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Diel activity and foraging mode of juvenile Arctic charr in fluctuating water flow

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Abstract

Streams fluctuate in water flow because of natural (e.g., rain) and human-induced events (e.g., hydropeaking). Magnitude, frequency, and predictability of these events can have drastic consequences for fish populations. We studied how rapid modifications of water flow affect diel activity and foraging mode of juvenile Arctic charr *Salvelinus alpinus* in stream enclosures exposed to either stable (intermediate) or fluctuating (low vs. high) water flow. Under stable conditions, Arctic charr showed limited activity (9.4%). In fluctuating water flow, charr increased activity during low flow periods, especially during the first hours after the flow decreased, but ceased activity almost completely at high flow. Charr were mostly nocturnal, and more nocturnal at low than intermediate water flow. Fish were more mobile and swam faster during prey search and attacked prey at longer distances at low water flow. Activity and foraging mode differed between the first and second day after reduced water flow, suggesting that Arctic charr require time to adjust their foraging behaviour. This study demonstrates the importance of behavioural flexibility for population ecology in fluctuating environments such as regulated rivers.

KEYWORDS

behavioural flexibility, current velocity, hydropeaking, *Salvelinus alpinus*, stream enclosures

1 | INTRODUCTION

Freshwater systems are characterized by fluctuations in ecological parameters like water temperature, depth, and current velocity (Poff et al., 1997). Such fluctuations affect the availability and distribution of suitable foraging microhabitats, to which organisms can respond directly by relocating (Clobert, Danchin, Dhondt, & Nichols, 2001), or modifying their foraging behaviour (Dill, 1983). Employing either tactic should impact individual fitness, for example, through foraging opportunities, growth, and survival (Dill, 1983). Stream salmonids are well suited to test the effect of environmental fluctuations on behaviour. They can move to new habitats rapidly (Armstrong, Braithwaite, & Fox, 1998) but can also show strong site fidelity, even after acute modifications of their habitat (Scruton et al., 2003), requiring them to adjust their behaviour accordingly. In spite of this flexibility, human-induced habitat modifications are expected to have drastic effects on salmonid populations (Jonsson & Jonsson, 2009), which highlights the importance of studying the behaviour of salmonids in rapidly changing conditions (Young, Cech Jr, & Thompson, 2011).

Although extensive variation exists in the flow regime of rivers at different spatial scales, some fluctuations in water flow are predictable in time (Poff et al., 1997), for instance, increases in water flow associated with spring snowmelt. Fluctuations in water flow may also result from unpredictable, sometimes extreme events such as floods and droughts (Magoulick & Kobza, 2003). Additionally, natural water flow can be altered by humans, for example, via hydroelectric dams. The magnitude, duration, and frequency of hydropeaking events depends on human demands for electricity and sometimes follow predictable patterns, for example, when the water is stored at night and released during the day or vice versa (Scruton et al., 2005). However, hydropeaking can alter the flow regime more drastically and

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unpredictably on a day-to-day basis (Murchie et al., 2008), with sometimes several peaks per day (Scruton et al., 2008). Whether salmonids can cope with disturbances caused by hydropeaking may depend on the frequency and predictability of associated water flow fluctuations and the behavioural flexibility of the fish.

Many studies examine the impact of hydroelectric dams on several aspects of salmonid ecology and physiology, including plasma levels (Flodmark et al., 2002), space use (Scruton et al., 2005; Vehanen, Bjerke, Heggenes, Huusko, & Mäki–Petäys, A., 2000), and growth (Flodmark, Vøllestad, & Forseth, 2004). Rapid fluctuations in water flow can also affect temporal aspects of stream fishes behaviour, for example, small and large-scale movements, relocation, and habitat use (Korman & Campana, 2009; Krimmer, Paul, Hontela, & Rasmussen, 2011; Riley, Maxwell, Pawson, & Ives, 2009; Scruton et al., 2005; Taylor et al., 2014). Other studies have suggested that salmonids also alter their diel feeding activity in response to hydropeaking (e.g., Rocaspana, Aparicio, Vinyoles, & Palau, 2016). Salmonids show extensive flexibility in diel activity (Reebs, 2002) and can adjust it in response to daily variations of food availability and predation risk (Larranaga & Steingrímsson, 2015; Orpwood, Griffiths, & Armstrong, 2006). This is of particular relevance in the context of hydropeaking rivers, because modifications of water flow can also affect several aspects of freshwater fish ecology. At low water depth or current velocity, less food is available, and fish are more conspicuous to avian and terrestrial predators (Lonzarich & Quinn, 1995; Nislow, Folt, & Seandel, 1998), which can affect the costs and benefits of different activity patterns.

