Energetics Related to Upstream Migration of Atlantic Salmon in Vertical Slot Fishways

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ENERGETICS RELATED TO UPSTREAM MIGRATION OF ATLANTIC SALMON IN VERTICAL SLOT FISHWAYS

by

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ABSTRACT

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Hydropower brings clear advantages as a renewable energy resource. Key impacts of hydropower development on rivers are physical obstructions causing the separation of habitats. Considerable efforts have been expended to construct fishways that allow fish to bypass the obstructions. However, fishway designs have seldom considered fish behavior and energetics. We used electromyogram (EMG) telemetry to analyze swimming energetics in relation to turbulent flow and passage success of 14 adult Atlantic salmon (*Salmo salar* L.) ascending two vertical slot fishways on the Exploits River, Newfoundland, Canada. Wild Atlantic salmon were collected at the fishway entrances, and EMG transmitters were surgically implanted in the fish with electrodes inserted into the red muscle. EMG signals were calibrated against swimming speed using a Blazka-type respirometer. After calibration, fish were released below the hydro dam. Data loggers continuously monitored EMG signals and migration time as Atlantic salmon approached, entered, and ascended the fishways at Bishop's Falls and Grand Falls. Turbulent flow in the fishway was measured using an Acoustic Doppler Velocimeter.

Of the 14 fish that were tagged, 11 individuals were recorded approaching the fishway but only five individuals were recorded ascending the fishway. The majority of the fish visited the tailrace more than once before ascending. After entering, all five individuals migrated successfully through the fishway on their first attempt. Our results further indicate that (1) tagging delayed the upriver migration of fish by up to a month, and (2) passage success differed between the two fishways.

RÉSUMÉ

Enders, E.C., Pennell, C.J., Booth, R.K. and Scruton, D.A. 2008. Energetics related to upstream migration of Atlantic salmon in vertical slot fishways. Can. Tech. Rep. Fish. Aquat. Sci. 2800: v + 22 p.

Étant une ressource renouvelable, l’énergie hydro-électrique présente des avantages indéniables. Néanmoins, en agissant comme des barrières qui divisent les habitats, les ouvrages hydro-électriques exercent des effets négatifs sur les cours d’eau et les populations de poisson. Des efforts considerables ont été fait afin de construire et de mettre en place des passes migratoires pour permettre aux poissons de franchir ces obstacles. Cependant, le comportement et la bioénergétique des poissons ont rarement été considérés lors du design de ces infrastructures. Sur la rivière Exploits de Terre-Neuve (Canada), nous avons analysé les coûts énergétiques de nage de 14 saumons atlantiques en fonction des conditions turbulentes de l’écoulement de passes migratoires. Cette étude a été réalisée en utilisant la télémétrie électromyographique (EMG). Les saumons ont été pêchés aux entrées de deux passes migratoires. Deux électrodes reliées à un transmetteur EMG ont été implantées dans les muscles rouges de chacun des poissons. Les signaux EMG ont été calibrés en fonction de la vitesse de nage dans un respiromètre Blazka. Suite à la calibration, les poissons ont été relâchés en aval des barrages hydro-électriques. Les enregistreurs de données ont continuellement enregistré les signaux EMG et l’heure de passage des poissons à des endroits stratégiques situées aux abords et à l’intérieur des passes migratoires de Bishop’s Falls et de Grand Falls. L’écoulement turbulent dans les passes migratoires a été mesuré en utilisant un vélocimètre acoustique Doppler.

Parmi les 14 individus étudiés, 11 poissons se sont approchés des passes migratoires, mais seulement 5 poissons ont franchi l’une des passes migratoires. La majorité des poissons se sont approchés plus d’une fois des passes migratoires avant d’entreprendre la montaison des ces dernières. Après être entré, ces 5 poissons ont franchi la passe au premier essaie. Nos résultats indiquent que (1) le marquage a retardé la migration des poissons jusqu’à un mois, et que (2) le succès de passage diffère entre les deux passes migratoires.

INTRODUCTION

Hydropower brings clear advantages as a renewable energy resource, however, possible unfavourable effects due to anthropogenic flow changes on fish populations must be considered (Poff et al. 1997; Saltveit et al. 2001). Among many potential environmental impacts associated with hydropower development, one of the key impacts relates to the creation of physical obstructions that result in separation and lack of access to habitats. Denying free migration between valuable habitats may consequently lead to decline or extinction of affected fish populations (Bain et al. 1988). To prevent these potential negative impacts from the separation of fish habitats, environmental policies [e.g. European Water Framework Directive (European Parliament 2000) and Canada's Fisheries Act, including principles outlined in Policy for the Management of Fish Habitat (DFO 1986)] ensure the provision of fish passage, where justified.

Constraining the ecological connectivity of riverine systems is especially critical for anadromous species, which spend part of their life cycle in freshwater and some part in the ocean and that require migration between spawning, rearing, feeding, and over wintering habitats. Ascending Atlantic salmon (*Salmo salar* L.) may migrate hundreds of kilometers to freshwater spawning grounds. Migrations are energetically demanding and Atlantic salmon do not feed during spawning migration. Consequently, they rely entirely on energy reserves acquired in the ocean to complete their spawning migration and to spawn successfully (Lucas and Baras 2001). At hydro dams, fish may be attracted to high flows associated with the tailraces, which can result in migration delays, higher stress, and increased predation risk (Clarke et al. 2008). Barriers to upstream migration may therefore affect the gonadal production and the ability to reach spawning grounds, which can negatively affect spawning success (Bernatchez and Dodson 1987).

Considerable efforts have been expended on the improvement of fishways to enhance the probability of fish negotiating them (Jungwirth et al. 1998). Unfortunately, these efforts have tended to rely on trial-and-error approaches based exclusively on hydrodynamic considerations that have often failed due to the exclusion of fish physiology and behaviour in the design (Clay 1995). Engineers have largely failed to incorporate fish swimming capacity into fish pass design. While many fishery biologists criticize the engineers' bias, in reality, little empirical data exists on fish performance in complex hydrodynamic fields that could be factored into the design. Recent research on energetics and kinematics of swimming in turbulent flow has shown that the energetic costs of swimming increases with turbulence (Enders et al. 2003). In contrast, Liao et al. (2003) have shown that under certain flow conditions, fish can take advantage of turbulence and significantly reduce the energetic costs of swimming. These apparently contradictory findings have important implications for fishway design: they strongly suggest that certain types and characteristics of turbulence may be conducive to passage, while others may be inhibitory. Therefore, knowledge on the effects of turbulence on the capacity of fish to negotiate fishways is needed.

A preliminary study on upstream migrating adult anadromous Atlantic salmon in the Exploits River, insular Newfoundland, Canada, that were tagged with physiological (electromyogram or EMG) radio telemetry transmitters has revealed that tailrace attraction may considerably delay migration timing and may lead to increased energetic expenditures (Scruton et al. 2007). The objective of this study was to (1) assess the behavior and energetics of anadromous Atlantic salmon ascending two different vertical slot fishways on the Exploits River using EMG radio telemetry, and (2) correlate the swimming energetics to the turbulent flow occurring in the fishways.

MATERIALS AND METHODS

STUDY SITES AND SPECIES

The Exploits River is Newfoundland’s largest river 322 km in length draining a catchment area of 11,272 km² (Fig. 1). It sustains one of the largest populations of anadromous Atlantic salmon in North America (Randal et al. 1989). In the early 1900’s, two hydro plants were established on the Exploits River in Bishop’s Falls (10 km from the estuary) and Grand Falls (22 km from the estuary) to power pulp and paper mills. Historically, anadromous Atlantic salmon were restricted to the lower 10% of the Exploits River. However, fishways were constructed at both hydro dams (Bishop’s Falls in 1959; Grand Falls in 1974) to provide anadromous Atlantic salmon with access to approximately 90% of the watershed. Parallel to the improved access, large numbers of juvenile Atlantic salmon were stocked and adult salmon were transferred to the upstream parts of the river (Mullins et al. 2003). Since then the Atlantic salmon population has increased from 1,200 adults returning in 1960 to a peak of 32,000 in 1996, averaging to 22,000 adults returning over the last decade (O'Connell et al. 2003).

