

Physiological, energetic and behavioural correlates of successful fishway passage of adult sockeye salmon *Oncorhynchus nerka* in the Seton River, British Columbia

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Electromyogram (EMG) radio telemetry was used in conjunction with physiological biopsy to relate prior physiological condition and subsequent swimming energetics and behaviours to passage success of 13 wild adult sockeye salmon *Oncorhynchus nerka* at a vertical-slot fishway on the Seton River, British Columbia. At the time of capture, plasma lactate, glucose and cortisol levels indicated that fish were not exhibiting unusually high levels of physiological stress. Very few differences existed between successful and unsuccessful fish in body size, initial plasma physiology and energy state and mean swim speed and energy use during passage. Generally, fish did not employ burst swimming during successful or failed attempts at passage, indicating that failure was probably not related to metabolic acidosis. Plasma Na⁺ concentration was significantly lower in unsuccessful fish ($P < 0.05$), which is suggestive of a depressed ionic state or a possible stress component, although values in all fish were within an expected range for migrant adult *O. nerka*. Nevertheless, six of 13 fish failed to reascend the fishway and remained in the tailrace of the dam for more than a day on average before moving downstream and away from the dam. During this time, fish were observed actively seeking a means of passage, suggesting that there may have been other, undetermined causes of passage failure.

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INTRODUCTION

Reproductive migrations of anadromous adult Pacific salmon *Oncorhynchus* spp. from ocean feeding grounds to natal freshwater streams are physiologically

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challenging and energetically demanding, particularly for populations that must travel long distances or pass through hydraulically complex reaches en route to spawning locations (Bernatchez & Dodson, 1987; Hinch *et al.*, 2006). Adult *Oncorhynchus* spp. bound for spawning grounds stop feeding prior to entering fresh water and rely exclusively on energy reserves to reach spawning grounds, complete sexual maturation and engage in spawning events (Brett, 1995). Because *Oncorhynchus* spp. are semelparous (*i.e.* die following reproduction), the ability to successfully reach spawning grounds with adequate energy reserves to complete gonad development and engage in spawning activities is imperative to their lifetime fitness.

Anthropogenic migration barriers have dramatically reduced the number and size of salmonid populations by making migration routes impassable or hindering *Oncorhynchus* spp. from reaching terminal spawning grounds (Nehlsen *et al.*, 1991; Slaney *et al.*, 1996). To mitigate this problem, fishways (or fish ladders) are often constructed to facilitate migrations past dams and other sites where passage has been obstructed by human activities (Clay, 1961). Nevertheless, segments of populations of migrating fishes are unable to pass despite the presence of a fishway. Estimates of passage failure among salmonids at dams along the Columbia River, U.S.A., generally range from 2 to 10% (Keefer *et al.*, 2007). At Hells Gate rapids on the Fraser River in Canada, 25% of tagged adult sockeye salmon *Oncorhynchus nerka* (Walbaum) were unable to enter and pass through fishways (Hinch & Bratty, 2000), and up to 37% of adult Atlantic salmon *Salmo salar* L. failed to pass through fishways on the River Conon system in Northern Scotland (Gowans *et al.*, 2003). In some cases, fishways may present velocity barriers to passage (Castro-Santos, 2005), but few studies have documented the scope of this issue, and such observations raise the question of why some adult migrants can successfully ascend fishways, while others are unsuccessful.

Hinch & Bratty (2000) observed differences between successful and unsuccessful adult *O. nerka* migrating through the Hells Gate rapids and fishway in the Fraser River using electromyogram (EMG) telemetry and behavioural observations. Unsuccessful fish were characterized by repeated attempts to enter the fishway, extended periods (*i.e.* several hours) of bursting to swimming speeds beyond critical swim speeds (U_{crit} ; *i.e.* anaerobic metabolism), and were frequently observed swimming in areas of relatively higher water velocity and turbulence in the approach to the fishway. In contrast, the successful fish entered the fishway upon first attempt, spent relatively little time swimming at fast speeds and swam in areas where water velocity was slower. Hinch & Bratty (2000) suggested that failure to pass into and through the Hells Gate fishway may have been related to elevated physiological stress and physical exhaustion in fish, which chose to migrate in fast and turbulent flows. Interestingly, some species of fishes are able to successfully migrate through fast flows using very slow swim speeds by utilizing reverse flow fields, boundary layers and other behavioural tactics (Hinch *et al.*, 2002; Liao *et al.*, 2003). There have been no studies, however, to assess how physiological condition may affect the behavioural tactics used in and around fishways with fast or turbulent flows.

