Effect of short-term regulated temperature variations on the swimming economy of Atlantic salmon smolts

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Migratory species travelling long distances between habitats to spawn or feed are well adapted to optimize their swimming economy. However, human activities, such as river regulation, represent potential threats to fish migration by changing environmental parameters that will have impact on their metabolism. The main objective of this study was to evaluate the changes in the swimming energetics of a salmonid species, Atlantic salmon (Salmo salar L.), caused by short-term temperature variations that usually result from the operation of hydroelectrical dams. Intermittent flow respirometry in swim tunnels allows to obtain high resolution data on oxygen consumption of swimming fish which can reflect aerobic and anaerobic metabolism. This method was used to compare the metabolic rates of oxygen consumption before, during and after sudden thermal change. Control (no temperature variation) and experimental (temperature variation of approximately 4 °C in 1 h) swimming trials were conducted to achieve the following objectives: (i) quantify the variations in oxygen consumption associated with abrupt temperature decrease, and (ii) assess if the tested fish return quickly to initial oxygen consumption rates. Main results revealed that Atlantic salmon smolts show a strong response to sudden temperature variation, significantly reducing the oxygen consumption rate up to a seven-fold change. Fish quickly returned to initial swimming costs shortly after reestablishment of temperature values. Results from this study can be used to evaluate the species-specific effects of the applied operation modes by hydroelectrical dams and to increase the success of conservation and management actions directed to fish species inhabiting regulated rivers.

Key words: Hydropeaking, intermittent respirometry, oxygen consumption, Salmo salar, streamflow regulation

Introduction

Short-term streamflow regulation performed by dams operating for hydropower production (i.e. hydropeaking) is a drastic form of regulation in which high amplitude changes in flow occur suddenly and at completely unnatural rates. Within only a few hours the discharge can become many-fold higher and lower again (Poff et al., 1997; Bunn and Arthington, 2002). Besides streamflow, the abiotic component of riverine ecosystems considered to be most affected by
hydropower dams is the thermal regime (Poff et al., 1997; Naiman et al., 2008). Usually, there are major shifts in thermal patterns downstream of dams because water is released from below the thermocline, which is often deoxygenated and considerably colder than the water that would be normally transported in the system (Olden and Naiman, 2010). Like streamflow, below these dams, riverine thermal variations usually occur abruptly and several times per day and specific components of the thermal regime (e.g. amplitude of variation, maxima and minima, etc.) also have relevance for the ecology and physiology of freshwater organisms (Poff et al., 1997). Therefore, the integrity of the thermal regime may be just as important as the integrity of the natural flow regime (Olden and Naiman, 2010) and should be given relevance and priority when studying the effects of hydropower production on aquatic organisms.

From the standpoint of ichthyofauna, the high and unpredictable environmental variability caused by hydropower generation is even more important than the simple alteration of flow magnitudes (Scruton et al., 2003; Vehanen et al., 2005). On one hand, ecological effects of hydropowering on fish behaviour are well known (Taylor et al., 2014; Alexandre et al., 2015; Boavida et al., 2016) On the other hand, physiological effects (e.g. swimming demand, oxygen consumption and internal temperature regulation) caused by the increased environmental variability are, until this date, still poorly understood (Geist et al., 2005; Taylor et al., 2014). Moreover, specifically concerning the thermal regime, very few studies (Preece and Jones, 2002; Todd et al., 2005) have attempted to explore the individual and interactive effects of abrupt thermal modification related with dam operation on the riverine biota, especially on freshwater fish.

Considering the scarcity of information about hydropowering effects on the biology and physiology of affected freshwater fish assemblages, this study marks one of the first attempts to study the swimming economy of a fish species when subjected to abruptly varying environmental factors, more specifically water temperature. We aimed to assess the changes in the oxygen consumption rate of Atlantic salmon (Salmo salar L.) smolts, in response to water temperature variations within the range that is usually associated to known hydropowering phenomena. When studying smolts, knowledge on the relationship between fish movement and environmental variation during downstream migration is of high concern. Streamflow and temperature regimes are the two most important variables controlling migration of salmonid smolts to marine waters (Aldvén et al., 2015), therefore, significant alterations to these patterns downstream of hydropower dams, caused by hydropowering operations, can severely impair this ecological process and affect juvenile Atlantic salmon’s growth and survival.