FISH TAGGING

EMG radio telemetry was used to analyze migration timing and associated energy expenditures of adult anadromous salmons at Bishop’s Falls and Grand Falls fishways on the Exploits River. Fourteen fish were in total from the fishways using dip nets [Bishop’s Falls (n=7) and Grand Falls (n=7)]. After capture, fish were transferred to holding facilities where they were anaesthetized (clove oil; 0.6 $mg \cdot l^{-1}$), weighed (kg wet), and measured (fork length L_F; cm; Table 1). Fish had a mean body mass of 1.7 kg ± 0.3 kg (range: 1.4 to 2.4 kg) and a mean fork length of 54.6 cm ± 2.9 cm (range: 49.5 to 59.5 cm). Fish were tagged with coded EMG transmitters (Fig. 2a). The cylindrical transmitters (model cEMG-R11-18 Lotek Wireless Inc.; 54 mm in length and 11 mm in diameter, mass in air of 10.0 g, guaranteed battery life of 54 d) were equipped with an antenna and two Teflon-coated electrodes. The end of each electrode was attached to a gold tip sensor (7 x 1 mm) that serves as electrical and mechanical contact with muscle tissue and secures the electrode in the musculature.

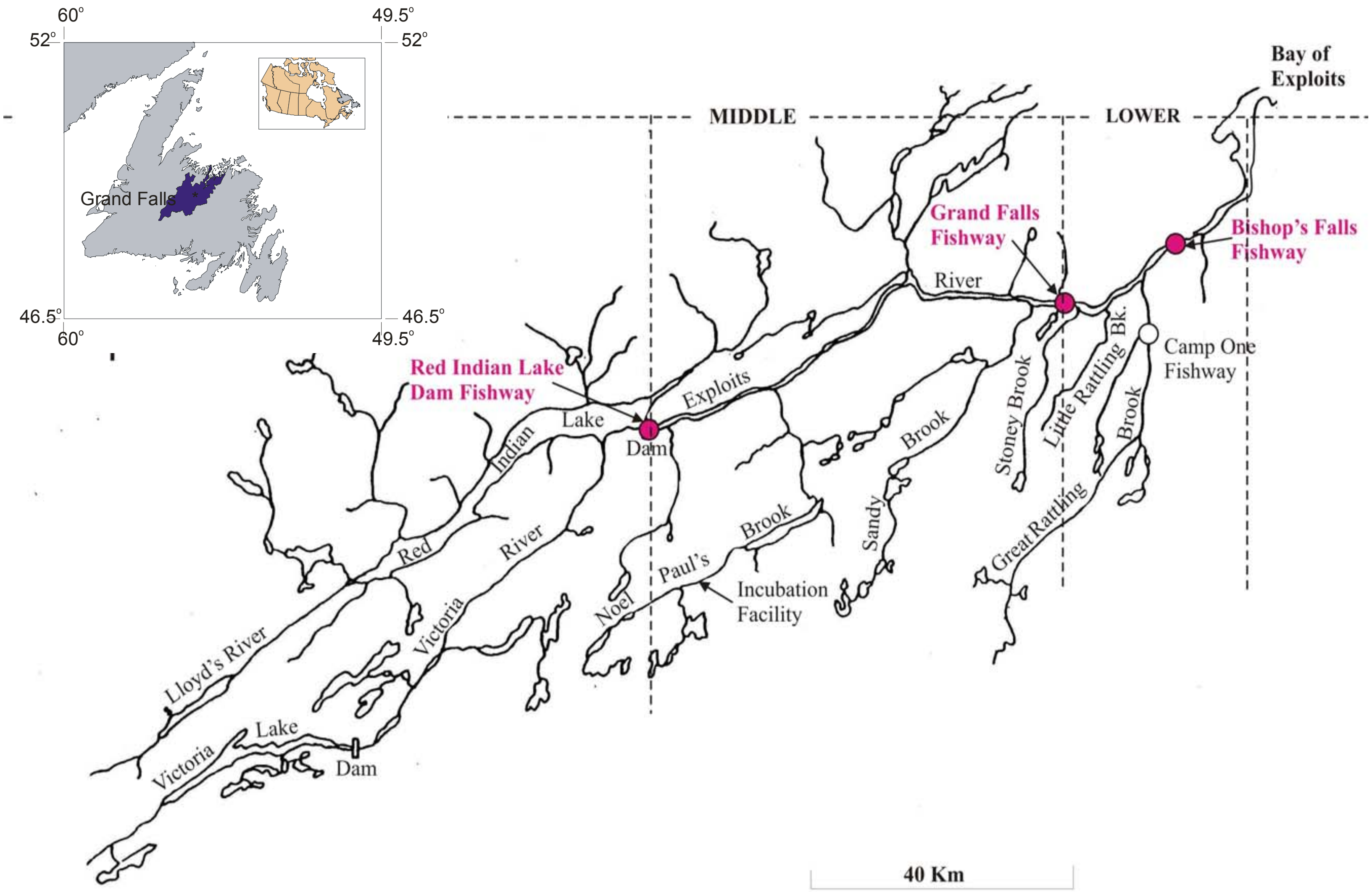

Figure 1. Distribution of fishways along the Exploits River in insular Newfoundland, Canada.

Table 1. Data of individual Atlantic salmon in Bishop's Falls (BF) and Grand Falls (GF) fishways: fish body mass (M), fork length (L_F), experimental water temperature (T), date of surgery, resting EMG values, linear regression statistics of the calibration of swim speed (U in $BL \cdot s^{-1}$) to EMG values, and number of EMG values obtained in the field.

Fish #	Fish-way	M (kg)	L_F (cm)	T (°C)	Date of surgery	Resting EMG	Regression equation	Statistics r^2	p	df	Field observation N of EMG
1	BF	2.2	57.5	16.2	7 July	7	$\text{EMG} = 12.69\ U_S - 6.35$	0.71	0.01	5	62487
2	BF	1.4	49.5	17.0	7 July	4	$\text{EMG} = 1.08\ U_S + 4.78$	0.05	0.28	6	666
3	BF	1.4	53.0	17.3	8 July	5	$\text{EMG} = 1.17\ U_S + 5.35$	0.39	0.06	6	1657
4	BF	2.0	57.5	17.5	8 July	7	$\text{EMG} = 2.59\ U_S + 5.08$	0.77	0.03	3	4763
5	BF	1.4	53.0	17.3	8 July	5	$\text{EMG} = 5.36\ U_S + 6.31$	0.97	0.01	2	6717
6	BF	1.4	51.5	17.1	8 July	5	$\text{EMG} = 2.29\ U_S + 4.69$	0.70	0.01	5	65535
7	BF	1.8	55.0	17.3	8 July	3	$\text{EMG} = -0.57\ U_S + 5.45$	0.01	0.35	5	1104
8	GF	2.0	55.0	17.0	6 July	9	$\text{EMG} = 1.16\ U_S + 9.50$	0.00	0.50	3	1301
9	GF	1.5	52.0	15.6	6 July	6	$\text{EMG} = 2.43\ U_S + 10.35$	0.14	0.35	2	8195
10	GF	1.9	58.0	15.6	6 July	3	$\text{EMG} = 3.48\ U_S + 1.06$	0.78	0.01	4	727
11	GF	1.8	57.0	18.0	6 July	1	$\text{EMG} = 1.52\ U_S + 0.95$	0.60	0.03	5	1006
12	GF	1.8	53.0	16.6	7 July	3	$\text{EMG} = 0.13\ U_S + 11.20$	0.00	0.91	2	5
13	GF	1.6	52.5	17.3	7 July	5	$\text{EMG} = 12.38\ U_S - 3.40$	0.98	0.06	1	23392
14	GF	2.4	59.5	16.6	7 July	7	$\text{EMG} = 4.05\ U_S + 6.52$	0.52	0.06	4	86