Recent biopsy-telemetry studies in the main stem of the Fraser River found that *O. nerka* that failed to reach spawning grounds had higher physiological

stress levels as indicated by elevated plasma lactate, glucose and plasma ions compared with fish that successfully reached spawning grounds (Cooke *et al.*, 2006; Young *et al.*, 2006). Thus, hydraulically challenging sections of rivers and fish passage structures may not only cause physiological exhaustion and stress but also act as bottlenecks for migrating fishes, specifically selecting against fishes that already have relatively higher levels of physiological stress. This is perhaps not an unexpected finding given a much larger data base for laboratory studies, which clearly show that fishes swimming at speeds in excess of U_{crit} for extended periods of time will experience physiological stress (Black *et al.*, 1962; Wood, 1991). Minimally, this type of exhaustive exercise impairs subsequent swimming capabilities and necessitates long recovery periods from exhaustion (Stevens & Black, 1966; Peake & Farrell, 2004). Thus, the ability to migrate through hydraulically fast and complex riverine areas, such as those near and in fishways, may be compromised in individuals that become physiologically exhausted and stressed (Hinch *et al.*, 2006).

The present study investigated the linkage between physiological condition, energetics and swimming behaviour and the ability of migrating adult *O. nerka* to successfully pass through a vertical-slot fishway en route to spawning grounds. EMG radio telemetry was used in combination with biopsy sampling to obtain tissue samples for physiological analysis (Cooke *et al.*, 2005) to test two predictions: (1) that *O. nerka* which successfully ascend a fishway are characterized by lower levels of physiological stress relative to fish that are unsuccessful in ascending and (2) that successful migrants display much lower swim speeds and consequently exhibit lower energy use than unsuccessful migrants.

MATERIALS AND METHODS

STUDY SITE

The study was conducted at a vertical-slot fishway at the Seton River dam (50°40' N; 121°58' W), c. 5 km south-west of Lillooet, British Columbia, Canada. The fishway consists of 32 pools separated by concrete baffles and makes two 180° turns and thus has two primary corner resting pools (Fig. 1). The fishway is 107 m long, with an elevation of 7.4 m, creating an effective slope of 6.9%. Maximum water discharge in the fishway can reach 1.3 m³ s⁻¹, and water velocities can range from negligible to 2.1 m s⁻¹ due to the complex nature of flow. Water flow-through the fishway is determined by the fore-bay head and is unregulated but was at a consistent height throughout the study period.

The present study focused on *O. nerka* bound for the Gates Creek spawning channel. Gates Creek fish are classified as an 'early summer-run' Fraser River stock, with upriver migrations taking place between late July and early September. To reach the dam and fishway, *O. nerka* have already travelled c. 350 river km upstream from the mouth of the Fraser River. Upstream of the Seton Dam, Gates Creek fish must travel a further 50 km through Seton and Anderson Lakes in order to reach spawning areas.

FISH CAPTURE, BIOPSY SAMPLING AND TAGGING

Thirteen adult *O. nerka* were captured by dip-net at the top pool of the fishway (Fig. 1) as they migrated upstream during the period of 11 to 28 August 2005 at the Seton Dam. This location was selected because fish could be captured quickly and

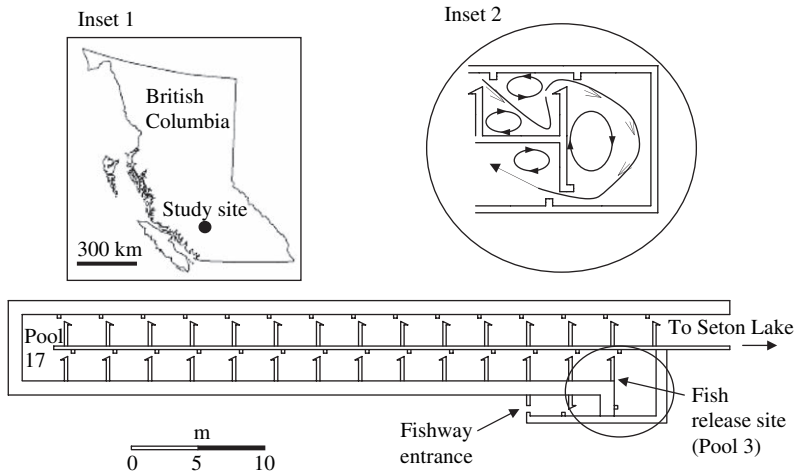


FIG. 1. Schematic of the Seton River fishway layout. Tagged fish were released in a low-velocity area within pool number three as indicated by the arrow. Fish movements were tracked by hand from the catwalk running the length of the fishway. Inset 1 shows the general location of the study site in British Columbia, Canada. Inset 2 details a generalized pattern of the flow within each of the two representative pool types found in the Seton Dam fishway.

