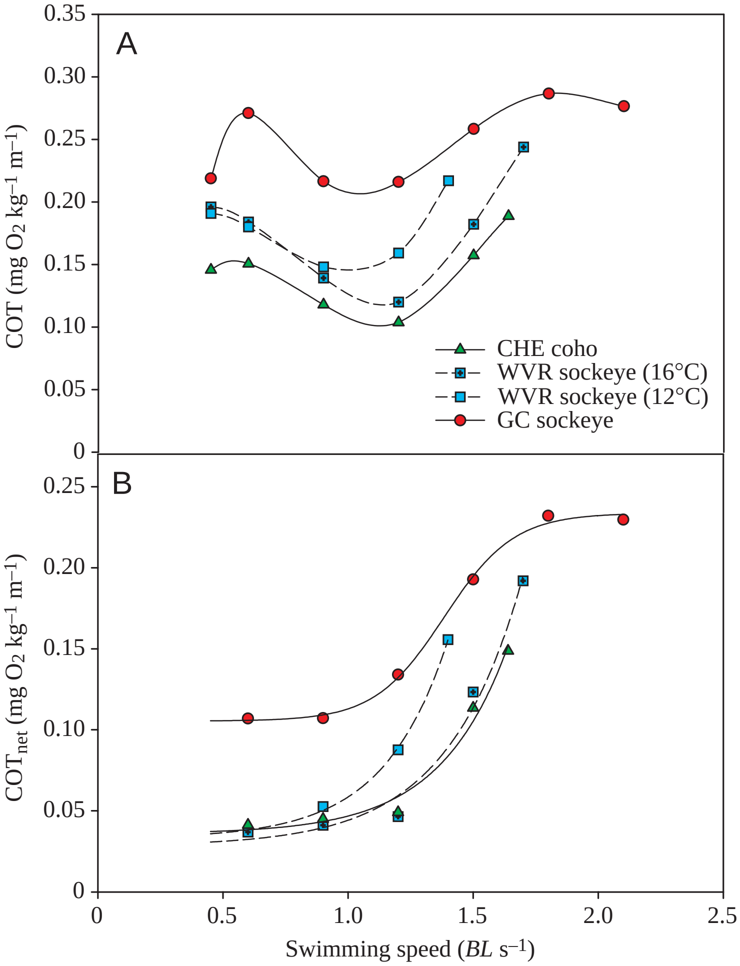

Fig. 3. Relationships between (A) cost of transport (COT) and (B) net cost of transport (COT$_{net}$) and swimming speed for three stocks of adult Pacific salmon using the total oxygen cost of swimming, calculated from $\dot{M}_{O_2}/U$. Net cost of transport was calculated from ($\dot{M}_{O_2}$–$\dot{M}_{O_2routine}$)/U and the values are based on those derived in Lee et al. (2003). For abbreviations, see Fig. 1.

chasing (Brett, 1964; Scarabello et al., 1992), but are more in line with the 1.5 h recovery time reported for adult Atlantic cod exhausted by either U_{crit} or burst swimming, as well as chasing (Reidy et al., 1995). While this finding adds weight to the possibility that adult fish have a shorter recovery time than juvenile salmonids, several caveats need to be considered.

The first caveat is that the shorter recovery time may reflect different rearing conditions among studies. Both the adult salmon used here and the Atlantic cod used by Reidy et al. (1995) were captured from wild stocks, whereas the earlier work on juvenile salmonids involved hatchery-raised stocks. Gamperl et al. (2002) showed that wild rainbow trout exhibit a level of aerobic fitness that is at least one-third greater than hatchery-raised individuals. This heightened aerobic fitness, presumably related to natural experiences of being exercised, may also favour a more rapid recovery rate. In addition, the practice swim prior to the U_{crit} test could have lowered EPOC, as seen earlier with juvenile rainbow trout (Scarabello et al., 1992). Scarabello et al. (1992) showed that chasing rainbow trout to exhaustion a second time, after a 6 h recovery period at 15°C, reduced recovery time to 2–3 h and almost halved EPOC to a value (252 mg O_2 kg^{-1}) that was in line with the EPOC for GC sockeye salmon at 18°C. Farlinger and Beamish (1977) similarly found that practice swims were beneficial for subsequent swimming performance. Adult, wild salmon may be naturally better aerobic swimmers with or without a practice swim because $\dot{M}_{\mathrm{O_2max}}$, EPOC and U_{crit} were the same for the first and second U_{crit}.