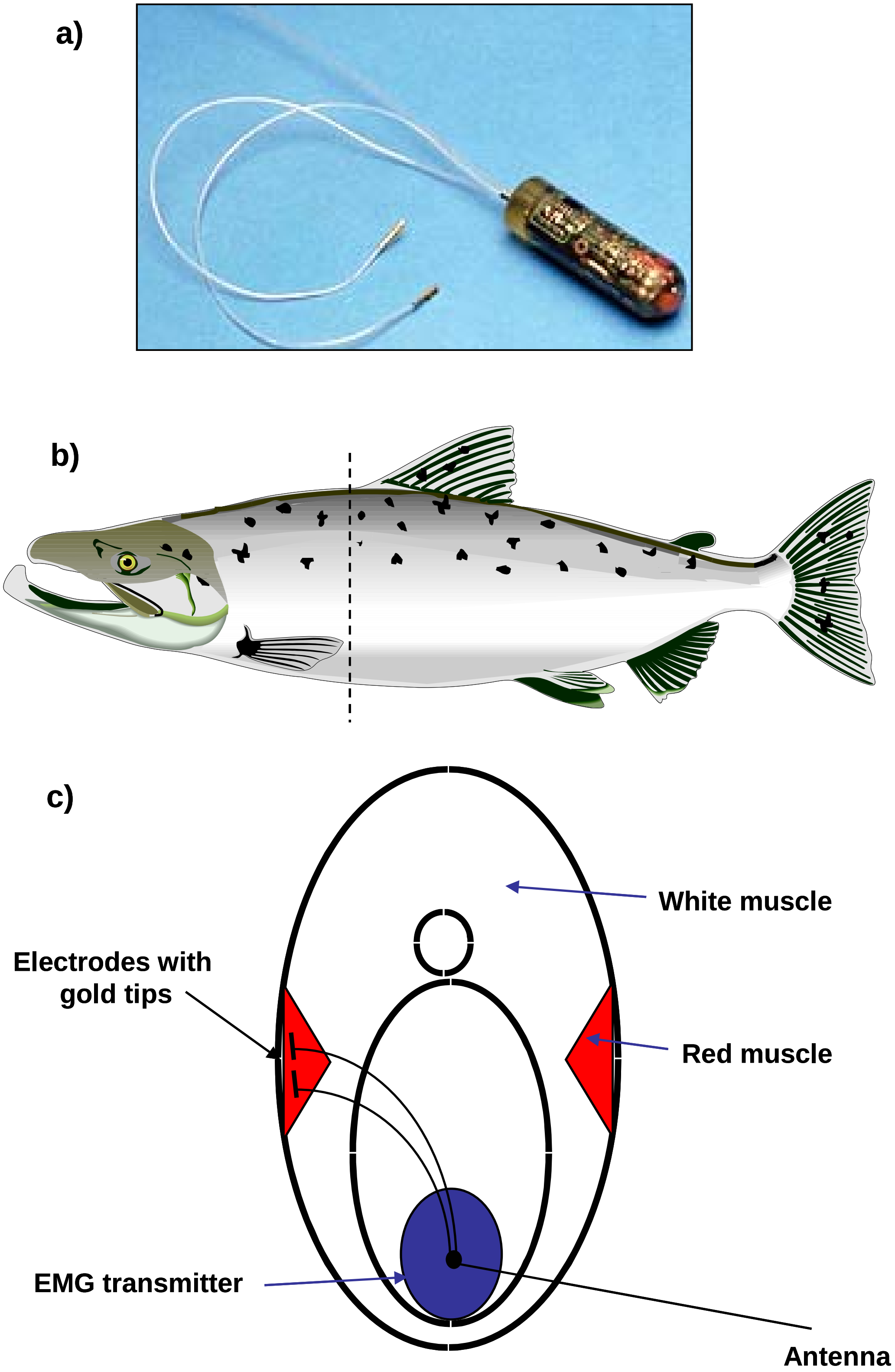

Figure 2. a) Coded electromyogram transmitter. Schematic diagrams of the b) placement of the insertion and c) the implantation of the EMG transmitter in the body cavity of the fish. Electrodes were inserted in red aerobic muscle.

Coded EMG transmitters sample the rectified and amplified bioelectrical potential changes between the two electrodes due to muscle contractions at a rate of 6000 Hz. In this study, we used tags with 1 and 5 s sampling rate, respectively. In both tags, an average voltage is calculated every second. The mean over one or five 1-s averages is subsequently converted in a relative activity level that ranges between 0 (no activity) and 50 (extreme activity). Due to noise and other variables, primarily the placement of the electrodes, the EMG output may vary significantly between individuals but also within individual fish.

EMG transmitters were surgically implanted via a 3 cm incision on the ventral surface posterior to the pelvic girdle (Fig. 2b). The transmitter was inserted through the incision and smoothly pushed forward into the body cavity. The antenna was threaded through the body wall using a hollow needle. The two gold electrodes were inserted 10 mm apart in the narrow band of red oxidative musculature just underneath the skin using a surgical plunger device similar to that described by Bunt (1999; Figure 2c). The incision was closed using three independent silk sutures (2-0 SofSilk^{TM}). Fish were allowed to recover over night in a holding tank and resting EMG values were obtained from fish observed at complete rest, without any swimming motions, at the bottom of the holding tank.

EMG CALIBRATION

Forced swim trials were used to establish relationships between swimming speed and EMG values. Swim trials were conducted using a 112 L Blazka-type swimming chamber (124 cm in length, 33 cm in internal diameter; Fig. 3). Water flow within the swimming chamber was generated by an impeller connected to an electrical motor. The impeller drew water passing the fish from the inner tube and pushed back through the outer tube. Calibration of the motor revolutions to flow velocities was performed in the mid-section of the swimming chamber using a flowmeter (Marsh-McBirney, model 2000 portable flowmeter). For further description of the swimming chamber, see Booth et al. (1997). Fish represented less than 4% of the cross-section surface of the swimming chamber; consequently blocking effect could be ignored (Bell and Terhune 1970; Beamish 1978). The EMG values were recorded every 1 or 5 s depending on the radio transmitter using a radio telemetry receiver (Lotek Wireless Inc., model SRX_400_W32CT).

Fish were placed in the swim chamber and allowed to acclimate for 2 h under flow through conditions at a swimming speed of 0.75 body length per second ($BL\cdot s^{-1}$). During each swim trial, flow velocity was increased by 0.25 $BL\cdot s^{-1}$ increments every 2 min until the fish exhibited obvious fatigue and fell back to the downstream grid. Simultaneously, fish were filmed and their EMG values recorded. Data were synchronised using the time stamps on both the video recording and the radio telemetry receiver. Water temperature during the swim trials ranged from 15.6 ºC to 18.0 ºC (mean ± S.D.: 16.9 ºC ± 0.7 ºC). Video recordings were used to assure that fish were swimming at the appropriate flow velocity. For each individual fish, linear regression analyses were used to obtain relationships between swimming speed and EMG values. The significance level for the statistical tests was $p \leq 0.05$.