consistently throughout the study period. Capture occurred quickly (<10 s), minimized the amount of time between capture and biopsy and minimized handling-induced alterations to the physiological variables that were measured (although it was recognized that capture created a response that was not measured). Fish were caught individually and immediately transferred (<10 s of net handling and air exposure) from the net to a foam-padded, V-shaped trough, which was continually supplied with fresh Seton River water directed through a tube aimed at the mouth of the fish. Once in the trough, fish were completely submerged in water and were only partially raised out for the biopsy procedures. Each fish was restrained in the trough by two people with bare, wet hands, while a third immediately sampled tissues. The biopsy sampling process included several procedures that have previously been validated as having no demonstrable effects on survival or migration rates of adult *O. nerka* released back to the ocean (Cooke *et al.*, 2005).

Blood (1.5 ml) was drawn from the caudal vein just posterior to the anal fin using a Vacutainer syringe [1.5" 21 gauge needle, 3 ml lithium heparin (Vacutainer; Becton Dickson & Co.; www.bd.com)] following the procedures outlined in Cooke *et al.* (2005). Fish were excluded from the study and released upstream of the dam if blood was not successfully drawn after 60 s. Fork length (L_F) was measured to the nearest 5 mm. Following these procedures (generally <1 min), the fish was gently transferred to an 80 l anaesthetic bath of MS-222 (tricaine methanesulphonate) (65 mg l^{-1}) buffered with CaCO_3 (65 mg l^{-1}) in preparation for surgical tag implantation. Once the fish was sedated, somatic lipid concentration was assessed using a microwave energy meter (Distell fish fatmeter, model 692; Distell Inc., Bath gate, West Lothian, Scotland, U.K.) following the procedure outlined in Crossin & Hinch (2005). A uniquely coded cinch tag (Floy Manufacturing; www.floytag.com) was attached to the anterior of the dorsal fin of the fully anaesthetized fish for external recognition purposes before the fish was transferred to the surgery trough where buffered anaesthetic ($30 \text{ mg MS-222 l}^{-1}$) was pumped through tubes inserted into the oral cavity and out across the gills of the fish to maintain an anaesthetized state.

Non-coded EMG transmitters (cylindrically shaped, 53 mm length, 16 mm diameter and 18.5 g mass and were equipped with 16 mm, 9 carat gold tips; Lotek Engineering;

www.lotek.com) were implanted followed techniques described in Hinch *et al.* (1996). Further descriptions of EMG transmitters can be found in Cooke *et al.* (2004). Following surgery, the fish was transferred to a 100 l recovery tank equipped with a constant flow of fresh water. The entire surgical procedure took 5–6 min to complete.

Fish were held in recovery for *c.* 2 h during which time, they were monitored for signs of recovery. This period of time was deemed adequate for recovery based on observations of regained equilibrium and increasing restlessness within the recovery tank. Following recovery, fish were released near the bottom of the fishway in pool number 3 (Fig. 1). This particular release site represented one of two pools within the fishway that turned 180° and was chosen because it had relatively large areas of low-flow velocities compared to the other pools near the downstream end of the fishway. To minimize the chance of disoriented fish being immediately flushed out of the fishway following release, fish were specifically released into a section of the pool where flow velocity was minimal (see inset Fig. 1). This provided a common challenge metric for all fish and eliminated variability associated with fish attempting to locate the fishway entrance. Fish were lowered to the water using a knotless nylon-lined basket that was wetted prior to introducing the fish. Air exposure immediately prior to release was <10 s. All procedures were approved by the UBC Animal Care Committee in accordance with the policies of the Canadian Council on Animal Care.