Intermittent flow respirometry (Steffensen, 1989) was used to compare oxygen consumption rate (MO2) before, during and after abrupt temperature variation with the following specific objectives: (i) quantify the aerobic energy consumption variations associated with temperature decrease, and (ii) assess if fish can resume quickly previous physiological swimming costs. This method was consistently used in recent years to successfully assess the effect of natural long-term or circadian temperature fluctuations in the swimming performance and metabolism of distinct fish species (Beauregard et al., 2013; Chabot et al., 2016; Enders and Boisclair, 2016), but, to our knowledge, none addressed the effects of sudden and more accentuated temperature fluctuations usually associated to hydropowering operations. This type of information assessed at a small physiological scale is almost always left out of hydropowering-related studies which are normally more ecologically oriented, but can represent the basal explanation for some of the described responses at the assemblage level. Therefore, insights from this study can be crucial for the management and conservation of fish populations from rivers that undergo this type of flow regulation.

**Methods**

Experimental protocols complied with the current laws of the Netherlands and were approved by the animal experimental committee (DEC nr. 2014064).

**Swimming trials and oxygen consumption rate measurements**

Experiments to assess the effects of abrupt temperature variation on the metabolic costs of the swimming target species, the Atlantic salmon, were conducted at Wageningen Marine Research (Yerseke, The Netherlands) facilities during the spring of 2015, using four 127 L Blazka-type swim tunnels (van den Thillart et al., 2004 for a detailed description). Swim tunnels were placed in a climate room (15°C) with water recirculating from ambient tanks placed near the tunnels. Before each experiment, the water in the ambient tanks was renewed with fresh tap water. Each swim tunnel had a bypass system where a galvanic oxygen electrode, connected to a 4-channel respirometry system (DAQ-PAC-G4; Loligo Systems, Tjele, Denmark), was inserted to allow recording of dissolved oxygen concentration. During respirometry, water in the swim tunnels was recirculated through the bypasses and oxygen concentration in the system decreased due to the oxygen consumption of the swimming fish. Swimming trials were conducted with farmed Atlantic salmon smolts (n = 48; standard Body Length (BL): 10.30 ± 0.93 cm (mean ± std deviation); Body Weight (BW): 19.78 ± 4.92 g) which were transported by truck from Norway to the IMARES facilities, under adequate conditions of temperature and oxygen, well in advance to the beginning of the experiments. Fish were housed in a 8001 tank with freshwater at a light regime of 14 h light:10 h dark, before and during the trial periods. Fish were fed twice per day ad lib with commercial feed pellets (crude protein 43%, ether extract 29%, ash 7%, 3 mm, Skretting), except when they resided in the swim tunnels.
We performed a total of four trials, using all four tunnels in each trial, to determine and compare Atlantic salmon’s oxygen consumption rate when subjected to stable (two control trials) and varying (two treatment trials) temperature. The amplitude and rate of temperature variation used in these treatment trials were in accordance with the imposed photoperiod regime, and were based on the thermal regime registered downstream of a typical hydroelectrical dam from the Central Portugal, the Raiva dam, located in River Mondego (WGS84—Lat: 40°18′33″; Long: 8°14′59″), one of the largest and most important watercourses of the Iberian Peninsula. Temperature variation parameters downstream from this dam were previously assessed during a year using temperature data loggers. Information gathered during this period revealed that hydropoeaking events in River Mondego caused a decrease in water temperature of ~4°C in approximately 1 h.

Before each swimming trial, 12 Atlantic salmon were anaesthetized by immersion in a bath with 2-phenoxethanol at a concentration of 0.4 mL L⁻¹, measured (standard BL ±1 mm), weighed (BW; ±0.1 g) and randomly distributed over the four swim tunnels. Considering potential biases that could result from using small fish in larger respirometer tunnels (Svendsen et al., 2016a,b), such as the one used in this study, we used three fish per tunnel to reduce the respirometer-to-fish volume ratio. Fish were left inside the tunnels, swimming in water at ambient temperature, until the next day (15 h), to acclimate to experimental conditions. Next day, each experiment was started exactly within the same hour period (9:00—10:00 a.m.) to avoid data biases related with circadian activity rhythms of the tested fish. In all trials fish were swimming below their critical swimming speed (Peake, 2008) at a moderate constant velocity of 4 BL. s⁻¹ (based on the mean standard length of the three fish per swim tunnel with a range between 37.3–44.8 cm.s⁻¹). The choice for the swimming velocity of 4 BL. s⁻¹ was made on basis of a preliminary quick test in which this speed was determined as the lowest speed fully forcing fish to swim. Below 4 BL. s⁻¹ fish could lay still on the bottom using the pectoral fins as anchors. The applied swimming speed of 4 BL. s⁻¹ was close to the optimal swimming speed of 3.77 ± 0.10 BL. s⁻¹ that was determined on fish from the same batch in the same set-up (Böhm and Palstra, unpublished data).