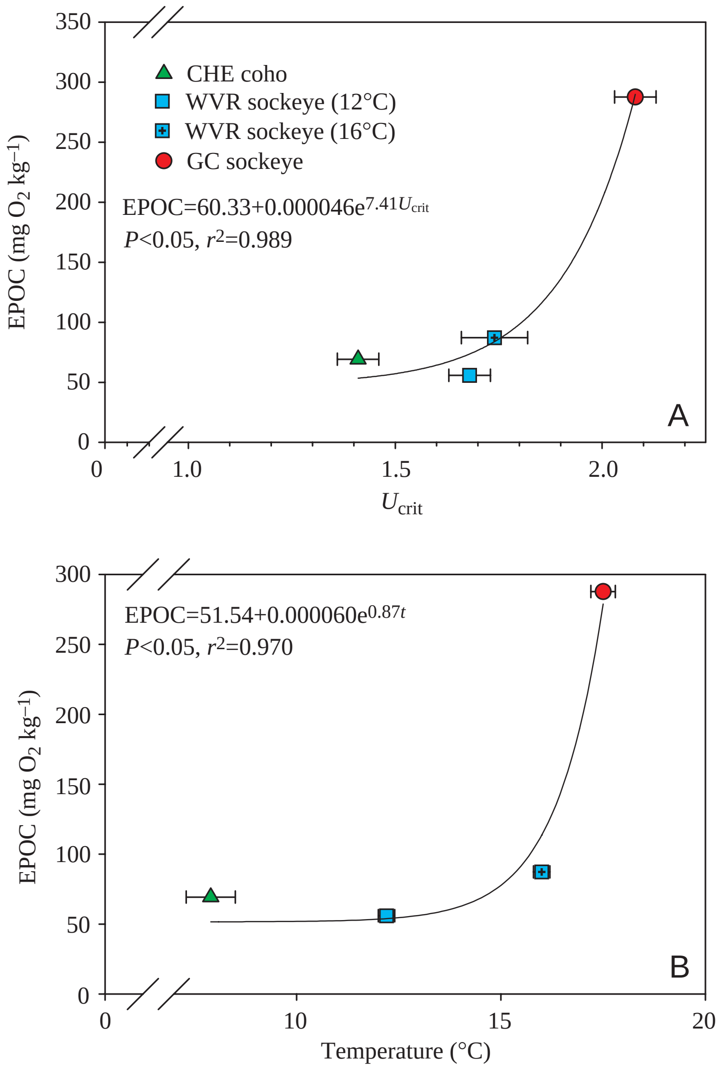

Fig. 4. Relationship among three stocks of adult Pacific salmon for post-exercise oxygen consumption (EPOC) and either (A) critical swimming speed (U_{crit}), or (B) ambient water temperature. For abbreviations, see Fig. 1.