Immediately after release, fish were tracked by hand throughout the fishway using data-logging receivers (Lotek model SRX_400) equipped with hand-held three-element Yagi antennas. Because all fish were manually tracked, the detailed movements of fish were closely followed with a high degree of precision to accurately describe specific movements such as forays into adjacent pools within the fishway structure. Fish were classified as either 'successful' if they ascended and exited the upstream end of the fishway or 'unsuccessful' if they did not reascend the fishway and fell back out of the fishway entrance into the tailrace of the dam. All fish were continuously tracked while in the fishway structure until they either reached the top pool of the fishway or moved downstream and into the dam tailrace.

PHYSIOLOGICAL ASSAYS

A small amount of the blood sample was transferred from the Vacutainer to a capillary tube to determine haematocrit (Hct). The balance of the blood sample was centrifuged and plasma was transferred into three separate 0.8 ml containers and locally stored on dry ice until they could be transferred to a –80° C freezer. Plasma ion concentrations (Na⁺, K⁺ and Cl⁻) and osmolality were measured following the procedures outlined in Farrell *et al.* (2001). Plasma lactate and glucose levels were measured using a YSI 2300 lactate/glucose analyser (Yellow Springs Instruments; www.ysi.com). Cortisol concentrations were measured in duplicate using 96-well enzyme-linked immunosorbent assay (ELISA) kits (Neogen Corp.; www.neogen.com). 17β-oestradiol (E2) was measured using heat extraction methods described in Scott *et al.* (1983) and 96-well ELISA kits (Carey & McCormick, 1998) and were used to assign sex to individual fish. E2 measurements were compared with those from another set of Gates Creek *O. nerka* caught in 2005, for which sex was confirmed, with females generally having E2 values >1.0 ng ml⁻¹ (J. Hills, pers. comm.).

DATA ANALYSIS AND STATISTICS

All recorded EMG pulse interval data were converted into instantaneous swim speeds (mm s⁻¹) following equations developed from the relationship between EMG pulse intervals and swim speeds, which are described in Hinch & Rand (1998). Using swim speed (mm s⁻¹), temperature (° C) and fish mass (g) data, energy use (J g⁻¹ h⁻¹) was estimated following the equation described in Healey *et al.* (2003). Because individual mass of study animals was not measured, it was estimated using sex-specific regressions developed from L_F and mass (M) data collected from other Gates Creek *O. nerka*

captured at Seton Dam in August 2005 (unpubl. data). L_F and M regression equations were developed for males: $M = 8.430L_F - 2871.3$ ($r^2 = 0.830$, $n = 18$) and for females: $M = 11.747L_F - 4835.6$ ($r^2 = 0.874$; $n = 21$). Exploratory analysis of the data revealed no differences between sexes (all physiological variables, swim speed and energy use) so sexes were pooled for subsequent analysis. This observation is generally consistent with previous studies on migrating adult *O. nerka* where sex-related differences have only been found in hormone levels and measurements of gross somatic energy (GSE) taken at early stages in the migration (Cooke *et al.*, 2006; Young *et al.*, 2006).

To examine the prediction that passage success was related to initial physiological condition, plasma metabolites, ion concentrations, cortisol, GSE and Hct were compared using a series of one-way ANOVA with fate (*i.e.* successful or unsuccessful) as the effect. To examine the predictions that energetics, swimming behaviour or swimming strategy affected fish fate, average individual swim speeds, energy use and duration of residency in the release pool were compared among successful and unsuccessful fish using a series of one-way ANOVAs. Fish size (*e.g.* L_F) was also compared among successful and unsuccessful fish using ANOVA. Due to low sample sizes, power analyses were conducted for all comparisons. All statistical analyses were conducted using SAS v. 9.1 (SAS Institute; www.sas.com). Results are reported for significance at $\alpha = 0.05$, with sequential Bonferroni corrections applied to groupings of statistical comparisons relevant to each prediction. Bonferroni corrections can be highly conservative where many variables are compared, so uncorrected P -values are also presented, allowing the reader to perform their own assessment of significance criteria (Moran, 2003).