During any type of swimming trial, one of the most commonly observed effects is solid blocking (SBE), which should be considered and corrected if needed, particularly when the ratio between fish square area and swim tunnel cross-sectional area is above 10% (Bell and Terhune, 1970). For this study, we performed a calculation of the error associated to solid block effect (SBE) to assess the need of a posterior correction of swim speed values. For all our trials, the ratio between the square area of the three fish and cross area of the swim tunnel working section was approximately 1%, so the SBE can be considered negligible (Bell and Terhune, 1970). When calculated, the associated fractional error is ca. 0.008 and the solid blocking correction factor is estimated as ca. 0.1, which would not change significantly the swimming speeds used. Therefore, swimming speeds applied in this study were not corrected for SBE.

In the treatment trials, water temperature of 15°C was kept constant for a 1-h period, after which water in the ambient tank was rapidly decreased (1 h) within the range previously defined as related with hydropoeaking events (4°C), until reaching 11°C. Fish were maintained swimming at this lower temperature for a period of 30 min, after which the temperature was again increased, during another hour period, until reaching the initial temperature of 15°C, mimicking what usually happens in the river/hydropower dam scenario from which the experimental pattern was derived. Sudden decrease and increase of water temperature was performed by using a set of two automatic chillers (HC-1000A, Valkenswaard, the Netherlands) and six submersible aquarium heaters, respectively. During the 230 h period of water temperature variation, this parameter was measured every 5 min in the ambient tank. Following this procedure, fish were kept swimming for three more hours, after which the trials were ended, resulting in a total trial duration of approximately 7 h. Oxygen content in the swim tunnels was continuously measured during the entire trial duration and so was the fish oxygen consumption, except for the flushing periods (i.e. 10 min) that were periodically performed to restore oxygen in the system to saturation levels before each new measuring period and to change temperature in the swim tunnel in accordance to the ambient tank. For the control trials, water temperature inside the ambient tank and swim tunnels was kept constant during the total duration of the experiment. We tried to maintain similar flushing periodicity between treatment and control trials but, since temperatures were kept constant in the latter, fewer periods were needed to measure oxygen values. The operator was the same for all the experiments and was constantly present to observe the behaviour of the swimming fish. The wall effect of the used swim tunnels comprises about two centimeters but fish were never observed to take advantage of it. At the end of the fish experiments, control and treatment blank trials (using a similar procedure but without fish swimming in the tunnels) were conducted to analyse, and if necessary compensate, for background oxygen consumption.

Data analysis

No background consumption was detected in the blank tests, so we could directly calculate the rate of O₂ consumption for each measuring period (and for all three smolts per tunnel) of each control and treatment trial (MO₂, mg.kg⁻¹.h⁻¹) without any compensation, using the following expression:

\[
MO₂ = \frac{∆sat(𝑡)}{BW},
\]

where: \( MO₂ \) is the oxygen consumption rate; \( ∆sat(𝑡) \) is the change in saturation level during the trial; and \( BW \) is the fish biomass.
where $\Delta$sat($t_{60}$) is the proportion (%) of decline in oxygen saturation inside the swim tunnels per hour, $mgO_2$ is the amount of oxygen in mg per % saturation under each respective temperature level, and BW is the total fish body mass in each swim tunnel. The average (mean ± SD) $r^2$ value associated with the slopes of $O_2$ variation over time (Table 1), considering all trials, was 0.894 ± 0.069. $MO_2$ calculations for each measuring period were performed and standardized for time periods with different durations throughout the trials (between 13 and 100 min). Non-linear oxygen depletion data during the mixing phase were omitted from analyses (Svendsen et al., 2016a).