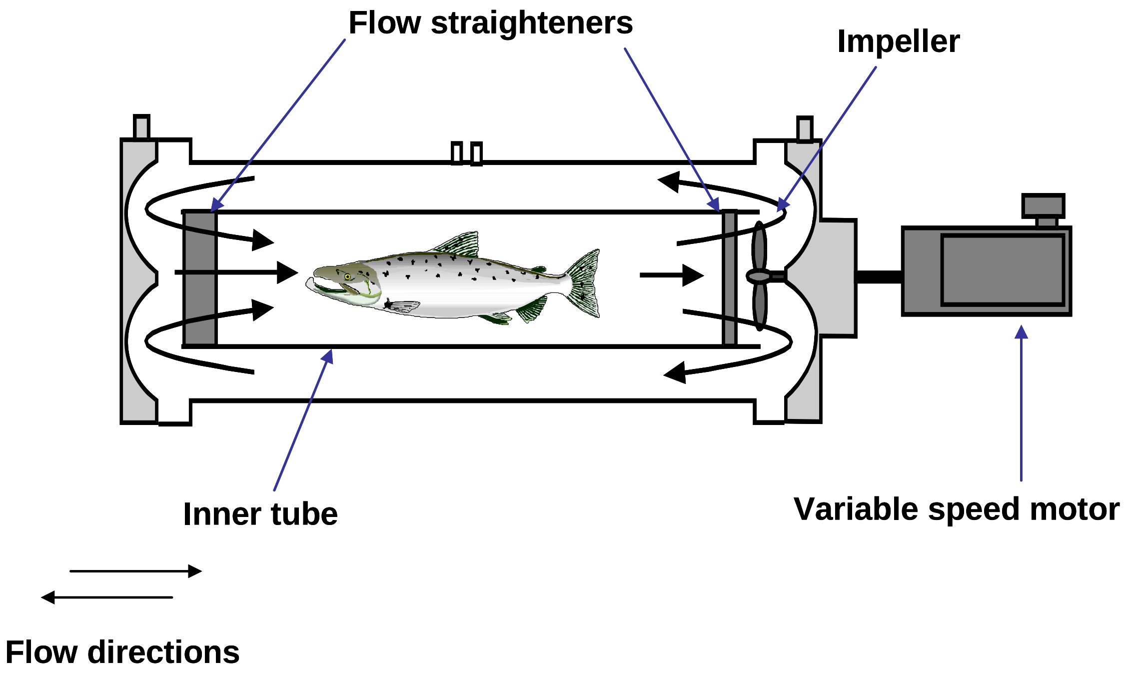

Figure 3. Schematic diagram of a Blazka-type respirometer used for the calibration of the EMG transmitters against swimming speed.

FISH TRACKING

After the swimming experiments, fish were allowed to recover over night in the holding tank and were released the next morning below the respective fishway. Tagged fish were tracked from 7 July to 5 September 2005 using fixed automatic data logging receivers (SRX_400 receiver; Lotek Wireless Inc.). The receivers were set up at strategic locations at the entrance and along Bishop's Falls and Grand Falls fishways (Fig. 4 and 5, respectively). EMG values were recorded continuously every 1 or 5 s depending on the radio transmitter.

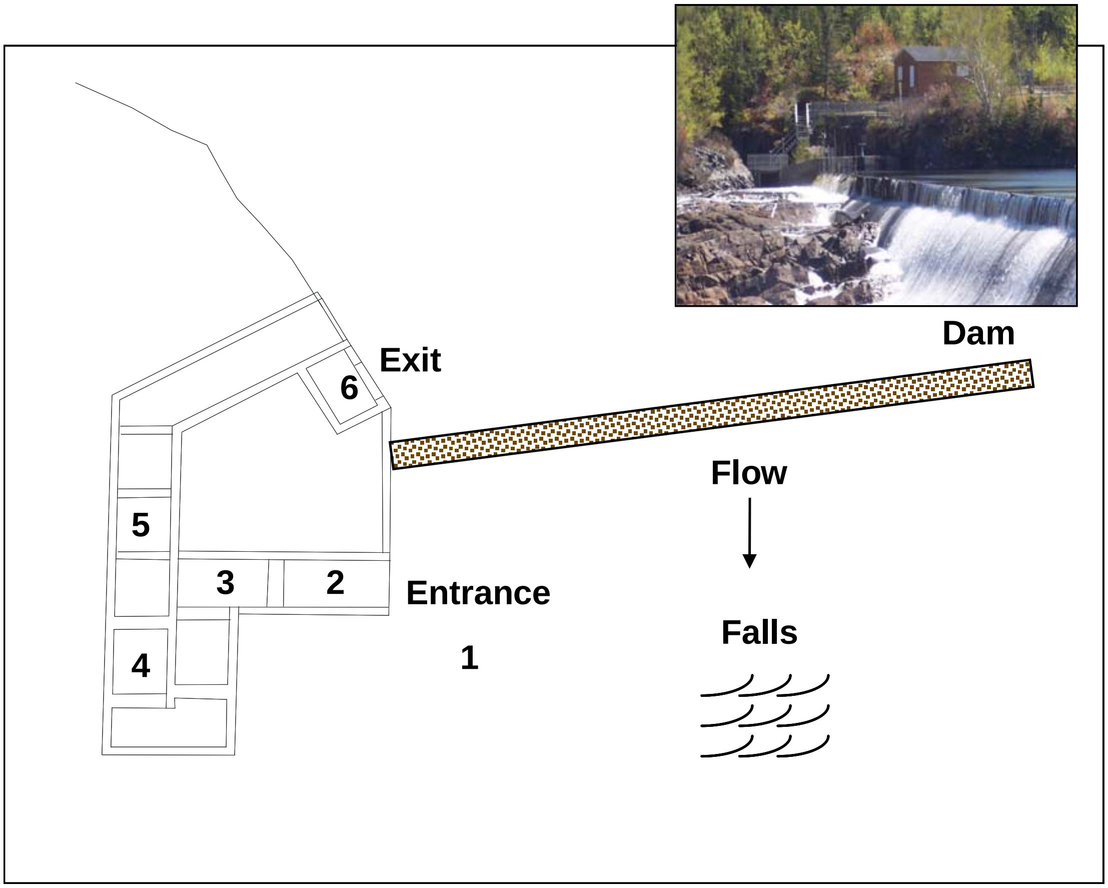

Figure 4. Bishop’s Falls fishway. Numbers give the positions of radio antennae and flow measurements.

