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In situ measurement of swimming performance of wild Atlantic salmon (*Salmo salar*) using radio transmitted electromyogram signals

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Abstract

Swimming capabilities and *in situ* measurement of muscle activity from adult Atlantic salmon (*Salmo salar*) at two seasonal temperatures were measured using radio transmitted electromyogram (EMG) signals. Forced sustained levels of activity and critical swimming speeds were determined and correlated to radio transmitted EMG signals using a modified Blazka swim speed chamber. There were no differences in swimming performance levels between tagged and untagged individuals. At 18°C, sustained activity and critical swimming speeds were approximately 70% and 20% higher than at 12°C, respectively. No differences in burst activity were observed at these temperatures. EMGs recorded from salmon during ascent of an artificial flume at cold temperatures revealed that overall muscle activity is greater than that observed for critical swimming speeds. This implies that white muscle may be recruited at this temperature. However, in contrast, most activity at 18°C is below that observed during critical swimming speed. Moreover, salmon required almost twice as long to traverse the flume at 18°C than at 12°C. Together, our data demonstrates that salmon may recruit white muscle fibres and incur an oxygen debt at colder temperature as a strategy for ascending velocity obstructions at a quicker rate.

Keywords: Atlantic salmon, telemetry, temperature, electromyogram, swimming performance.

Mesures in situ *des performances de nage du saumon atlantique sauvage* (Salmo salar) *au moyen de signaux radio-transmis d'électromyogrammes.*

Résumé

Les mesures de la capacité de nage et de l'activité musculaire *in situ* du saumon atlantique (*Salmo salar*) à deux températures différentes ont été effectuées au moyen de signaux radio-transmis d'électromyogrammes (EMG). Les niveaux d'activité soutenue et les vitesses de nage ont été déterminés et corrélés aux électromyogrammes en utilisant une chambre de nage de Blazka modifiée. Il n'y a pas de différence de performance de nage entre individus marqués ou non. A 18 °C, l'activité soutenue et les vitesses critiques de nage sont approximativement 70 et 20 % plus élevées qu'à 12 °C, respectivement. Aucune différence en activité intensive n'a été notée à ces températures. Les électromyogrammes enregistrés durant la formation d'un flux artifificiel à basses températures révèlent que l'activité musculaire est plus importante que celle observée pour des vitesses critiques. Ceci implique que le muscle blanc pourrait être sollicité à cette température. En revanche, la majeure partie de l'activité à 18 °C est inférieure à celle observée durant une

vitesse de nage critique. D'ailleurs, le saumon demande au moins 2 fois la longueur pour traverser le courant à 18 °C qu'à 12 °C. L'ensemble de nos données démontre que le saumon peut solliciter ses fibres de muscle blanc et subir un débit d'oxygène à des températures plus froides, comme stratégie pour lutter contre une vitesse croissante de façon plus efficace.

Mots-clés : Saumon atlantique, télémétrie, température, électromyogramme, performance de nage.

INTRODUCTION

Hydroelectric development is a ubiquitous occurrence on many rivers along the east coast of Canada. Moreover, a large number of these rivers are also used as migratory routes to spawning grounds by numerous fishes, including Atlantic salmon. To minimise the effects of dam construction on upstream fish passage, bypass systems (fishways) have been constructed at many sites to facilitate upstream migration. Unfortunately, many of these fishways fail to integrate designed operational characteristics of the fishway with the swimming performance of the migratory species in question.