Before any data analysis, assumptions for the use of appropriate parametric statistical methodologies, data normality and homogeneity of variances, were tested using the Shapiro–Wilk and Levene tests, respectively. Before the analysis of $MO_2$ variation within each type of trials, univariate analyses of variance (ANOVA) were applied to check for differences in fish size (SL), fish weight (BW) and fish body condition (Fulton’s Condition Index, $K = 100 \times BW/SL^3$) between control and treatment trials. After these preliminary analyses, and since multiple and consecutive $O_2$ measurements were conducted for the same group of fish, a repeated-measures ANOVA was used to test for significant differences in fish $MO_2$ between measuring periods within each trial, control and treatment, followed by Tukey post-hoc tests to identify significantly different periods.

**Results**

Fish size (ANOVA, $F_{1,46} = 1.25; P > 0.05$), weight (ANOVA, $F_{1,46} = 3.45; P > 0.05$) and Fulton’s Body Condition Factor (ANOVA, $F_{1,46} = 3.83; P > 0.05$) were not significantly different between control and experimental trials (Table 1), allowing us to continue with the planned $MO_2$ comparisons without considering potential bias from these factors in the results.

Atlantic salmon’s $MO_2$ showed significant differences between measuring periods during the control trials (Repeated-measures ANOVA, $F_{4,28} = 4.41; P < 0.05$). Temperature was kept constant during these trials but significant differences in $MO_2$ existed between the first (Period 1) and last (Period 5) measuring period, as revealed by following Tukey post-hoc tests, with higher $MO_2$ at the start (Fig. 1a). During the treatment trials, the pattern of $MO_2$ by the tested Atlantic salmons was quite distinct from the controls, clearly responding to the temperature variation protocol (Fig. 1b). In this case, highly significant differences between the experimental measuring periods were identified (Repeated-measures ANOVA, $F_{5,35} = 55.46; P < 0.001$). More specifically, Tukey post-hoc tests revealed the existence of $MO_2$ consumption between the lower $MO_2$ values during Periods 3 and 4, corresponding to the phases of sudden temperature variation, and the other measuring periods with significantly higher $MO_2$ values. Average $O_2$ consumption values registered during Periods 3 and 4 were clearly well below the average $MO_2$ at the regular water temperature of 15°C ($514 \, mg.kg^{-1} \, h^{-1}$). Oxygen consumption by Atlantic salmons during measuring Periods 5 and 6, recorded after the increase of water temperature back to initial values, was statistically similar ($P > 0.05$) to the first two measuring periods, recorded before the sudden decrease of water temperature.

**Discussion**

**Metabolic responses to temperature changes**

Many studies describe water temperature as the master variable controlling fishes’ swimming metabolism and energetic costs (Brett, 1965; Beaufregard et al., 2013; Enders and Boisclair, 2016). General assumptions state that, when fish are exposed to temperature changes during a sufficiently long period, they can obtain optimal performance by altering either their behaviour (preference/avoidance) or their physiology (adaptation/acclimation) (Bernatchez and Dodson, 1985; Lee et al., 2003; Oligny-Hébert et al., 2015). However, certain short-term variations in temperature, such as the ones occurring periodically in rivers regulated for hydroelectric production, may be unavoidable and their effects on the swimming metabolism of fish are much less known than the impacts of long-term thermal changes. Usually, a decrease in temperature results in a decrease in the rates of enzymatic reactions resulting in a reduction in metabolic rate of oxygen consumption (Hochachka and Somero, 2001). This is a well-established assumption in the field of fish physiology and our data corroborate it. In the control trials, Atlantic salmon’s $MO_2$ remained stable except for a significant decrease after nearly 6–7 h of swimming, probably due to training and/or habituation (Beamish, 1978; Janz et al., 1991). In the treatment trials, $MO_2$ followed the trend of environmental variation and significantly decreased (drop of ca. 70–80%) almost immediately after the sudden 4°C decrease in water temperature. After this, $MO_2$ rose again to previous values when temperature resumed its initial value. The overall pattern observed in this study, in which higher $MO_2$ values were associated to higher temperatures, and vice-versa, is consistent with previous studies for other fish species, namely rainbow trout (Oncorhynchus mykiss, Dickson and Kramer, 1971), sockeye salmon (Oncorhynchus nerka, Brett and Glass, 1973), largemouth-bass (Micropterus salmoides, Beamish, 1978; Cooke et al., 2001) and coho salmon (Oncorhynchus kisutch, Lee et al., 2003). When studying Atlantic salmon with similar length as ours (ca. 10–15 cm) Enders et al. (2003) obtained $MO_2$ values between 146 and 442 mg.kg$^{-1}$.h$^{-1}$ for fish swimming at 15°C, of which values for the smaller fish are comparable to the average $MO_2$ value of 514 mg.kg$^{-1}$.h$^{-1}$ obtained in our study. Beaufregard et al. (2013) and Oligny-Hébert et al. (2015), when studying Atlantic salmon juveniles, also reported a significant effect of diel temperature fluctuations ($±2.5°C$) on fish standard metabolic rate. Results from these studies indicate that circadian
Table 1: Biometrics of the Atlantic salmon smolts used in the respirometry trials