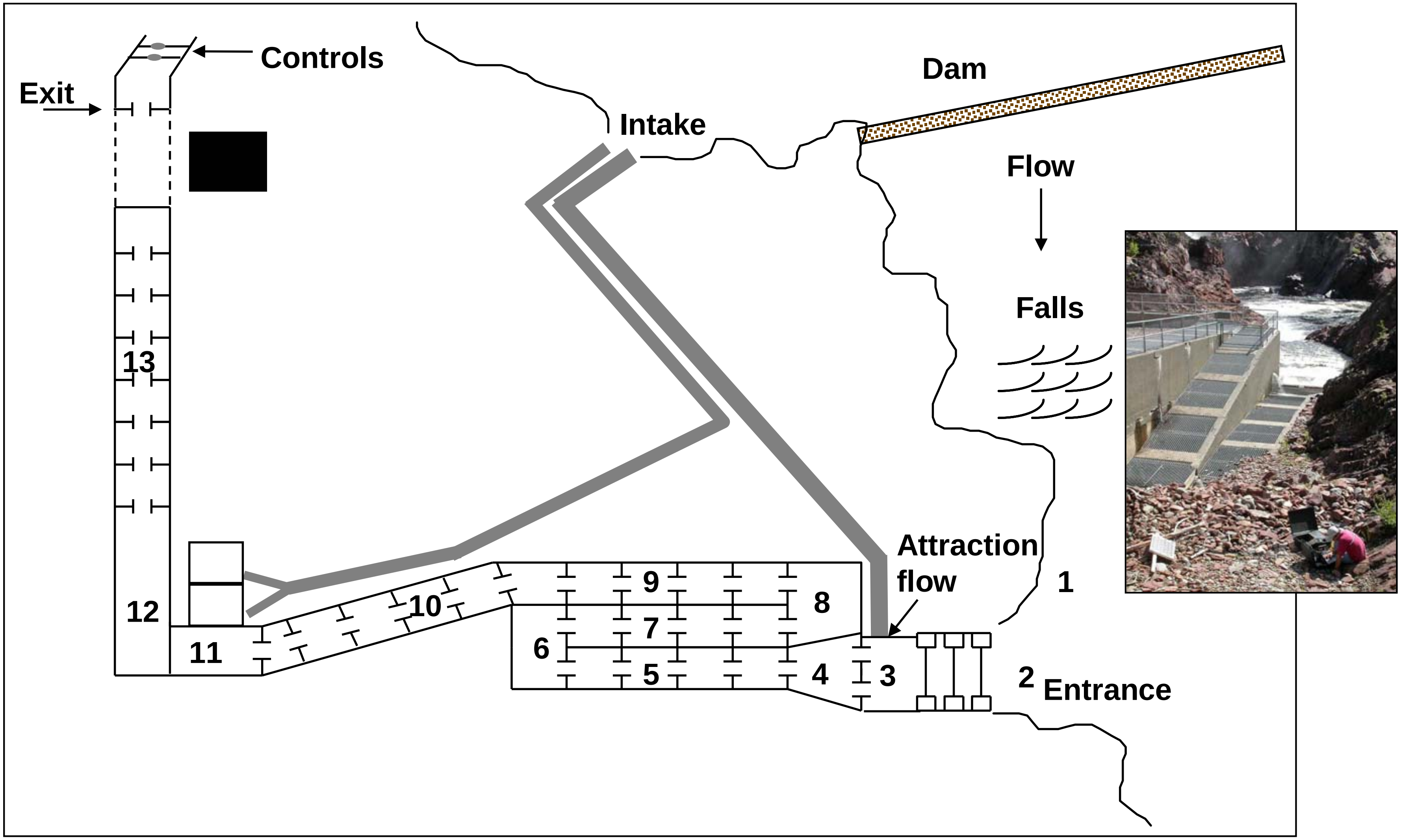

Figure 5. Grand Falls fishway. Numbers give the positions of radio antennae and flow measurements.

Due to an equipment failure of one of the data logging stations installed at Grand Falls fishway, EMG data of ascending fish were only recorded in the chambers with uneven numbers. Data analyses included determination of presence/absence within the entrance area and in the fishways, length of residency in the entrance area, length of upstream movement (h), comparison of EMG values between the Exploits River and fishway, and relation of EMG values in fishway with turbulent flow variables.

FLOW VELOCITY MEASUREMENTS

Turbulent flow around structures in the fishway were measured using an acoustic Doppler velocimeter (ADV, Sontek). The ADV allowed for the simultaneous measurements of three dimensional flow velocity components (longitudinal u, lateral v, and vertical w) at a frequency of 25 Hz. Velocity measurements were taken over periods of 60 s. In Bishop's Falls fishway, only 21 velocity point measurements could be obtained due to high water depth in the fishway and difficulties of access. In Grand Falls fishway, 190 velocity point measurements were taken in 10 chambers on strategic positions along the fishway that corresponded to the positions of the radio antennae (Fig. 3). Flow velocity was measured as mean flow velocity at 0.6 of the water depth on a 50 cm by 50 cm grid within a given chamber.

FLOW VELOCITY TIME SERIES ANALYSIS

The velocity time series were visually scrutinised to detect any anomaly in the signal. The four variables used to describe the flow characteristics were (1) mean flow velocity (u), (2) standard deviation of flow velocity (u_{SD}), (3) magnitude of the mean flow velocity vector (V) and (4) turbulent kinetic energy (TKE).

The magnitude V of the mean flow velocity vector in three dimensions is given by

$$(1) \qquad V = \sqrt{(\overline{u}^2 + \overline{v}^2 + \overline{w}^2}$$

where $\overline{u}$, $\overline{v}$ and $\overline{w}$ are respectively the mean longitudinal, lateral and vertical flow velocity components in $\text{cm}\cdot\text{s}^{-1}$.

The turbulent kinetic energy is a measure that combines the variances of the velocity fluctuations of all three velocity components in $\text{cm}^2\cdot\text{s}^{-2}$:

$$(2) \qquad TKE = 0.5\ (u_{SD}^2 + v_{SD}^2 + w_{SD}^2)$$

where u_{SD}, v_{SD}, and w_{SD}, are respectively the standard deviations of the longitudinal, lateral, and vertical flow velocity components. TKE is an overall measure of turbulence intensity (Enders et al. 2005).

From the EMG values observed in the fishways, fish swimming speeds were estimated, which were then correlated with mean flow velocity, standard deviation of flow velocity, magnitude of the mean flow velocity vector, and turbulent kinetic energy in order to examine the energetic expenditures related to upstream migration in the vertical slot fishways.

RESULTS

EMG CALIBRATION IN THE LABORATORY

Resting EMG values varied 9-fold (range 1-9) among individual Atlantic salmon. For six individuals (#1, 4, 5, 6, 10, and 11), EMG values increased significantly with an increase in swimming speed ($p < 0.05$; Table 1). For another three fish (#3, 13, and 14), the relationship between swimming speed and EMG values approached significance. Unfortunately, for the remaining five fish (#2, 7, 8, 9, and 12) no significant calibration curve could be obtained. With an increase in the flow velocity from 0.75 BL·s^{-1} to 2.75 BL·s^{-1}, EMG values increased by on average 2.4-fold (range 0.8 to 9.0-fold; Fig. 6).

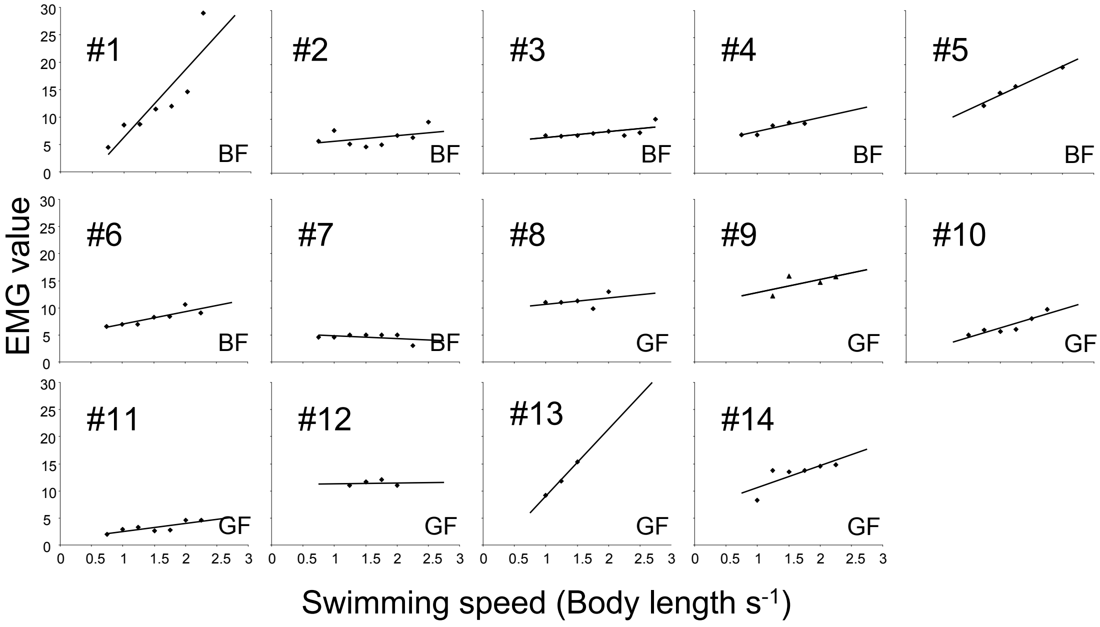

Figure 6. Relationships between swimming speed (BL·s^{-1}) and mean EMG value for fourteen Atlantic salmon.