RESULTS

Of the 13 tagged fish, seven successfully reascended the fishway. Of those, EMG recordings of passage were made for all but one whose transmitter was not functioning correctly. Six fish were unsuccessful in reascending the fishway, and all eventually fell back out of the fishway and into the tailrace area. All but one of the unsuccessful fish were able to maintain position within pool 3 for at least 7 min following release, and all fish were observed actively swimming in the vicinity of the entrance to pool 4, suggesting that fish were indeed attempting to move up the fishway. After falling back from the fishway, unsuccessful fish were observed to remain in the tailrace for 36.6 ± 14.4 h (mean \pm s.e.), and during this time, fish appeared to be attempting to find a means of upstream passage by swimming in turbulent water discharged from the dam near the fishway entrance. No difference in L_F was found between successful and unsuccessful fish (ANOVA, d.f. = 6,5, $P > 0.05$). Sample sizes were too small to statistically assess for sex-related effects on passage success (successful fish: four females and three males; unsuccessful fish: two females and four males).

The average residency time spent at the release site (pool 3) prior to moving either up the fishway or falling back downstream was similar between successful and unsuccessful fish (ANOVA, d.f. = 5,4, $P > 0.05$) as was mean swim speed (ANOVA, d.f. = 5,4, $P > 0.05$) and mean energy expenditure (ANOVA, d.f. = 5,4, $P > 0.05$) (Table I). Mean individual swim speeds varied substantially for both successful fish and unsuccessful fish during observation in pool 3 (Fig. 2). This variability may be explained in part by the degree to which a fish was able to take advantage of low-velocity areas within the fishway. Some fish [Fig. 2 (b), (c), (e)] appeared to hold in low-velocity areas, as evidenced by very low swim speeds, until attempting to move up the fishway.

In contrast, other fish appeared to swim in the stronger currents and employed frequent bursts of swimming effort to maintain their position and avoid being washed down the fishway [Fig. 2 (a), (f), (h)].

Physiological measures revealed few statistical differences between successful and unsuccessful fish (Table I), but statistical power was generally low for all comparisons ranging from 0.05 to 0.69. Even so, unsuccessful fish had lower plasma concentrations of Na^+ ions than successful fish (mean \pm s.e.: 143.33 ± 1.54 and 149.64 ± 1.74 mmol l^{-1} , respectively; ANOVA, d.f. = 6,5, $P < 0.01$; this was not significant under Bonferroni correction). No differences were

TABLE I. Summary of the one-way ANOVAs performed on physiological measurements taken from successful (pass) and unsuccessful (fallback) fish, as well as swim speed, energy use, residency time in pool 3 and fork length (L_F). Data are shown as mean \pm s.e. Statistical significance was assessed with a Bonferroni corrected $\alpha = 0.05$; for stress $\alpha = 0.006$ (lactate, glucose, cortisol, ions and haematocrit), for fish condition $\alpha = 0.025$ (gross somatic energy and L_F) and for swim behaviour $\alpha = 0.02$ (swim speed, energy use and time in release pool). No significant differences were found after Bonferroni corrections were applied; however, uncorrected significant P -values are denoted by †. *Measurements were \log_{10} -transformed prior to analysis but pre-transformed means and s.e. are presented

Measurement	Fate	Mean \pm s.e.	n	Statistical output		
				F	P	Power
Plasma lactate (mmol l^{-1})	Pass	1.83 ± 0.32	7	1.23	0.29	0.16
	Fallback	2.75 ± 0.81	6			
Plasma glucose (mmol l^{-1})	Pass	4.66 ± 0.30	7	<0.01	0.98	0.05
	Fallback	4.68 ± 0.53	6			
*Plasma cortisol (ng ml^{-1})	Pass	219.38 ± 64.11	7	0.29	0.60	0.06
	Fallback	240.94 ± 49.20	6			
Plasma [Na^+] (mmol l^{-1})	Pass	149.64 ± 1.74	7	7.12	0.02†	0.69
	Fallback	143.33 ± 1.54	6			
Plasma [Cl^-] (mmol l^{-1})	Pass	140.09 ± 0.88	7	2.44	0.15	0.30
	Fallback	135.49 ± 3.04	6			
Plasma [K^+] (mmol l^{-1})	Pass	2.91 ± 0.22	7	1.22	0.29	0.18
	Fallback	3.31 ± 0.29	6			
Osmolality (mosmol l^{-1})	Pass	306.21 ± 1.92	7	2.11	0.17	0.28
	Fallback	300.00 ± 4.06	6			
Haematocrit (%)	Pass	40.57 ± 1.13	7	0.15	0.71	0.07
	Fallback	40.00 ± 0.93	6			
Gross somatic energy (MJ kg^{-1})	Pass	6.49 ± 0.27	7	0.46	0.51	0.09
	Fallback	6.79 ± 0.37	6			
L_F (mm)	Pass	581.4 ± 10.00	7	0.18	0.68	0.07
	Fallback	586.7 ± 6.10	6			
*Swim speed (mm s^{-1})	Pass	292.7 ± 130.30	6	0.25	0.63	0.27
	Fallback	101.8 ± 21.40	5			
*Energy use rate ($\text{J g}^{-1} \text{h}^{-1}$)	Pass	3.35 ± 1.55	6	0.69	0.43	0.28
	Fallback	1.30 ± 0.29	5			
Time in release pool (min)	Pass	11.41 ± 2.88	6	0.24	0.64	0.07
	Fallback	13.66 ± 3.71	5			