| Fish ID | SL (cm) | BW (g)  | K     | Swim tunnel | Type of trial | $r^2$ values (mean ± SD) |
|---------|---------|---------|-------|-------------|---------------|-------------------------|
| #1      | 10.5    | 20.6    | 1.78  | 1           | Control       | 0.993 ± 0.003           |
| #2      | 10.0    | 18.6    | 1.86  |             |               |                         |
| #3      | 9.5     | 14.8    | 1.73  |             |               |                         |
| #4      | 9.5     | 15.3    | 1.78  | 2           | Control       | 0.973 ± 0.024           |
| #5      | 10.7    | 19.3    | 1.57  |             |               |                         |
| #6      | 9.0     | 12.4    | 1.70  |             |               |                         |
| #7      | 10.0    | 16.6    | 1.66  | 3           | Control       | 0.975 ± 0.016           |
| #8      | 9.6     | 15.4    | 1.74  |             |               |                         |
| #9      | 8.4     | 10.5    | 1.77  |             |               |                         |
| #10     | 10.7    | 23.2    | 1.89  | 4           | Control       | 0.993 ± 0.003           |
| #11     | 8.5     | 11.1    | 1.81  |             |               |                         |
| #12     | 10.4    | 20.8    | 1.85  |             |               |                         |
| #13     | 10.8    | 22.5    | 1.79  | 1           | Control       | 0.956 ± 0.030           |
| #14     | 11.5    | 25.1    | 1.65  |             |               |                         |
| #15     | 8.9     | 13.5    | 1.91  |             |               |                         |
| #16     | 11.4    | 25.4    | 1.71  | 2           | Control       | 0.956 ± 0.030           |
| #17     | 11.3    | 21.5    | 1.49  |             |               |                         |
| #18     | 8.9     | 11.5    | 1.63  |             |               |                         |
| #19     | 11.0    | 20.4    | 1.53  | 3           | Control       | 0.889 ± 0.196           |
| #20     | 10.1    | 20.0    | 1.94  |             |               |                         |
| #21     | 10.1    | 18.8    | 1.82  |             |               |                         |
| #22     | 11.4    | 25.5    | 1.72  | 4           | Control       | 0.889 ± 0.196           |
| #23     | 11.4    | 23.5    | 1.59  |             |               |                         |
| #24     | 9.8     | 15.5    | 1.65  |             |               |                         |
| #25     | 11.1    | 24.6    | 1.80  | 1           | Treatment     | 0.862 ± 0.102           |
| #26     | 9.4     | 13.7    | 1.65  |             |               |                         |
| #27     | 10.3    | 18.4    | 1.68  |             |               |                         |
| #28     | 10.2    | 22.1    | 2.08  | 2           | Treatment     | 0.862 ± 0.102           |
| #29     | 10.5    | 21.4    | 1.85  |             |               |                         |
| #30     | 8.4     | 10.7    | 1.81  |             |               |                         |
| #31     | 10.5    | 21.5    | 1.86  | 3           | Treatment     | 0.853 ± 0.100           |
| #32     | 10.1    | 19.5    | 1.89  |             |               |                         |
| #33     | 10.2    | 19.5    | 1.84  |             |               |                         |
| #34     | 11.1    | 24.1    | 1.76  | 4           | Treatment     | 0.852 ± 0.163           |
| #35     | 10.4    | 18.5    | 1.64  |             |               |                         |
| #36     | 9.4     | 14.3    | 1.72  |             |               |                         |
| #37     | 11.9    | 32.4    | 1.92  | 1           | Treatment     | 0.852 ± 0.153           |
| #38     | 11.3    | 24.3    | 1.68  |             |               |                         |