TIMING OF FISH MIGRATION

Of the 14 fish that were tagged, 7 individuals were recorded approaching the fishways (Bishop's Falls: n = 3, #1, 5, and 6; Grand Falls: n = 4, #9, 10, 11, and 13) but only five individuals (Bishop's Falls: n = 1, #5; Grand Falls: n = 4, #9, 10, 11, and 13) were recorded ascending the fishway. The majority of the fish visited the fish entrance area more than once before ascending. At the Bishop's Falls dam, one fish moved up the fishway soon after release (#5), two more fish were observed until August, 20 and 22 close to the dam (#6 and 1, respectively). In contrast, at the Grand Falls fishway, fish left the area for considerable time (up to 29 days) before four fish migrated upstream through the fishway.

Consequently, our results suggest that tagging delayed the upstream migration of fish by up to a month (Fig. 7). After entering the fishway, all five individuals migrated successfully through the fishway on their first attempt. Residence time of the fish that ascended the Bishop's Falls fishway was 2.5 days, whereas the four fish that the Grand Falls fishway only took 1.5 to 2 h to pass through the fishway. Interestingly, the four fish that successfully ascended Grand Falls fishway were trapped in a challenging rocky passage area ("Upper Falls") just above the fishway for up to 35 days (Fig. 7).

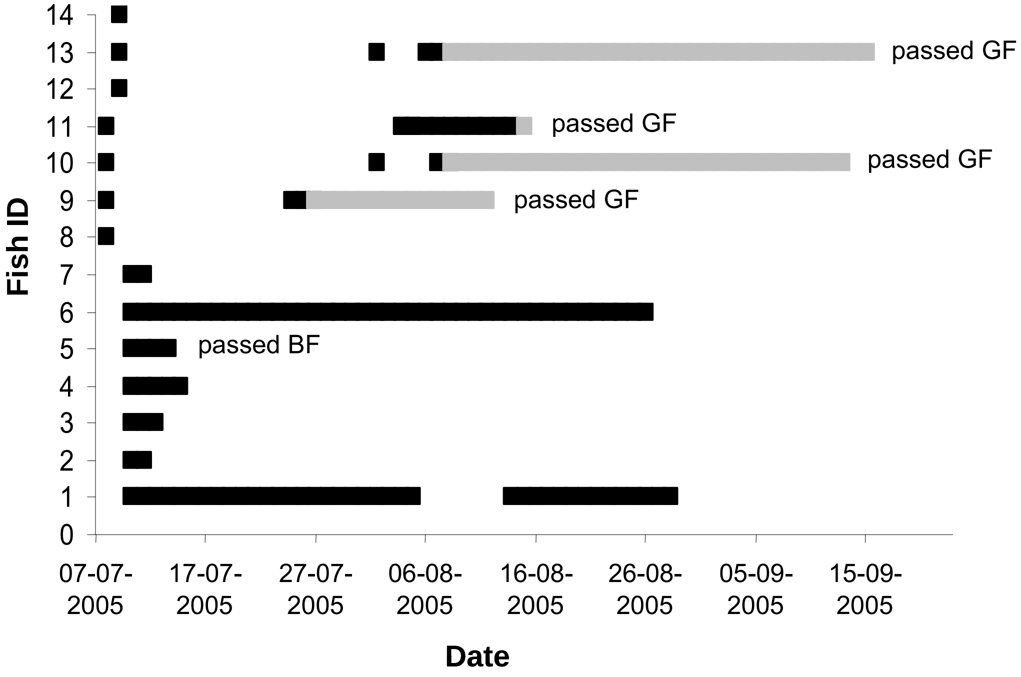

Figure 7. Timeline of fish observations in the Exploits River and in Bishop's Falls (BF; Fish #1 to 7) and Grand Falls (GF; Fish #8 to 14) fishways. Fish observations in a challenging section above the Grand Falls fishway are indicated in light grey.

FLOW VELOCITIES IN FISHWAYS

Mean flow velocity u in Bishop's Falls fishway was 25.2 $\text{cm}\cdot\text{s}^{-1}$ ± 26.7 $\text{cm}\cdot\text{s}^{-1}$ (range: -17.3 $\text{cm}\cdot\text{s}^{-1}$ to 74.4 $\text{cm}\cdot\text{s}^{-1}$). In Grand Falls fishway, mean flow velocities varied between the different chambers from 5.2 $\text{cm}\cdot\text{s}^{-1}$ to 26 $\text{cm}\cdot\text{s}^{-1}$ (Table 2). Negative flow velocities were observed in the recirculation zones of the fishway chambers. Flow velocities were highly variable within the swimming chambers demonstrated by a standard deviation greater than the mean for most of the swimming chambers.

The mean magnitude V of the mean flow velocity vector in three dimensions was 34.7 $\text{cm}\cdot\text{s}^{-1}$ ± 29.2 $\text{cm}\cdot\text{s}^{-1}$ (range: -1.4 $\text{cm}\cdot\text{s}^{-1}$ to 91.7 $\text{cm}\cdot\text{s}^{-1}$) in Bishop's Falls fishway. A smaller range of magnitude was observed in Grand Falls fishway were magnitude ranged between 11.8 $\text{cm}\cdot\text{s}^{-1}$ to 62.5 $\text{cm}\cdot\text{s}^{-1}$. In Bishop's Falls fishway mean turbulent kinetic energy TKE was 1769.8 $\text{cm}^2\cdot\text{s}^{-2}$ ± 4856.2 $\text{cm}^2\cdot\text{s}^{-2}$. Depending on the chamber, TKE varied between 78.3 $\text{cm}^2\,\text{s}^{-2}$ and 2822.6 $\text{cm}^2\cdot\text{s}^{-2}$ in Grand Falls fishway.

ENERGETICS RELATED TO MIGRATION AND FISHWAY PASSAGE

In comparison to the resting EMG values observed in the laboratory, fish had increased EMG values in the Exploits River (Table 3). For the five fish that passed a fishway significant differences in the EMG values while swimming in the Exploits River and the different swimming chambers were observed (Wilcoxon test, p always < 0.05).

Table 2. Turbulent flow data of Bishop's Falls (BF) fishway and in several chambers (Ch#) of Grand Falls fishway (GF) on mean, standard deviation (S.D.), minimum (min) and maximum (max) of flow velocity (u, cm·s^{-1}), standard deviation of flow velocity (u_{SD}, cm·s^{-1}), magnitude of the mean flow velocity vector (V, cm·s^{-1}), and turbulent kinetic energy (TKE, cm^2·s^{-2}).

	u				***u***				***V***				*TKE*			
Fishway	mean	S.D.	min	max	mean	S.D.	min	max	mean	S.D.	min	max	mean	S.D.	min	max
BF	25.2	26.7	-17.3	74.4	23.4	37.2	4.0	135.3	34.7	29.2	1.4	91.7	1769.8	4856.2	24.9	16851.3
GF Ch#4	16.6	30.9	-21.6	79.2	16.5	7.5	8.2	32.5	30.9	24.2	3.4	79.4	385.5	320.7	69.7	1190.9
GF Ch#5	16.5	39.3	-46.8	73.5	23.8	8.0	13.1	36.7	53.3	22.5	18.4	96.9	799.5	478.8	235.4	1720.0
GF Ch# 6	26.5	30.2	-25.4	81.6	15.7	7.9	8.9	36.7	42.0	19.3	13.8	86.1	326.1	314.3	89.6	1111.3
GF Ch# 7	13.4	35.5	-48.5	71.3	39.8	35.1	13.2	155.3	48.2	27.1	14.7	102.8	2822.6	6222.5	213.5	24908.6
GF Ch# 8	22.2	34.4	-56.6	78.7	25.7	29.4	9.2	180.4	62.5	33.8	18.2	207.5	1466.3	4760.5	107.1	27770.9
GF Ch# 9	5.2	37.6	-59.0	84.1	30.3	11.8	15.6	56.9	53.8	28.3	16.2	120.0	1189.0	705.2	298.1	2843.0
GF Ch#10	16.0	37.0	-54.8	79.9	34.5	32.1	14.5	121.9	54.7	24.6	16.7	88.6	1977.8	3724.9	257.5	13670.9
GF Ch#11	11.5	14.4	-11.8	33.9	39.3	40.8	9.3	143.0	21.8	8.8	5.6	34.7	2794.7	5685.4	110.0	18676.3
GF Ch#12	9.1	7.0	-10.2	18.0	8.7	0.8	7.3	10.6	11.8	5.4	0.6	20.7	78.3	17.0	51.9	125.6

Table 3. Resting EMG from the calibration experiments and mean (± S.D.) EMG values observed in the Exploits River for all fish, and mean (± S.D.) EMG values in the different chambers of Bishop's Falls (BF) and Grand Falls (GF) fishways for the five fish that passed the fishway(s).