A second caveat is that the short recovery times may reflect limited anaerobic swimming in adult, wild fish because they were either less willing or less able to do so. Our EPOC values, ranging from 55 to 290 mg O_2 kg^{-1} at temperatures between 8°C and 18°C, are lower than those either for U_{crit} tests with juvenile (33–63 g) sockeye salmon (252 mg O_2 kg^{-1} at 5°C to 504 mg O_2 kg^{-1} at 15°C; Brett, 1964) or for chased juvenile (6 g) rainbow trout (454 mg O_2 kg^{-1} at 15°C; Scarabello et al., 1992). We did not establish the level of anaerobic effort by measuring lactate concentration in either muscle or blood, for a variety of reasons. Some of the fish had to be returned to the stream to spawn and this precluded invasive experiments. In any event, opening up the swim tunnel to obtain a muscle sample would have precluded accurate measurements of $\dot{M}_{\mathrm{O_2}}$ during the recovery period, and would have jeopardized the second swim. Furthermore, plasma lactate does not peak until about 1 h after exhaustion, i.e. after EPOC had subsided, and lactate release from tissue into the blood is suppressed by moderate swimming during recovery, since plasma lactate increases by only 2–7 mmol l^{-1} *versus* 12–25 mmol l^{-1} (Milligan et al., 2000; Farrell et al., 2001a). Nevertheless, we have previously swum adult, wild sockeye salmon and found appreciable increases in plasma lactate concentrations both at U_{crit} and during recovery (3–4 mmol l^{-1}) (Farrell et al., 1998), even with the fish swimming to a lower U_{crit} and $\dot{M}_{\mathrm{O_2max}}$ than in the present study. In view of this, we feel that the burst-and-coast swimming gait observed in the present study when the fish approached U_{crit} reflected a substantial contribution of anaerobic swimming. In fact, the unusual plateau in the $\dot{M}_{\mathrm{O_2}}$ *versus* swimming speed curve for GC sockeye salmon can only be explained by an unusually high anaerobic effort as the fish approached U_{crit}.

It is very unlikely that adult, wild salmon are incapable of high levels of anaerobic effort when forced to do so. In fact, the opposite is more likely, because both Pacific and Atlantic adult salmon can become even more severely exhausted than hatchery-raised rainbow trout, as judged by higher muscle lactate levels after capture by either angling or commercial fisheries (Wilkie et al., 1997; Farrell et al., 2001a,b). Nevertheless, wild salmon naturally cease feeding and, because these salmon had stopped feeding up to 3 weeks prior to the experiments, we cannot eliminate the possibility that dwindling energy stores could have limited anaerobic effort to some degree. However, while a 5 day starvation period has been shown to decrease total body glycogen stores and the accumulation of muscle lactate at exhaustion, it had no effect on EPOC (Scarabello et al., 1991).

The third caveat is that we may have underestimated both EPOC and recovery time because of an elevated $\dot{M}_{O_2\mathrm{routine}}$. Earlier Brett (1964) obtained a ‘minimum’ $\dot{M}_{O_2\mathrm{routine}}$ by omitting any fish exhibiting ‘restless behaviors’. While we ensured that fish were undisturbed when $\dot{M}_{O_2\mathrm{routine}}$ was measured, no attempt was made to identify ‘outliers’. Even so, our $\dot{M}_{O_2\mathrm{routine}}$ values (2.47–$4.35\,\mathrm{mg\,O_2\,min^{-1}\,kg^{-1}}$; Table 1) were in the range of previous estimates (1.21–$2.92\,\mathrm{mg\,O_2\,min^{-1}\,kg^{-1}}$; Brett, 1964; $3.36\,\mathrm{mg\,O_2\,min^{-1}\,kg^{-1}}$, Scarabello et al., 1991), and so the error due to an elevated $\dot{M}_{O_2\mathrm{routine}}$ cannot be large. Furthermore, if our measurement of $\dot{M}_{O_2\mathrm{routine}}$ was problematic, then a lower EPOC would be associated with a higher $\dot{M}_{O_2\mathrm{routine}}$. This was not the case for GC sockeye salmon, which had the highest $\dot{M}_{O_2\mathrm{routine}}$ as well as the highest EPOC.