(Continued)
temperature fluctuations can incur an additional metabolic cost to salmons, consequently affecting their growth. Our study showed that hydropeaking-related temperature changes are also affecting salmons’ swimming metabolism. These type of artificial temperature changes occur more suddenly and at higher magnitudes than natural diel temperature variations. Therefore, effects of human-induce thermal regulation on fish bio-ecology, namely growth patterns, can also occur, perhaps at a larger extent. However, most of the existent studies report on swimming trials where fish were subjected to distinct experimental protocols (i.e. performing several trials at different temperatures rather than performing one trial with a sudden temperature variation, or inducing temperature changes of lower magnitude) making it difficult to compare results. Lee et al. (2003) also analysed the effect of temperature on swimming performance and oxygen consumption of two salmonid species (sockeye and coho salmon). These authors showed that temperature changes of approximately 5°C were responsible for a significant drop of routine $\dot{M}O_2$, about 50% of the initial $\dot{M}O_2$ value, corroborating the results obtained in the present study. Differences between our study and Lee et al. (2003) regarding the drop of oxygen consumption as a percentage of the initial values may reflect the type of protocol applied, since in the Lee et al. study, temperature variations were applied between and not within swim trials, probably reducing the degree of immediate impact on tested fish.

The results gathered for the second objective of this study, to assess the recovery of the target species after being subjected to short-term temperature changes, provide new and valuable insights about the way freshwater fish react to this phenomenon. After being subjected to a sudden 4°C decrease in water temperature, Atlantic salmons lowered $\dot{M}O_2$ values and rapidly re-established their regular metabolism when temperature returned to initial values. Earlier laboratory-based studies, also developed with hatchery-raised salmonid specimens (rainbow trout and sockeye salmon), show that these species can recover quickly when subjected to swimming speed tests. A 45-min recovery period was sufficient for these fishes to be able to repeat their previous swimming performance, both in terms of critical speed and $\dot{M}O_2$, even when they swam to exhaustion, which was not the case in our study (Jain et al., 1997; Farrell et al., 1998). As for the recovery period in our study, between the period of lower

**Table 1: continued**

| Fish ID | SL (cm) | BW (g) | K       | Swim tunnel | Type of trial | $r^2$ values (mean ± SD) |
|--------|---------|--------|---------|-------------|---------------|-------------------------|
| #39    | 10.4    | 19.7   | 1.75    |             |               |                         |
| #40    | 10.5    | 22.6   | 1.95    |             | Treatment     |                         |
| #41    | 11.3    | 26.7   | 1.85    |             |               | 0.862 ± 0.103           |
| #42    | 11.0    | 24.2   | 1.82    |             |               | 0.898 ± 0.090           |
| #43    | 11.2    | 24.8   | 1.76    |             |               |                         |
| #44    | 10.9    | 22.5   | 1.74    |             |               |                         |
| #45    | 10.5    | 19.9   | 1.72    |             |               |                         |
| #46    | 11.0    | 24.6   | 1.85    |             | Treatment     | 0.891 ± 0.123           |
| #47    | 10.9    | 21.8   | 1.68    |             |               |                         |
| #48    | 8.1     | 11.7   | 2.21    |             |               |                         |

Average $r^2$ values for slopes of $O_2$ variation over time are also presented for each trial. SL—Standard length; BW—Body Weight; K—Fulton’s Body Condition Factor.