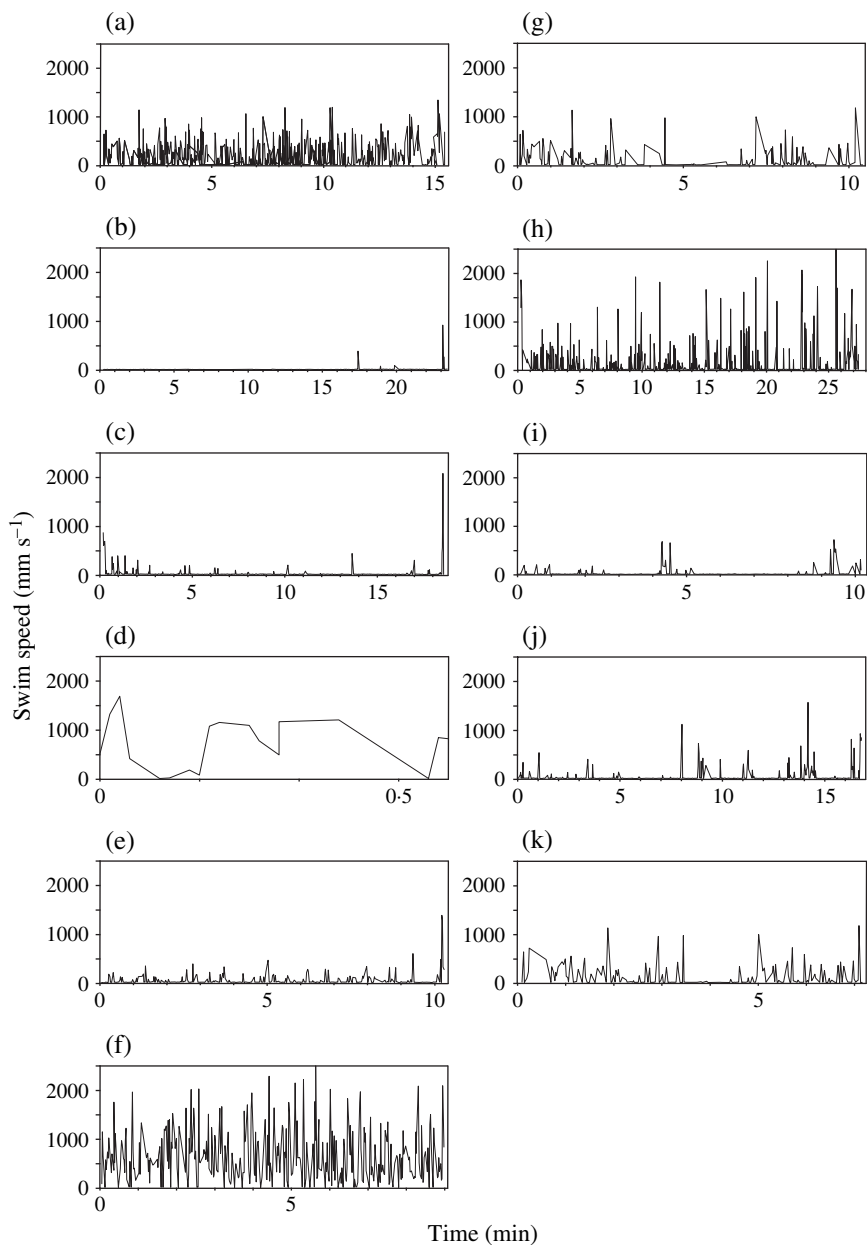


FIG. 2. Plots of instantaneous swim speed estimates from EMG pulse interval data contrasting (a)–(f) successful fish and (g)–(k) unsuccessful fish. Each graph represents the total time spent at the release site (*i.e.* pool 3) prior to upstream or downstream movement. Note that the *x*-axes vary among individual graphs.

detected between unsuccessful and successful fish for plasma osmolality and other plasma ions (K^+ and Cl^-), lactate, glucose and cortisol concentrations, gross somatic energy content and Hct (all ANOVA, d.f. = 6,5, $P > 0.05$; Table I).