How stream fishes respond to fluctuating water flow may depend on how well they perform in different habitats. There is extensive variation in habitat use among salmonid species (Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003). For instance, our study species, the Arctic charr *Salvelinus alpinus*, tends to use slow habitats (Heggenes & Saltveit, 2007; Tunney & Steingrímsson, 2012), although this may reflect competitive exclusion by other salmonids rather than habitat preferences per se. If habitat availability is limited, which should occur under strong fluctuations of water flow, one may thus expect that Arctic charr should restrict their activity to periods of low water flow (LWF) and that species with preferences for faster-running water should display the opposite pattern.

Stream salmonids are visual predators feeding on drifting invertebrates (Tunney & Steingrímsson, 2012). Their ability to detect and capture prey is highest during the day (Elliott, 2011). At night, low visibility decreases aggression (Cromwell & Kennedy, 2011) and the distance between individuals (Valdimarsson & Metcalfe, 2001). Depending on water temperature, prey attack distance is typically shorter at night (Nicieza & Metcalfe, 1997). Salmonids can mitigate reduced night-time foraging efficiency by selecting slower waters where drifting food is easier to detect (Polacek & James, 2003). In turn, they can modify their mobility while searching for and attacking prey in different habitats to increase their energetic intake (Grant & Noakes, 1988; Tunney & Steingrímsson, 2012). Fluctuations due to hydropeaking affect the temporal availability and distribution of optimal habitats, as well as food availability, which may affect how salmonids distribute their foraging effort in time (e.g., diel activity).

We conducted a 10-day experiment to study the effect of fluctuating water flow on the diel activity and foraging mode (mobility and speed while searching for prey, foraging radius, and prey attack rates) of individually tagged juvenile Arctic charr. We used stream enclosures where fish were constrained to habitats where water flow was stable and intermediate, or fluctuated between high and low water level every other day. On the basis of Arctic charr's preference for slow-running habitats (Heggenes & Saltveit, 2007) and on contrasting costs associated with daytime and night-time activity (Metcalfe, Fraser, & Burns, 1999), we tested the predictions that, under fluctuating flows, (a) fish will alter their activity patterns so that they are more active and more nocturnal during low flow periods, and (b) foraging mode will likewise be altered so that fish will display more mobility and faster swimming during prey searches in low water level conditions.

2 | MATERIALS AND METHODS

2.1 | Sampling

On July 24–25, 2014, we sampled 60 parr (age 1+) Arctic charr, respectively, via electrofishing (Smith-Root LR-24) in a tributary of the river Deildará in northern Iceland (N 65.849379, W 19.222297). Fish were anaesthetized with phenoxyethanol, measured for fork length to the closest 0.1 mm (with calipers) and body mass to the closest 0.01 g (PESOLA® PPS200). On average (±standard deviation), the study fish were 59.5 (±5.9) mm and 1.91 (±0.68) g. Age was determined based on the size distribution of Arctic charr in the stream. Fish were individually tagged using combinations of visible implant elastomers (red, green, orange, and yellow) injected in two specific positions of the dorsal fin (Steingrímsson & Grant, 2003). The tags spread along the fin rays, which permitted identification during overhead observations. Arctic charr were randomly assigned to one of six stream enclosures and given 24 hr to adjust to the experimental conditions before starting behavioural observations. The experiment was terminated on August 5, 2014 when fish were captured and measured for final body length and mass. All 1+ fish were successfully retrieved, and no tag had faded to the point of impeding individual identifications during observations. On average, fish were 60.1 (±6.7) mm and 1.99 (±0.75) g at the end of the study. Initially, we also placed four young-of-the-year Arctic charr, average 32.4 (±1.3) mm and 0.23 (±0.03) g, in each enclosure, but these were not detected until all, except three, were recaptured at the end of the study.