Fishway evaluations have typically used existing swimming performance data reported for Pacific salmonids (*Oncorhynchus* sp.). Furthermore, many of these studies have been undertaken under laboratory conditions and using hatchery reared fish, which can possess very different swimming capabilities compared with wild fish (Bosclair and Legget, 1989). However, acquiring direct assessments of the amount and intensity of locomotory activity displayed by wild fish is extremely difficult (Fry, 1947; Beamish, 1978; Brett and Groves, 1979). Conventional telemetry practices have provided some crude estimates of fish activity in the field (Winter, 1983). Limited studies involving physiological telemetry have produced several techniques for directly estimating the activity and energetics of free living fish (Lucas *et al.*, 1993; McKinley and Power, 1992; Weatherly *et al.*, 1996). Previous studies have utilised correlations of heart rate (Priede and Young, 1977; Armstrong *et al.*, 1989; Lucas *et al.*, 1993), opercular rate (Rogers and Weatherly, 1983), and locomotor muscle electromyograms (Kaseloo *et al.*, 1992; McKinley and Power, 1992; Demers *et al.*, 1996; Weatherly *et al.*, 1996) to successfully estimate activity patterns of fish in the field.

Much of a fish's routine activity involves sustained and prolonged swimming and is typically supported by the red muscle (Beamish, 1978). Energy required for this activity is obtained through the metabolism of energy-rich substrates such as fats and proteins acquired during feeding. In migratory species such as the Atlantic salmon (*Salmo salar* L.), feeding is suspended for several months during their spawning period. Consequently, the energy required to support locomotion must be obtained solely from endogenous stores. This situation is complicated further by a period of sexual development which also occurs during the migratory period. Gonadal development requires enormous amounts of energy and may leave little for other needs such as body maintenance and courtship activities. Consequently, changes to either the intensity or duration of migration could significantly accelerate the rate at which energy is used and could result in unsuccessful spawning, low egg viability and, hence, poor recruitment and even death of spawning adults.

The objective of this study was to investigate the use of physiological telemetry as a method for estimating swimming performance of wild Atlantic salmon in an experimental flume under non-forced conditions. We chose to use electromyograms from the axial musculature as an indicator of swimming performance of wild Atlantic salmon.

MATERIALS AND METHODS

Animals and study site

Wild adult Atlantic salmon (55-60 cm) were collected at fishway traps located on the Exploits River, Newfoundland, Canada (49° N, 57° W) between 15 July and 10 October, 1995. Collection occurred between 21 and 27 July when ambient water temperatures averaged 18 °C and 27 September to 3 October when water temperatures averaged 12°C. Fish were transported to a salmon hatchery situated on a tributary of the Exploits River - the Noel Paul River. Individuals were held in large rectangular outdoor pens (8 m wide, 15 m long and 0.8 m deep). These pens were positioned in a 100 m long raceway adjacent to the river. Water flow in the raceway was regulated using a pair of upstream positioned control valves which diverted water from the river to the raceway. Water velocity in the raceway was maintained at 40 $m.s^{-1}$. All animals were allowed to recover from transportation for three days prior to swim speed trials.

Surgical procedures

Individual Atlantic salmon were removed from a common enclosure and anaesthetized in an aerated and buffered solution of MS-222 (50-75 $mg.l^{-1}$, pH 7.0).

When a slow irregular operculum was observed, surgery was initiated. This stage of anaesthesia was generally reached in four minutes. Anaesthetized individuals were placed ventral side up onto a non-abrasive V-shaped surgical table and the gills were irrigated with fresh oxygenated water.

A 3 cm incision was made on the ventral surface at a position posterior to the pelvic girdle. The transmitter was gently inserted through the incision and pushed anteriorly into the body cavity above the pelvic girdle. Electrodes were positioned approximately 5 mm apart in the lateral muscle below the lateral line using 21 gauge rods. Once the electrodes were secure in the muscle, the rods were removed. The antenna wire was exited from the body via a 2 mm incision located just prior to the anal fin. The incision was closed using three independent sutures (2/0 Ethicon silk) and, prior to the last suture, an injection of Liquamycin LP (1 ml. kg^{-1} antibiotic) was injected intraperitoneally. Surgical time averaged 4-5 minutes.