Power analyses typically revealed low power levels for all statistical tests (Table I).

DISCUSSION

Although 46% of tagged and biopsied *O. nerka* were unable to reascend the fishway, few differences were found in support of a mechanism behind passage failure. Though stress was postulated as a potential factor, only plasma Na^+ concentrations differed between successful and unsuccessful fish. No other differences were observed among the suite of physiological variables measured. The original prediction that lower swim speeds and energy use would favour successful ascent was made on the basis that exercise-related fatigue was less likely to occur among these fish. No differences in these metrics, however, were observed among successful and unsuccessful fish.

During the present study, river temperatures were quite favourable to migrant *O. nerka*, with Seton River water (16.3°C) nearly identical to the optimal temperature for aerobic scope in adult Gates Creek *O. nerka* (*i.e.* 16.5°C ; Lee *et al.*, 2003). These conditions were probably reflected in the measurements of physiological stress. Specifically, plasma glucose levels were similar and lactate levels lower than values reported from migrant adult Adams River *O. nerka*, which were similarly intercepted and biopsied in 2003; a year when river temperatures were slightly warmer than average (Young *et al.*, 2006). More specifically, the average lactate levels observed in the present study were closer to 'routine levels' (*c.* 2 mmol l^{-1}) derived from laboratory-held adult *O. nerka* than measurements made after these same fish swam to U_{crit} test speeds (*c.* 6 mmol l^{-1}) (Wagner *et al.*, 2006). Plasma cortisol results were within the range of values from previous biopsy results for other Fraser River *O. nerka* stocks sampled near terminal spawning grounds (Crossin *et al.*, 2008) as were Hct levels (Magnoni *et al.*, 2006). Generally, plasma ion concentrations were similar to previously reported values for migrant adult *O. nerka* (Crossin *et al.*, 2008), although these values tend to naturally decrease over the course of freshwater migration and therefore may be difficult to compare across stocks (Shrimpton *et al.*, 2005). Thus, the physiological state of adult Gates Creek *O. nerka* in 2005 seemed to be consistent with that of other stocks of migrating Fraser River fish in other years when environmental conditions were not unusual and was indicative of migrants with low levels of physiological stress related to exhaustive exercise.

Nevertheless, the lower concentrations of Na^+ observed in unsuccessful fish may indicate some degree of stress in these animals, and while not significant, similar trends in Cl^- and osmolality corroborated a depressed ionic condition. Deviations from baseline ion values can be related to previous 'stressful' conditions or significant exercise and may persist over a period of 8–12 h, though this may be extended under chronic exposure to unfavourable conditions (Postlethwaite & McDonald, 1995; McDonald & Milligan, 1997). Given the lack of strong differences between successful and unsuccessful fish in the non-ionic stress indicators, the ion results are probably indicative of recent migration experience leading up to capture (*i.e.* migration towards the dam and initial passage through the fishway).

Stress and exercise can cause a net loss of ions primarily *via* an elevated brachial efflux associated with elevated circulating catecholamines in fishes (Wood & Randall, 1973; McDonald & Milligan, 1997). Plasma ion concentrations tend to decrease following aerobic exercise (Postlethwaite & McDonald, 1995), though they may increase following anaerobic exercise (Graham *et al.*, 1982; Wood, 1991). Swim speed data, however, revealed little evidence of continuous anaerobic swimming activity associated with fishway ascent or during efforts made in the tailrace area. If the fish's first ascent of the fishway had involved similar swimming behaviours, the expectation would be that any stress-related or exercise-related ion fluctuations associated with *O. nerka* migrating past the Seton Dam would not have been excessive or related to anaerobic exercise, and likely to decrease ion concentrations, which is consistent with the observed values. There is the expectation that an ionic imbalance can contribute to the inability of fish to reascend the fishway as ion imbalances are generally thought to hinder swimming performance by reducing the scope for activity (Barton & Schreck, 1987). Swimming performance metrics such as U_{crit} have been shown to vary with plasma Na^+ concentrations, with optimal U_{crit} occurring at 147 mEq l^{-1} in experiments with freshwater salmonids (Randall & Brauner, 1991; Brauner *et al.*, 1992). In the present study, plasma Na^+ concentrations were close to this optimum in successful fish.