2.2 | Experimental design

Six stream enclosures (4 m long, 1 m wide, and 0.75 m high) were installed where the study tributary separates into two channels. Two enclosures were situated 10 m upstream from the divide, side by side, where the water flow showed natural and limited fluctuation. Two enclosures were situated in separate locations along each channel downstream of the divide. During the first 2 days of the study (control phase), we ensured that the water flow was similar in all enclosures (ANOVA, p = .358 for current velocity and p = .383 for water depth). On the third day of the experiment (water flow manipulation phase), at 13:30, we placed a barrier of cobbles, boulders, and black plastic tarp at the upstream end of the right channel thus diverting water to the left channel (facing downstream) for two subsequent days. After this switch, two enclosures had deeper and faster habitats than the stable flow enclosures, while the other two had shallower and slower habitats. After 48 hr, the flow was switched to the right side for another 2 days, by moving the barrier upstream on the left side. This was repeated a second time, so that each channel had 4 (2 × 2) days of low flow and 4 days of high flow.

Enclosures were made of 5 mm nylon mesh, that is, large enough for invertebrates to drift through and small enough to ensure 1+ fish remained within their enclosure. Enclosures were covered with substrate from the study stream. A string was tied across the top of each enclosure to deter avian predators, presumably without affecting the risk perceived by fish (Larranaga & Steingrímsson, 2015). Each enclosure had ten 1+ individuals (and four young-of-the-year), which is a high enough density to create competition for food and space in a 4 m^2 enclosure (Fingerle, Larranaga, & Steingrímsson, 2016; Larranaga & Steingrímsson, 2015).

2.3 | Habitat and food availability

Throughout the experiment, water depth and current velocity in all treatments remained within the reported range of habitats used by Arctic charr (Heggenes & Saltveit, 2007; Tunney & Steingrímsson, 2012). Water depth and current velocity (at 40% of the water depth, measured from the bottom, Davis & Barmuta, 1989) were measured at the beginning of the experiment. Water depth was measured at 100 *x*–*y* coordinates in each enclosure (at 20-cm intervals on each axis, starting 10 cm from the sides). Current velocity was measured at five points along four parallel transects separated by 1 m, starting 50 cm from the top with a Flo-MateTM Model 2000CM (Marsh-McBirney Inc., Frederick, MD) current velocity metre. During the initial 2-day control phase, the average depth across the six enclosures was 23.5 (±3.9) cm, and the average current velocity was 14.7 (± 6.0) cm/s.

After each switch of water flow from one channel to the other, water depth and current velocity were measured at 24 random locations in each enclosure (4 times during this period). In the stable flow enclosures, water depth was 24.7 (±8.7) cm, and current velocity was 12.5 (±7.0) cm/s. In the LWF treatment, mean water depth was 14.2 (±2.7) cm, and current velocity was 5.2 (±1.9) cm/s. At high water flow (HWF), water depth was 33.5 (±3.6) cm, and current velocity was 21.1 (±3.3) cm/s. Two enclosures within the same treatment always had similar habitats ($p > .05$ in all cases). Habitat availability within all three treatments of water flow did not differ between the rounds of measurements (ANOVA, $p > .1$, for water depth and current velocity in all cases), indicating that the average discharge in the stream remained stable.

We measured the density of drifting invertebrates in each enclosure during the control phase (August 26 between 12:00 and 13:00) via a drift net (40 cm wide and 25 cm high) immersed for 5 min. Fewer organisms drifted in the upstream (35.7 and 7.1 organisms m^{-3}) than in the downstream enclosures (205.3, 83.0, 123.0, and 57.2 organisms m^{-3}). However, these short measurements may not reflect the variability in drift rates among enclosures. In addition, the difference should be limited compared with differences in food availability (no. of organisms flowing through a transection of the water column) induced by the extremes in water flow. Indeed, water discharge varied about 9.6 fold between the low and HWF conditions.