Fish #	Fish-way	Resting EMG	Exploits River	Chamber 2	Chamber 3	Chamber 4	Chamber 5	Chamber 6		
1	BF	7	35.0 ± 5.6							
2	BF	4	25.9 ± 10.4							
3	BF	5	5.6 ± 1.7							
4	BF	7	33.9 ± 7.5							
5	BF	5	10.1 ± 3.8	10.3 ± 0.7	10.6 ± 1.0	12.0 ± 0.0	10.2 ± 0.6	10.5 ± 1.2		
6	BF	5	6.4 ± 2.3							
7	BF	3	3.7 ± 1.5							
			Exploits River	**Chamber 2**	**Chamber 5**	**Chamber 7**	**Chamber 9**	**Chamber 11**	**Chamber 13**	**Above fishway**
8	GF	9	17.5 ± 5.6							
9	GF	6	13.0 ± 6.6	12.3 ± 5.3	14.3 ± 9.2	16.8 ± 9.8	8.2 ± 1.9	10.1 ± 2.0	12.6 ± 2.8	11_6 ± 2.9
10	GF	3	5.7 ± 2.9	5.5 ± 2.2	6.8 ± 2.3	4.7 ± 0.5	4.1 ± 1.7	4.5 ± 1.9	4.5 ± 2.3	6.8 ± 5.4
11	GF	1	5.3 ± 5.6	6.4 ± 6.3	4.3 ± 1.7	4.6 ± 3.9	3.1 ± 0.5	3.1 ± 0.9	6.4 ± 7.6	3.0 ± 1.5
12	GF	3	16.7 ± 7.6							
13	GF	5	32.1 ± 12.3	32.6 ± 11.6	13.7 ± 14.0	34.0 ± 8.8	35.4 ± 8.6	45.0 ± 2.3	34.6 ± 9.7	32.7 ± 11.9
14	GF	7	13.8 ± 2.4							

Estimated mean swimming speed, for fish #5 ascending Bishop's Falls fishway, varied by 1.5-fold and was highest in Chamber No. 4 (Table 4). This corresponded to the highest measured water velocity of 97.3 cm·s^{-1} in the Bishop's Falls fishway.

Table 4. Estimated mean swimming speed (cm·s^{-1}) of four fish observed in the Exploits River and in the different chambers of Bishop's Falls (BF) and Grand Falls (GF) fishways estimated using the EMG-calibration curves.

Fish #	**Fishway**	**Exploits River**	**Chamber 2**	**Chamber 3**	**Chamber 4**	**Chamber 5**	**Chamber 6**		
5	BF	37.5	39.5	42.4	56.3	38.5	41.4		
		Exploits River	**Chamber 2**	**Chamber 5**	**Chamber 7**	**Chamber 9**	**Chamber 11**	**Chamber 13**	**above fishway**
10	GF	77.3	74.0	95.7	60.7	50.7	57.3	57.3	95.7
11	GF	163.1	204.4	125.6	136.9	80.6	80.6	204.4	76.9
13	GF	150.5	152.7	72.5	158.6	164.5	205.3	161.1	153.1

***Note:** Fish #9 was excluded because the EMG calibration curve was not significant (*p*=0.35).

For fish passing the Grand Falls fishway, mean swimming speeds were only estimated for fish #10, 11, and 13. Consequently, estimated mean swimming speeds in the different chambers were correlated to four flow variables mean flow velocity, deviation of flow velocity, magnitude of the mean flow velocity vector, and turbulent kinetic energy (Fig. 8). However, no clear trend could be observed between the estimated swimming speed and the mean flow velocity, standard deviation of flow velocity, magnitude of the mean flow velocity vector, and turbulent kinetic energy. This is most likely due to the high variability in flow velocities within the chambers.

DISCUSSION

Electromyogram telemetry has been suggested to provide valuable insights into migration and associated energy expenditures of fish (Cooke et al. 2004) by directly measuring the muscle activity of free swimming fish *in situ* in relation to various environmental conditions. In the present study, EMG telemetry was used to identify the energetic expenditures related to upstream migration of adult anadromous Atlantic salmon in two vertical-slot fishways on the Exploits River. EMG values have to be calibrated using swimming performance tests to obtain estimates on the swimming speed. As relationships may differ for individual fish and between species, individual calibration of EMG values for each fish is necessary to obtain quantitative estimates of energy expenditure (Økland et al. 1997; Thorstad et al. 2000). Unfortunately, in the present study significant relationships between swimming speed and EMG values were only obtained for six out of the fourteen fish, but for another three fish the relationships approached significance. Consequently, correlation of EMG values to swimming speed could only be calculated for a reduced number of fish. We did not measure EMG values in relation to oxygen consumption, a measure of the metabolic rate, because these measurements would have required longer swimming trails and at a relative high water temperature, this would have lead to an additional stress of the experimental fish.