Many studies have examined fish moving past hydraulically challenging areas (Gowans *et al.*, 2003; Brown *et al.*, 2006), but only Hinch & Bratty (2000), who had sample sizes similar to the present study, have documented differences between successful and unsuccessful fish. Unlike their study, however, no difference in mean swim speed was detected between successful and unsuccessful migrants at the Seton fishway. This discrepancy may reflect the substantially lower maximum water velocities of $c. 2 \text{ m s}^{-1}$ in the Seton River fishway compared with average surface velocities of 6 m s^{-1} (Hinch & Bratty, 2000). The lower water velocities in the Seton River fishway may have necessitated less anaerobic swimming, which is generally needed at speeds exceeding 60–70% of the individuals' U_{crit} (Lee *et al.*, 2003). For Gates Creek *O. nerka*, anaerobic activity would be invoked at speeds $>930 \text{ mm s}^{-1}$ based on U_{crit} estimates of Lee *et al.* (2003), but fish were rarely observed continually swimming at speeds above this value while ascending the fishway. Indeed, the observation of oscillating swim speeds suggested that many fish appeared to employ a burst-coast swim pattern, which has been previously observed in migrating *O. nerka* (Hinch *et al.*, 2002). This behaviour may partially explain the relatively low mean swim speeds, which translated into similarly low mean energy use rates during residency in pool 3. In fact, energy use rates were lower than those calculated for upriver migration of other Fraser River *O. nerka* stocks with similar migration distances to Gates Creek *O. nerka* (Brett, 1995). As these stocks begin upriver migration with $c. 8.3 \text{ MJ kg}^{-1}$ of somatic energy (Crossin *et al.*, 2004) and can consume $>50\%$ of this during their migrations (Brett, 1995), it is unlikely that passage through the Seton Dam fishway would result in energetic exhaustion.

Other studies examining adult *O. nerka* passing through the Seton Dam fishway (Pon *et al.*, 2006; Roscoe & Hinch, 2008) have reported lower passage failure rates ($c. 20\%$) than the present study, though there are several key points

worth noting here. All aforementioned studies used identical capture and biopsy techniques, but unlike the present study, the others used gastrically inserted radio transmitters. Therefore, the handling procedures could have been a contributing factor in the present study as EMG tag insertion is a more invasive procedure than gastric tag insertion. It is important, however, to note that the unsuccessful fish in the present study did not simply give up and drift downstream. On the contrary, these fish remained in the tailrace of the dam for several hours to days during which time they were observed actively seeking passage upstream in visibly turbulent water spilled from the dam (Pon *et al.*, 2006). Additionally, fish from the present study were released directly into the fishway, as opposed to a location downstream of the fishway entrance (Pon *et al.*, 2006; Roscoe & Hinch, 2008). The fact that some fish dropped out of the lower section of the fishway shortly after release should not be considered as an indication of migration failure. Indeed, fallback of such a short distance is not uncommon in tagging studies (Hinch & Rand, 1998). Finally, the fact that handling-related stress indicators were not unusually elevated in these fish support the notion that handling procedures were not a primary cause of passage failure. That fish were able to ascend the fishway with relatively low mean swim speeds and without becoming physiologically stressed suggest that the design of the fishway suits fish that can successfully navigate their way up it. The limiting factor may instead be associated with attraction of fish into the fishway.

The integrative use of physiological biopsy and EMG telemetry, as used here, has been recently advocated by Murchie *et al.* (2008) as an effective means of assessing mechanisms of fishway passage difficulty or mortality. These approaches, however, may not be able to provide enough information on the physiological underpinnings of passage failure, and so, care should be used in their application with respect to the expected effect size. Indeed, there were also no clear physiological correlates of passage failure in the other recent studies on *O. nerka* passage through the Seton River hydropower system (Pon *et al.*, 2006; Roscoe & Hinch, 2008). It is possible that physiological factors that were not examined had predisposed individual fish to passage failure in the present study and the others. Additional biochemical approaches such as gene array technology, which can simultaneously examine the function and activity of thousands of genes and which enable a more detailed and powerful means of examining the physiological limitations of salmonid passage, should be explored (Miller *et al.*, 2007).

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