Water temperature was recorded every hour to the closest 0.2 °C during the experiment by data loggers positioned at each enclosure (Onset® HOBO® UTBI-001 TidBiTv2). Light intensity was also measured every hour by data loggers positioned at the most upstream and downstream enclosures (UA-002-08 HOBO Pendant® Temp/Light, 8K). As there were only minor differences in water temperature and light intensity among enclosures (smaller than the accuracy of the data loggers), we used values from the data loggers positioned in the stable flow enclosures. On average, water temperature was 6.7 (±1.0, range = 5.1–9.0) °C and light intensity was 19.7 (±18.3, range = 0.1–69.3) kilolux.

2.4 | Behavioural observations

Observations started on July 26, 2014 (15:00) and finished on August 4 (12:00). Two persons observed fish in all enclosures every 3 hr (00:00, 03:00, etc.) during 10 days, yielding a total of 80 measurements of activity per enclosure. Bright summer nights in Iceland permitted visual observations and individual identification without the aid of artificial light. Observers alternated every day and hence distributed the observations equally throughout the study. Algae and debris were removed from all enclosures after a round of observations to ensure unhindered water flow. Enclosures were visited in a random order during each observation period, but the two enclosures in each treatment were always visited consecutively. During each observation, we remained motionless in front of an enclosure for 5 min and then recorded activity for 10 min. We measured overall activity rates as the proportion of fish active in each enclosure during each scan. An individual was considered active during a particular observation if it was observed feeding actively. Hence, inactive fish were either hiding, or in rare cases, remained motionless on the bottom without showing any foraging effort (Larranaga & Steingrímsson, 2015). Once a fish emerged, it was usually active for the rest of the 15 min observation.

We collected data on foraging mode for all active individuals. During each observation, we recorded the foraging mode of all active individuals during 3 min (McLaughlin, Grant, & Kramer, 1992). When more than three individuals were active simultaneously in an enclosure, observations of foraging mode, but not activity, were extended beyond 15 min. Time was kept with a digital timer that emitted a pulse every 5 s. Each observation alternated between one to three consecutive 5-s intervals of monitoring and a 5-s interval where these data were recorded. Each 5-s interval was classified as either pursuit or search. Pursuit intervals correspond to a situation where a focal individual made at least one feeding attempt, whereas search intervals correspond to periods where fish did not attack prey (McLaughlin et al., 1992; Tunney & Steingrímsson, 2012). Multiple feeding attempts in a single 5-s interval were rare throughout the study and were not distinguished from single attempts. Similarly, the rare 5-s intervals where aggression was detected were excluded from the analyses ($N = 55$ and 0.58% of the 5-s intervals). We quantified the mobility during search intervals in number of body lengths. Search mobility corresponds to the proportion of search intervals during which an individual moved one or more body lengths (McLaughlin et al., 1992). Search speed corresponds to the number of body lengths moved during a 5-s search interval (McLaughlin et al., 1992). During pursuit intervals, we measured the foraging radius (in body lengths) as the distance between the locations where an attack was initiated and where the prey was intercepted. We measured prey attack rates as the proportion of intervals when a focal fish attacked at least one prey (Larranaga & Steingrímsson, 2015).

2.5 | Data analysis

The distribution of activity rates, expressed as the number of individuals active per enclosure, was right-skewed because there were many observations with no or few fish active. We used a Generalized Linear Mixed Models (GLMM) with a Poisson distribution to assess the effect of water flow treatment, time of day (day from 06:00 to 18:00, night from 21:00 to 03:00), and their interaction on activity rates. We used a similar model (GLMM) to test if there was a difference in activity rates between the first and second switch of water flow and between the first and second day after the switch in the enclosures with fluctuating water flow. Enclosures were considered as a random factor in both models.

The four foraging mode variables were normally distributed. We built linear mixed models (LMM) to estimate the association between explanatory variables (treatment, time of day, and interaction), and search mobility, search speed, foraging radius, and prey attack rates. A second series of LMM was used to detect potential differences between the first and second switch to LWF, and the first and second day after a switch to LWF. For each of the four foraging mode models, enclosure, as well as individual fish ID were included as random factors. For every model, we tested all possible combinations of variables using the function *dredge* from the *MuMin* package in R (Barton, 2009) and selected the best model based on its Akaike Information Criterion (AIC; REML was fixed as false). The difference in AIC values between the best and second best model was always higher than 2, suggesting a single best model in each dataset (Burnham & Anderson, 2002). Hence, four types of models were used and were of the form:

Model 1. Activity (GLMM) ~ Water flow treatment + Time of day + Water flow treatment × Time of day + enclosure (random)

Model 2. Foraging mode (LMM) ~ Water flow treatment + Time of day + Water flow treatment × Time of day + enclosure (random) + Fish ID (random)

Model 3. Activity at LWF (GLMM) ~ Switch + Number of days since switch + enclosure (random)

Model 4. Foraging mode at LWF (LMM) ~ Switch + Number of days since switch + enclosure (random) + Fish ID (random)

Based on the non-normal distribution of overall activity rates, we compared activity among enclosures during the control phase of the study, and throughout the study in the upstream enclosures using Wilcoxon signed-rank tests or Kruskal–Wallis tests. For all tests, a *p* value lower than 0.05 was used to determine the significance of effects.

For each individual, we calculated the circular mean and standard deviation as indexes of the mean time of activity and the dispersion of activity, respectively (Larranaga & Steingrímsson, 2015). The mean time of activity indicates the position of an individual's span of activity around the clock, and the dispersion is a descriptor of its tendency to spread its activity over long or short periods. We used a circular ANOVA (Batschelet, 1981) to compare the distribution of mean times of activity between treatments. A Wilcoxon signed-rank test was used to assess the effect of water flow on the dispersion of activity.

3 | RESULTS

We report behavioural data only for fish of age 1+, as YOY were not detected throughout the study. During the control phase, the mean overall activity rate was 9.4 ± 12.3% (Figure 1), and similar among enclosures except for one of the two upstream enclosures where fish were significantly more active (Wilcoxon signed-rank test, p < .001 when compared with all five other enclosures, p > .05 for all other comparisons). During the water flow manipulation phase, the mean overall activity rate was 10.9 ± 11.1% in the upstream enclosures with stable intermediate water flow (IWF). Overall activity rate was 13.8 ± 14.5% at LWF, and similar among enclosures (Wilcoxon signed-rank test, p = .998). However, at HWF, only one fish was observed active and only once (Figure 1). Therefore, we did not consider data from HWF in the rest of our analyses. Fish were more active at LWF than IWF (GLMM, p < .001, Table 1, Figure 1). Overall activity rates remained similar in the stable flow enclosures throughout the study (Kruskal–Wallis test, p = .133, Figure 1). More fish were active during the first day after a switch to LWF than during the second day (Figure 3, Table 2).

During the manipulation phase, and as expected, fish were significantly more active at night than during the day, at both IWF and LWF (Table 1, Figure 2). Overall, the mean time of activity was 22:10 (±6:27, hh:mm), but it differed significantly between IWF (21:20 ± 5:51) and LWF (23:27 ± 6:51, circular ANOVA, p < .001). The dispersion of activity was 4:32 (±2:09) overall, 5:10 (±1:57) at IWF, and 4:13 (±2:12) at LWF and was similar across water flow conditions (Wilcoxon signed-rank test, p = .136).

Because only one fish was detected active at HWF, we only measured foraging mode at IWF and LWF. As predicted, fish were more mobile during prey search at LWF (0.68 ± 0.21), than IWF (0.54 ± 0.19, Table 1, Figure 2). Search mobility was similar during the day and the night overall, but there was a significant difference between treatments, such that fish were more mobile during the day than at night under LWF, but not IWF (Table 1, Figure 2). Arctic charr were also less mobile after the second switch to LWF (Table 2, Figure 3). Fish swam faster at LWF (1.59 ± 0.29 body lengths/5 s) than at IWF (1.42 ± 0.36 body lengths/5 s) and also