Radio telemetry equipment

Transmitters measured 50 mm in length and 13 mm in diameter and measured less than 2% of the experimental animal's body weight (Lotek Engineering Inc., Newmarket, Ontario). Muscle activity signals were detected via 18 carat gold tip sensors and transmitted along insulated stainless steel electrodes. A precision half wave rectifier and integrator processed the input EMG signals within the bandwidth 30-350 MHz. EMG signals were processed through an integrator and a radio pulse corresponding to the pulse interval in milliseconds (ms) was transmitted when the integrated EMG (*i.e.* EMGi) equalled the predetermined threshold value of 150 μV. Increasing muscle activity resulted in a corresponding decrease in the interval between successive radio pulses. Transmitters were designed to broadcast at frequency intervals of 10 kHz within an operating band of 148 to 150 MHz. Lifespan (battery life) of the transmitters was approximately two to three months. Transmitted signals were detected and recorded automatically using a W20 radio receiver/datalogger (Lotek Engineering Inc., Newmarket, Ontario) and downloaded to a laptop computer via an RS232 serial communication port. The receiver was programmed to record all EMGi signals from each tagged individual.

Calibration of muscle activity to swimming speed

Muscle activity obtained from Atlantic salmon was correlated against sustained and prolonged swimming speeds. We chose to express the muscle activity of salmon using an activity index (pulse interval ms) based on previous studies of muscle activity in lake sturgeon (McKinley and Power, 1992).

Swimming performance trials were conducted (at least one week after surgery) using a Blazka-type swim speed chamber/respirometer (Blazka *et al.*, 1960). This type of swim speed chamber is characterised by a tube within a tube design which permits water to be circulated within a smaller volume compared to Brett-type tunnel swim speed chambers (Brett, 1964). The cross sectional diameter of the inner tube was 28 cm with a cross sectional area of 615 cm^2 and the outer tube was 44 cm with a cross sectional area of 1 519 cm^2, total volume of the chamber being 120 litres. Water flow within the chamber was generated using an electric motor connected to an impeller and was rheostatically controlled. Calibration of motor speed and water velocity was performed at eight locations along the vertical mid-section of the swim chamber. The relationship between motor speed and water velocity at the centre of the swim chamber is described by Equation 1:

$$\text{water velocity} = 0.00312 + 0.00189 \times \text{motor speed}, \quad R^2 = 0.99 \qquad (1)$$

where, water speed is measured in $m.s^{-1}$ and motor speed in revolutions per minute.

The chamber could generate water velocities up to 2.6 $m.s^{-1}$ within two seconds. Cross-sectional velocity profiles revealed that there was a minimal edge effect, less than 4 cm at any speed. Ambient, untreated river water was pumped into the chamber. Maximum cross-sectional area of salmon used in swim trials was measured to ensure that adjustments could be made for the influence of the fish's body on water flow within the chamber, if necessary (Smit *et al.*, 1971).

The swimming performance of both tagged and untagged salmon was evaluated by measuring critical swimming speeds. Critical speed was determined after salmon had been in the swim chamber for three hours at a velocity of 1 body length. s^{-1}, after which water velocity was increased in a constant, stepwise progression. Critical swimming speeds (*U*crit) at 12 °C and 18°C were calculated using Brett's (1964) equation:

$$U\text{crit} = V + (t_i / t_{ii})u_i \qquad (2)$$

where, V is the highest velocity maintained for the prescribed period ($m.s^{-1}$), t_i is the time elapsed at final velocity (min), t_{ii} is the time increment (min) and u_i is the velocity increment ($m.s^{-1}$). A ten minute time interval and a 0.1 $m.s^{-1}$ velocity increment was used.

Endurance was measured at velocities just above the maximum sustainable swim speeds at 12°C and 18°C. Tests involved placing individuals into the chamber for an acclimation period of one hour after which the speed was immediately adjusted to the test velocity and time to fatigue noted. Five individuals were tested at each test velocity and temperature.