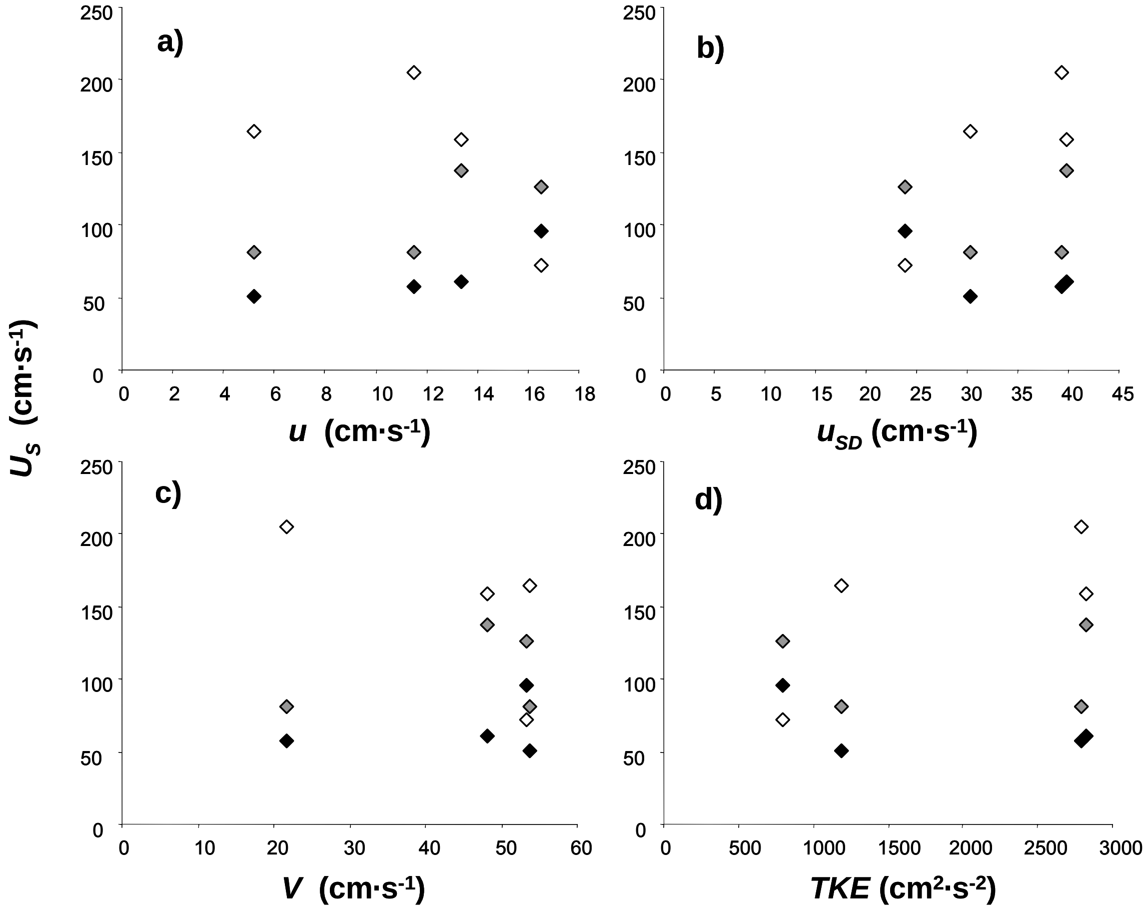

Figure 8. Estimated mean swimming speed U_S of fish #10 in solid diamonds, fish #11 in shaded diamonds, and fish #13 in open diamonds in relation to a) mean flow velocity u, b) standard deviation of flow velocity u_{SD}, c) magnitude of the mean flow velocity vector V, and d) turbulent kinetic energy TKE in the different chambers No. 5, 7, 9, and 11.

The coded EMG tags (model cEMG-R11-18, Lotek Wireless Inc.) that were used in the present study measure the bioelectrical voltage due to muscle activity over a 1 or 5 s period and then calculate a mean value over this period. The mean value is subsequently converted to an EMG value that ranges from 0 to 50. The EMG value is then transmitted to the radio-telemetry receiver and has to be calibrated in laboratory experiments such as for example swim trails to be biological meaningful.

The integration of bioelectrical voltage over several seconds in the 5 s burst rate tags may attenuate the effects of short term burst swimming motions, which may last only one second. Therefore we recommend the use of the 1 s burst rate tags that average EMG values only over 1 s. These tags may have a larger range of EMG values than measurable with the 5 s burst rate tags.

Interestingly, we observed that only 35.7% of the fish successfully migrated through the fishways. Success rate was lower at Bishop's Falls fishway (14.3%) than in Grand Falls fishway; although Bishop's Falls fishway (57.1%) is shorter and would appear to be less challenging from a hydraulic point of view. In this study, only one salmon migrated upstream the Bishop's Falls fishway and this was immediately after release. Two other fish at the Bishop's Falls dam seemed to be attracted to the tailrace for a prolonged period of time and stayed in the tailrace for over a month without resuming their migration. At Grand Falls fishway, the four fish that migrated upstream of the fishway were delayed in the migration by up to a month, which may have had a considerable effect on their reproductive success. Migration delays of Atlantic salmon in tagging studies have been previously reported in the Exploits River (Scruton et al. 2007), in Scotland (Gowans et al. 1999) and in Norway (Thorstad et al. 2003). Such delays may affect the spawning success depending on the location of the spawning site, the difficulty of the remaining migration, the energy consumed, the state of maturity, and other environmental conditions (Bernatchez and Dodson 1987). In the present study, fish migration was additionally delayed in a section between the lower and the upper fishway at Grand Falls dam. This constricted section represented a severe bottleneck in the migration route with intense flow velocities and a challenging jump. However, the section was modified in 2006 to facilitate the upstream migration.

It is noteworthy that six fish were not detected at the hydro dam or on any upstream telemetry antennae. One of fish tagged at Grand Falls fishway moved downstream and was found dead in the plunge pool of Bishop's Falls fishway. Some level of mortality seems to be common in telemetry studies and might be associated with the surgical implantation of the EMG transmitters and the subsequent calibration procedure (Adams et al. 1998; Cooke et al. 2004). The river sections at Bishop's Falls and Grand Falls are part of the most challenging river sections in the Exploits River for fish migration. The combined effect of stresses due to migration, capture, transportation, handling, and surgery, as well as the high water temperatures during the field session may have led to the fact that fish did not resume their migration. Alternatively, fish may have stayed and potentially spawned in downstream river sections after having experienced an important delay in their migration (Bernatchez and Dodson 1987). In a comparative study, in which fish were collected from both upstream and downstream of a hydro dam, consequently tagged and released below the dam, Thorstad et al. (2003) demonstrated that there was no difference in migratory behavior between fish that had previously passed the fishway and those that had not. It may therefore be assumed that fish in the present study that did resume their migration to and past the fishway, are representative of the behavior of untagged fish. However, we have no data on the natural rate of mortality and successful migration rates in the Exploits River to confirm this assumption.

EMG telemetry was used to provide insight into migratory energetics and behavior. EMG values were used as relative energetic costs of migration to compare energetic costs in the entrance of the fishway (tailrace) and the fishway itself. We observed relatively high energy expenditures associated with tailrace attraction and residency, which was previously shown by Scruton et al. (2007). River reaches with relatively complex hydraulic environments due to high riverbed gradient and associated high flow velocities, as well as fishways, may represent difficult points of passage (Hinch and Bratty 2000; Hinch et al. 2002; Standen et al. 2002). In the present study, the high EMG values observed below the hydro dams suggest that the constricted river sections with high riverbed gradients and highly turbulent flows were challenging for the fish and difficult to pass. The energetic costs may be actually even higher than documented because fish swimming in these highly turbulent and fast flowing river sections may be also be utilizing white muscle (stored energy reserves, anaerobic metabolism) in addition to aerobic metabolism (red swimming muscle) for short bursts. Activity costs that are fuelled by the anaerobic metabolism, are not measured by the EMG electrodes that are situated in the red, aerobic muscles. Consequently, the obtained measured EMG values from red muscle may underestimate the actual energy expenditures of swimming (Cooke et al. 2004). Interestingly, fish passed fairly quickly the Grand Falls fishway with residence times ranging from 1.5 to 2 h resulting in low relative energy expenditures. Similarly, Hinch et al. (2002) had observed that upstream migrating pink and sockeye salmon increased their swimming speed in river sections with complex hydraulics associated with more turbulence and faster flow velocities. This suggests that fish search within the surrounding flow field for alternative migration routes using flow heterogeneity such as recirculation zones to decrease their energy expenditures during their upstream migration (Standen et al. 2002).

CONCLUSIONS

The improvement of fishways is a continual challenge for both industry and government in order to minimize potential negative impacts of hydro development on anadromous fish populations. The present study has shown that hydro dams may delay to some extent the upstream migration of adult Atlantic salmon, however it is not clear to which extent the experimental procedure used in this study may have caused or contributed to this delay. Some fish experienced prolonged tailrace attraction, which led to the resumption of the upstream migration. Energetic expenditures associated with tailrace attraction seemed to be slightly higher than the energetic expenditures within the fishways. Delays in migration and the associated energetic expenditures may negatively affect the spawning success of individual Atlantic salmon in the Exploits River although it is difficult to attribute the delays entirely to the power plants given the potential stress introduced by the surgical procedures. However, once fish started upstream migration through the fishways, they passed quickly, especially the Grand Falls fishway. However, improved attraction to the fishway entrance could potentially improve the passage success of adult anadromous Atlantic salmon on Bishop’s Falls and Grand Falls fishways on the Exploits River.

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