Our data concur with those of Brett (1964) for juvenile sockeye salmon, who showed that EPOC and U_{crit} were directly related to water temperature. This conclusion is consistent with the plateau observed for the $\dot{M}_{O_2}$ curve for GC sockeye salmon, which is most likely to be due to a greater anaerobic effort of white muscle fibres at a higher temperature (Kieffer et al., 1994; Wilkie et al., 1997). However, unlike Brett (1964), we found that a larger EPOC was associated with a longer recovery time. A longer recovery rate at warmer temperatures is inconsistent with the faster recovery rates reported for muscle ATP and glycogen in rainbow trout and Atlantic salmon (Kieffer et al., 1994; Wilkie et al., 1997).

Electromyography has shown that white muscle fibre recruitment in cyprinids occurs at 80% U_{crit} (e.g. Rome et al., 1984). In rainbow trout, accumulation of muscle lactate became a statistically significant oxygen cost at 80% U_{crit}, and though not statistically significant, the oxygen cost at 70% U_{crit} was 24% above routine (Burgetz et al., 1998). We estimated that EPOC began to contribute to the oxygen cost of swimming at 59–62% U_{crit}. This lower transition speed compared with that for an anaerobic swimming gait may be related to disruptions, other than anaerobic swimming, that contribute to EPOC (Scarabello et al., 1992). For example, the so-called ‘osmo-respiratory compromise’ during exercise (Randall et al., 1972; Nilsson, 1986), almost doubles with exercise, with one sodium ion being lost across the gills for every five molecules of oxygen taken up *versus* one sodium ion being lost for every eight molecules of oxygen at rest (Gonzalez and MacDonald, 1992). Our modeling, however, does not support the idea that this type of ionic disruption may add up to 20% to the net oxygen cost of swimming (Febry and Lutz, 1987), because maximally the non-aerobic oxygen cost of swimming added only 24–51% to $\dot{M}_{O_2}$ (Table 2). By comparison, Burgetz et al. (1998) predicted that anaerobic swimming alone added a 79% oxygen cost at U_{crit}, based on a conversion of whole body lactate to an oxygen equivalent in hatchery raised rainbow trout. Despite these differences among studies, it is important to note that the non-aerobic costs of swimming in adult salmon had apparently very little consequence for the minimum cost of transport (Fig. 4).

We are unaware of comparable information on adult, wild salmon that would allow EPOC to be incorporated into an ecologically relevant estimate of the total oxygen cost of locomotory activity during adult salmon migrations. Nevertheless, an understanding of the energetic costs of anaerobic swimming is critical to our understanding of the migration ecology and management of Pacific salmon. Adult Pacific salmon do not feed during their up-river migration; they must fuel swimming, maturation of gonads and spawning behaviours from energy stores, and use bouts of anaerobic swimming (Hinch et al., 2002). Rand and Hinch (1998) developed a bioenergetics model to predict energy depletion, and the associated risk of energy exhaustion and premature mortality for up-river migrating Early Stuart sockeye salmon, to help fisheries managers who make decisions about whether fisheries should be opened or closed. Their model assumed that anaerobic swimming was 15% more expensive than aerobic swimming. The present study clearly shows that this is a significant underestimate (up to three times) of the true relationship. Anaerobic swimming is thus much more critical to the energy budgets of sockeye salmon than was previously thought and this fact must be recognized by fisheries managers who assess the impacts of changing river flows and temperatures on energy use and hence migration success.

In summary, we have provided the first measurements of EPOC and estimates of the total cost of swimming to U_{crit} among different stocks of adult, wild salmon. While EPOC varied among fish stocks, $\dot{M}_{O_2\mathrm{routine}}$ was always restored within approximately 1 h. Potential explanations for the shorter recovery times and lower EPOC values for adult, wild salmon compared with juvenile, hatchery-reared salmonids are presented. EPOC was estimated to add 24.1–50.5% to the $\dot{M}_{O_2\mathrm{max}}$ measured at U_{crit}, depending on the species, and because this cost can be three times as high as that used for energetic modeling of salmon migration up-river, these energetic models may have to be revisited.

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