Measurements of critical speed and endurance depend on accurate and consistent recognition and definition of fish fatigue. The procedure used to determine metabolic fatigue involved stimulating individuals to

continue swimming using rapid changes in water velocity. In all cases, fish were considered fatigued when they failed to leave the downstream screen despite two to three attempts to stimulate them.

Correlation of salmon muscle activity of Atlantic salmon (N = 4 at each temperature) to swim performance was determined under forced swim conditions in the swim chamber described previously. Salmon fitted with transmitters were placed individually into the swim chamber and swum over the following range of water velocities: 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.0 and 2.2 $m.s^{-1}$. The relationship between muscle activity and swimming speed was determined using linear regression analyses.

In situ measurements within an experimental fishway

Swimming behaviour and performance of wild Atlantic salmon was recorded during their ascent of an experimental fishway. The fishway was constructed of plywood and plexiglass and consisted of a head pond and tail pond connected by a 20 m long sluice (30 cm wide and 20 cm high). The slope of the sluice was 1%, representing an offset vertical distance of approximately 44 cm. The water velocity within the flume ranged from 2.6 $m.s^{-1}$ at the downstream end to 1.85 $m.s^{-1}$ at the upstream end (average 2.1 $m.s^{-1}$). Flow within the fishway was not uniform and water velocities at the sides and bottom were typically 0.1-0.15 $m.s^{-1}$ less than in the centre of the fishway. Atlantic salmon (N = 4 at each temperature) were placed into the tail pond and were left to ascend the fishway at will. Most of the fish attempted to ascend the flume in the evening and, therefore, continuous recordings were made during the evening hours.

Statistical analyses

All values are represented as means ± standard error. Linear regression analysis was used to correlate swimming speed and muscle activity. Unpaired *t*-tests were used to compare swimming endurance of 12°C fish with that of 18°C fish. In all cases, $p < 0.05$ was the accepted level of significance.

RESULTS

Relationship of muscle activity to swimming speed

Swim performance of wild Atlantic salmon was lower at 12°C than at 18°C (Fig. 1). Maximum sustained swimming speed decreased by 1 $m.s^{-1}$ as temperature decreased from 18°C to 12°C. Sustained swimming speed of salmon at 12°C was also significantly lower than at 18°C. At burst velocities, swimming performance was independent of temperature, as

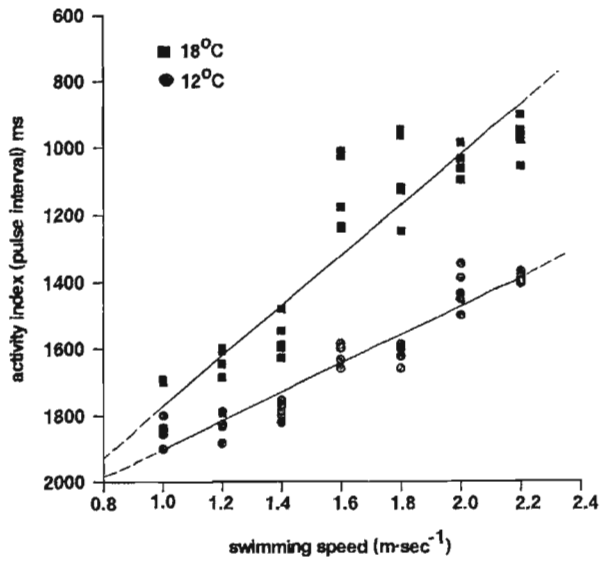

Figure 1. – Fatigue tests of swimming performance in wild Atlantic salmon (N = 5) conducted at 18°C and 12°C. Transition to exhaustion has been sub-divided into the following components: sustained, prolonged and burst swimming speeds. Dotted lines represent swimming endurance (*i.e.* time to fatigue) greater than 120 min.

indicated by the inability of salmon to maintain swimming speeds in excess of 2.40 $m.s^{-1}$ for periods greater than 10 s at either temperature (Fig. 1).