**Figure 1:** Average oxygen consumption ($\dot{M}O_2$ average ± SD; mg.kg$^{-1}$.h$^{-1}$) for each measuring period in control (a) and treatment (b) fish swimming trials; Distinct letters (a and b) above bars indicate significantly different measuring periods; Steps of temperature variation steps during the experiments are represented by the black short lines; Average $\dot{M}O_2$ calculated for the control trials, at 15°C (514 mg.kg$^{-1}$.h$^{-1}$) is represented by the black dashed line.
Water temperature (Period 3) and the period in which temperature resumed its initial values (Period 5), \( \text{MO}_2 \) remained low (c.f. Period 4 in Fig. 1b) although fish were swimming for an entire hour. If there was a ‘quasi’-linear relationship between temperature and \( \text{MO}_2 \) (Hochachka and Somero, 2001), Periods 2 and 4 (both at ~12°C) would be expected to be similar in terms of swimming costs but this was not the case in our study. During temperature rise, there is an apparent delay of its effect on Atlantic salmon’ \( \text{MO}_2 \), but this delay seems to disappear when fish resume their initial \( \text{MO}_2 \) level as soon as temperature is back to 15°C. More experiments are needed to support these data but, from our study, it can be concluded that typical scenarios of sudden thermal changes, like hydropeaking events, do not have a durable effect on swimming salmon smolts. As is shown by our results, after environmental conditions have returned to normal, fish regain rapidly previous metabolic rate levels. Absence of higher \( \text{MO}_2 \) than the initial values after return may indicate the absence of stress induced by a short-term regulated temperature variation of 4°C but cortisol measurements may support this conclusion in future experiments.

**Conservation issues and future directions**

The results obtained in this study can be the starting point for collection of a large set of physiological data that can be used to improve the management of hydroelectrical dams to promote more effective conservation and protection actions for affected fish species and populations. Migratory species such as the Atlantic salmon travel long distances between habitats to spawn or feed and are well adapted to optimize swimming economy (Lennox et al., 2016). Unexpected extreme values and short-term variations of either temperature or water velocity, such as the ones that usually happen in rivers regulated for hydropower production, can alter active metabolic rates and contribute to incomplete or delayed fish migrations through difficult stretches of impounded river systems (Macdonald et al., 2000). Knowledge about the physiological responses and recovery rates of fishes to sudden environmental changes is extremely important to promote timely migratory passages and reproduction success, when salmonids, as well as other migratory fish, face repetitive hydraulic and thermal challenges during their upstream migration in flow regulated rivers (Farrell et al., 2003).

In this study, we tested the effect of thermal variation but there are other biological (e.g. sex, energy reserves, gonad maturation) and environmental (e.g. dissolved oxygen, turbidity and current velocity) factors that may also influence oxygen consumption rates of individual migratory fish (Dickson and Kramer, 1971). Concerning specifically the described environmental factors, most of them can be severely and suddenly altered when hydropower dams operate. Future studies should evaluate the effects of these factors, individually and multifactorially, on the swimming economy of fish. Besides that, more insights should be gained on the species-specific effects of hydropeaking to increase the representativeness and applicability of obtained results and the suitability of conservation and management measures. Future work should address the effects of hydropeaking-related abiotic changes in other fish species, particularly cyprinids, which are abundant in world regions currently facing increasing hydroelectric exploitation (e.g. Europe and Australia; Arthington, 2012).

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**References**

Aldvén D, Degerman E, Höjesjö J (2015) Environmental cues and downstream migration of anadromous brown trout (Salmo trutta) and Atlantic salmon (Salmo salar) smolts. Boreal Environ Res 20: 35–44.

Alexandre CM, Almeida PR, Neves T, Mateus CS, Costa JL, Quintella BR (2015) Effects of flow regulation on the movement patterns and habitat use of a potamodromous cyprinid species. Ecohydrology. doi:10.1002/eco.1638.

Arthington AH (2012) Environmental Flows: Saving Rivers in the Third Millennium. University of California Press, Los Angeles, California, USA.

Beamish FWH (1978) Swimming capacity. In Hoar WS, Randall DJ, eds, *Fish Physiology*, Vol. 7. Academic Press, New York, pp 101–187.

Beauregard D, Enders E, Boisclair D (2013) Consequences of circadian fluctuations in water temperature on the standard metabolic rate of Atlantic salmon parr (Salmo salar). Can J Fish Aquat Sci 70: 1072–1081.

Bell WH, Terhune LDB (1970) Water tunnel designs for fisheries research. *Fisheries Research Board of Canada*. Technical Report 195.

Bernatchez L, Dodson JJ (1985) Influence of temperature and current speed on the swimming capacity of lake whitefish (Coregonus clupeaformis) and cisco (C. arctic). Can J Fish Aquat Sci 42: 1522–1529.
Boavida I, Harby A, Clarke KD, Heggenes J (2016) Move or stay: habitat use and movements by Atlantic salmon parr (Salmo salar) during induced rapid flow variations. Hydrobiologia. doi:10.1007/s10750-016-2931-3.