Critical swimming speed (U_{crit}) of salmon at 18°C and 12°C was 2.16 ± 0.18 $m.s^{-1}$ and 1.76 ± 0.06 $m.s^{-1}$, respectively ($p < 0.05$). Critical swimming velocities of untagged individuals were found to be 2.16 ± 0.18 $m.s^{-1}$ at 18°C and 1.76 ± 0.06 $m.s^{-1}$ at 12°C, while those of tagged salmon were 2.10 ± 0.05 $m.s^{-1}$ at 18°C and 1.80 ± 0.03 $m.s^{-1}$ at 12°C. There were no statistical differences between tagged and untagged salmon at either temperature ($p < 0.05$).

Regression analyses indicate that muscle activity was positively correlated to swimming performance at both temperatures (Fig. 2). The relationships between muscle activity and swimming speed are described by the following equations:

At 18°C,
muscle activity = 2 521.1 – 7.51 × swimming speed,
$R^2 = 0.85$ (4)

At 12 °C,
muscle activity = 2 330.8 – 4.29 × swimming speed,
$R^2 = 0.91$ (5)

where, muscle activity is in milliseconds and swimming speed is in $m.s^{-1}$. Temperature dependent differences in the muscle activity relative to swimming speed were only apparent beyond the critical swimming speeds indicated by the divergence of the regression lines. The relationship between swimming speed

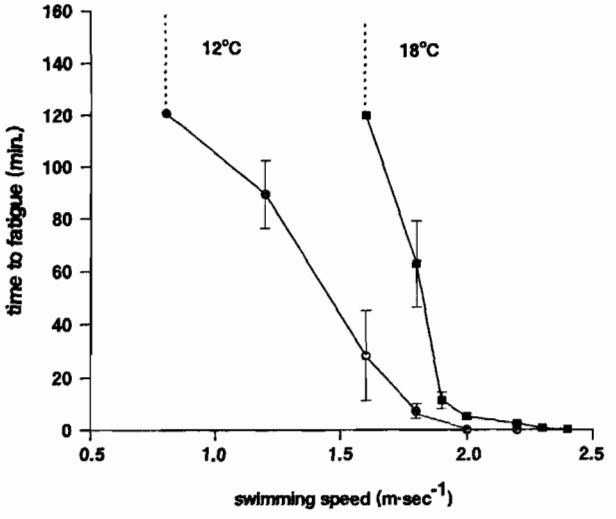

Figure 2. – Calibration of muscle activity with swimming performance in wild Atlantic salmon (N = 5), at 18°C and 12°C. Muscle activity was measured using radio transmitted electromyogram signals from the musculature of adult salmon under forced swimming conditions using a Blazka-type swim chamber.

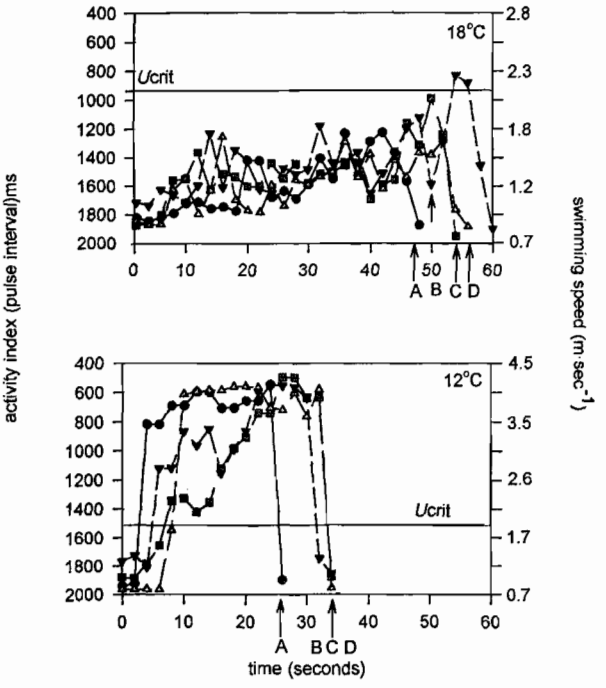

Figure 3. – Muscle activity recorded in wild Atlantic salmon (N = 4) during ascent of a 20 m long experimental fishway. Data were recorded in late summer (*i.e.* 18°C) and early fall (*i.e.* 12°C). Each symbol represents actual measurements of activity for an individual salmon. Critical swimming speeds and calculated swimming speeds corresponding to observed EMGi's are shown on the Y axis. A, B, C, D represent the exit times of each salmon from the flume.

and muscle activity was significantly different (slope 7.51) at 18°C than at 12°C (slope 4.51). The greater slope of the relationship at 18°C indicates that, at warmer temperatures, greater muscle activity results in higher overall swimming speeds.

Cross sectional area of fish used

Salmon possess an elliptical body shape with a dorsal ventral height ranging between 10 and 14 cm and a lateral width ranging between 9 and 12 cm, corresponding to cross sectional areas ranging from 58 to 66 cm^2. According to Smit *et al.* (1971), fish with cross sectional areas greater than 10% of the swim chamber must have swimming speeds corrected for influence of body size. Using the following equation from Smit *et al.* (1971), 'blocking effect' of salmon in our study would increase the actual swimming velocity by no more than 0.04 for the smallest salmon and 0.12 $m.s^{-1}$ for the largest. Therefore, conservative estimates of swimming performance were used and no correction was made for cross sectional area.

$$U_{corrected} = U_{measured} (1 + Area_{fish}/Area_{chamber}) \quad (3)$$

where, velocity is measured in $m.s^{-1}$, and U is the critical swimming speed ($m.s^{-1}$) of the corrected and actual measurement, respectively.

Experimental fishway study

Adult salmon exhibited two distinct patterns of swimming behaviour during ascent of the flume. At 18°C, swimming was continuous and characterised by a constant increase in muscle activity throughout the ascent. In contrast, at 12°C, the swimming behaviour of salmon was characterised by a rapid increase in muscle activity (within 10 s) to above U_{crit} levels, which then remained elevated throughout the ascent (Fig. 3).

At 18°C, ascent of the experimental fishway by salmon was achieved within the salmon's aerobic limits and below its critical swimming speed, indicating that an oxygen debt may have been incurred during ascent.

Overall, salmon traversed the fishway significantly faster at 12°C than at 18°C, requiring 31 ± 7 s and 47 ± 12 s, respectively. Part of the reason for the quicker ascent at 12°C is that fish swim at higher velocities. From equation 1 and 2, the respective mean swimming speed of salmon at 18°C is 1.4 $m.s^{-1}$, while the mean at 12°C is 2.87 $m.s^{-1}$. Because we could not use discreet positional telemetry, some of the activity recorded from salmon may be while fish were holding position. During these periods, swimming speeds may be high, while ground speeds are low or zero.

DISCUSSION

During the spawning migration of Atlantic salmon no food is consumed and all the energy required to migrate, sexually mature and spawn is derived from reserves stored in the body (Jonssen *et al.*, 1991). In some cases, the energetic costs associated with migration and spawning result in death, such as in Pacific salmon. In Atlantic salmon, however, migration and spawning does not result in death to all individuals and, indeed, some salmon may spawn several times during their lifetime. Consequently, additional energetic obstacles such as those induced anthropogenically (*i.e.* fishways) may result in a depletion of fishes' limited energy reserves and, in extreme cases, high post spawning mortality could occur.