Brett JR (1965). The relation of size to rate of oxygen consumption and sustained swimming performance of sockeye salmon (Oncorhynchus nerka). J Fish Res Board Can 22: 1491–1501.

Brett JR, Glass NR (1973) Metabolic rates and critical swimming speeds of sockeye salmon, Oncorhynchus nerka, in relation to size and temperature. J Fish Res Board Can 30: 379–387.

Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ Manage 30: 492–507.

Chabot D, McKenzie DJ, Craig JF (2016) Metabolic rate in fishes: definitions, methods and significance for conservation physiology. J Fish Biol 88: 1–9.

Cooke SJ, Kassler TW, Philipp DP (2001) Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management. J Fish Biol 59: 248–268.

Dickson IW, Kramer RH (1971) Factors influencing scope for activity and active and standard metabolism of rainbow trout (Salmo gairdneri). J Fish Res Board Can 28: 587–592.

Enders EC, Boisclair D, Roy AG (2003) The effect of turbulence on the performance of sockeye salmon (Oncorhynchus nerka) during induced migration. J Exp Biol 206: 3239–3251.

Lennox RJ, Chapman JM, Souliere CM, Tudorache C, Wikelski M, Metcalfe JD, Cooke SJ (2016) Conservation physiology of animal migration. Conserv Physiol 4: 1–15.

Macdonald JS, Foreman MGG, Farrell T, Williams IV, Gout J, Cass A, Woodley JC, Enzenhofer H, Clarke WC, Houtman R, et al. (2000) The influence of extreme water temperatures on migrating Fraser River sockeye salmon during the 1998 spawning season. Can Tec Rep Fish Aquat Sci 2326: 1–117.

Naiman RJ, Latterell JJ, Pettit NE, Olden JD (2008) Flow variability and the vitality of river system. CR Geosci 340: 629–643.

Olden JD, Naiman RJ (2010) Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. Freshwater Biol 55: 86–107.

Oligny-Hébert H, Senay C, Enders EC, Boisclair D (2015) Effects of diel temperature fluctuation on the standard metabolic rate of juvenile Atlantic salmon (Salmo salar): influence of acclimation temperature and provenience. Can J Fish Aquat Sci 72: 1–10.

Peake SJ (2008) Swimming performance and behavior of fish species endemic to Newfoundland and Labrador: a literature review for the purpose of establishing design and water velocity criteria for fishways and culverts. Can J Fish Aquat Sci 2843: v1–52.

Poff NL, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. Bioscience 47: 769–784.

Preece RM, Jones HA (2002) The effect of Keepit Dam on the temperature regime of the Namoi River, Australia. River Res Appl 18: 397–414.

Scrupton DA, Ollerhead LMN, Clarke KD, Pennell C, Alfredsen K, Harby A, Kelley D (2003) The environmental response of juvenile Atlantic salmon (Salmo salar) and brook trout (Salvelinus fontinalis) to experimental hydropeaking on a Newfoundland (Canada) river. River Res Appl 19: 577–587.

Steffensen JF (1989) Some errors in respirometry of aquatic breathers: how to avoid and correct for them. Fish Physiol Biochem 6: 49–59.

Swendsen MBS, Bushnell PG, Christensen EAF, Steffensen JF (2016b) Sources of variation in oxygen consumption of aquatic animals demonstrated by simulated constant oxygen consumption and respirometers of different sizes. J Fish Biol 88: 51–64.

Taylor MK, Hasler CT, Findlay CS, Lewis B, Schmidt DC, Hinch SG, Cooke SJ (2014) Hydrologic correlates of bull trout (Salvelinus
confluentus) swimming activity in a hydropoaking river. River Res Appl 30: 756–765.

Todd CR, Ryan T, Nicol SJ, Bearlin AR (2005) The impact of cold water releases on the critical period of post-spawning survival and its implications for Murray cod (Maccullochella peeli peelii); a case study of the Mitta Mitta River, southeastern Australia. River Res Appl 21: 1035–1052.

van den Thillart G, van Ginneken V, Körner F, Heijmans R, VanDerLinden R, Gluvers A (2004) Endurance swimming of European eel. J Fish Biol 65: 312–318.

Vehanen T, Jurvelius J, Lahti M (2005) Habitat utilization by fish community in a short-term regulated river reservoir. Hydrobiologia 545: 257–270.