Fishways represent a potential barrier to the upstream migration of Atlantic salmon. The limited numbers of studies concerning the effects of fishway design and water velocities on migratory fish, however, have resulted in controversy regarding the ability of salmon to navigate fishways. Fish are ectothermic and the energetic cost of activity is determined, to a large extent, by water temperature. Decreases in water temperature have been shown to significantly reduce a fishes' aerobic swimming capacity (Brett and Glass, 1973; Jayne and Lauder, 1994). Similarly, in this study the critical swimming speeds of wild Atlantic salmon were significantly reduced by temperature, decreasing from 2.16 ± 0.18 $m.s^{-1}$ to 1.76 ± 0.06 $m.s^{-1}$ at 18°C and 12°C, respectively. Below water velocities of 1.0 $m.s^{-1}$, salmon appear to possess a 'swimming block' and, regardless of temperature, many salmon chose to sit on the bottom of the chamber and did not swim. As a result, accurate data for swimming speeds below 1.0 m. s^{-1} was not obtained.

Low speed swimming, which includes sustained and prolonged activity, is supported by the red muscle fibres under aerobic conditions. Beamish (1978) defines sustained activity as that which fish can maintain for a minimum of 200 minutes and prolonged as that which can be maintained for less than 200 minutes but more than 30 seconds. Activity that can only be maintained for < 30 seconds is defined as burst activity, which is supported by the white musculature using anaerobic pathways.

The sustained and prolonged swimming velocities of Atlantic salmon also decreased significantly with decreased temperature but burst activity appeared unaffected. Thus, one may speculate that salmon required to swim at high water velocities when water temperatures are cold may depend more heavily on the use of white muscle fibres, fuelled through anaerobic metabolism. Previous studies have shown that a significant oxygen debt is acquired during anaerobic activity (Wood *et al.*, 1983). Beamish (1978) reported that the energetic costs of repaying this oxygen debt may be greater than the aerobic scope of the fish and exhaustive exercise may contribute to delayed mortality (Wood *et al.*, 1983). Consequently, ascent of fishways by Atlantic salmon requiring activity beyond their prolonged capabilities could result in increased levels of mortality.

To date, there have been few studies of swimming activity in wild fish. Physiological telemetry has been used previously to monitor the activity of fish in the wild. However, the number of studies are limited (Priede and Young, 1977; McKinley and Power, 1992; Demers *et al.*, 1996; Weatherly *et al.*, 1996). What information that is available is representative of very different species with different behaviours and swimming capabilities and no previous studies have been conducted on activity of Atlantic salmon. Successful calibration of radio transmitted EMGi signals with swimming performance allowed us to utilise measurement of *in situ* muscle activity to assess the activity of free swimming Atlantic salmon at two temperatures while successfully ascending an experimental fishway. At 18°C, the water velocity within the fishway (*i.e.* 2.1 $m.s^{-1}$) was below the critical swimming speed of salmon, and is reflected in the ability of salmon to ascend the flume with constant muscle activity and within aerobic capacity. In contrast, the muscle activity measured in salmon ascending the fishway at 12°C was more vigorous than at 18°C and probably reflects the reduced swimming capabilities of Atlantic salmon at 12°C, as determined under laboratory conditions. Furthermore, the majority of muscle activity exhibited by salmon at colder temperatures indicated that ascent of the fishway may have involved activity beyond its aerobic scope.

In the fall, water temperature decreased quickly and late migrants may, therefore, be subjected to additional stress when ascending fishways and navigating rapids. Barriers, either mechanical or hydraulic, routinely impede the natural migratory progress of salmon. On rivers which support large scale dams and utilise water for industry, the amount of energy used by salmon during migration may increase and limit spawning success. How much influence barriers will have on the energy expenditure of migrating salmon during fishway passage and, thus, ultimately affect the allocation of energy for reproduction requires further investigation.

CONCLUSION

This study demonstrated that radio transmitted EMGi signals can be correlated with swimming performance in Atlantic salmon. Using this procedure, salmon ascended an experimental fishway despite having to utilise high intensity, burst swimming and, therefore, may have incurred an oxygen debt. Collectively, our results suggest that physiological telemetry involving measurements of muscle activity can be used to evaluate fishway design relative to the swimming performance of wild Atlantic salmon.

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