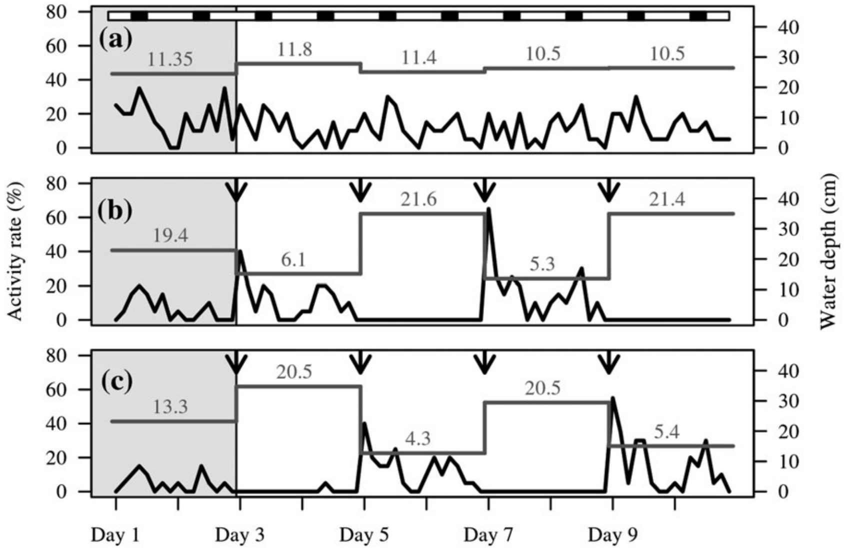

FIGURE 1 Overall activity rates (black lines) of age 1+ Arctic charr measured every 3 hr under contrasting water flow regimes ((a): Upstream enclosures with stable, intermediate water flow; (b) and (c): Two channels where the flow was diverted repeatedly from one channel to the other). During the control phase (2 days, grey areas), water flow was similar in all three sections. Water flow was switched (arrows) at 13:30 on the respective day and was maintained for 48 hr. Grey lines indicate the average water depth in a particular section throughout the experiment. Numbers above the grey lines indicate the average current velocity (cm/s). Black and white rectangles at the top of the figure represent night (21:00 to 03:00) and day (06:00 to 18:00), respectively

TABLE 1 Effect of water flow treatment (intermediate vs. low) on overall activity rates (number of active individuals) and foraging mode of juvenile Arctic charr

Response variable	Explanatory variable	Estimate	Standard error	*z* or *t* value	Pr (>|z|) or Pr (>|t|)
Overall activity rate	Intercept	−0.548	0.197	−2.776	0.006
	Water flow	0.816	0.178	4.532	<0.001
	Time of day	0.564	0.100	5.713	<0.001
Search mobility	Intercept	0.565	0.020	28.243	<0.001
	Water flow	−0.028	0.027	−1.039	0.300
	Time of day	0.174	0.029	6.013	<0.001
	Water flow × time of day	−0.085	0.041	−2.099	0.037
Speed while moving	Intercept	1.422	0.060	23.847	<0.001
	Water flow	−0.125	0.033	−3.828	<0.001
	Time of day	0.283	0.056	5.082	<0.001
Foraging radius	Intercept	1.157	0.036	31.781	<0.001
	Water flow	0.155	0.044	3.482	0.004
Foraging rate	-	-	-	-	-

Note. A GLMM was used for the analysis of activity rates and LMMs for the analysis of foraging mode. Default values are "low" for water flow and "night" for the time of day. Enclosures were included as a random factor in all models. Individuals were also included as a random factor in models of foraging mode. Hyphens indicate that the null model best explained the data based on AIC.

TABLE 2 Analysis of differences in overall activity rates (number of active individuals) and foraging mode of juvenile Arctic charr between the first and second switch to low water flow and the first and second day after the switch

Response variable	Explanatory variable	Estimate	Standard error	z or t value	Pr (>|z|) or Pr (>|t|)
Overall activity rate	Intercept	1.534	0.230	6.667	<0.001
	Days since switch	−0.553	1.555	−3.564	<0.001
Search mobility	Intercept	0.972	0.044	22.320	<0.001
	Switch	−0.204	0.029	−7.010	<0.001
Speed while moving	-	-	-	-	-
Foraging radius	-	-	-	-	-
Foraging rate	Intercept	0.146	0.016	9.264	<0.001
	Days since switch	0.039	0.009	4.598	<0.001

Note. A GLMM was used for the analysis of activity rates and LMMs for the analysis of foraging mode. Default value is "first" for both explanatory variables. Enclosures were included as a random factor in all models. Individuals were also included as a random factor in models of foraging mode. Hyphens indicate that the null model best explained the data based on AIC.

swam faster during the day regardless of the water flow treatment (Table 1, Figure 2). They attacked prey at longer distances at LWF (1.30 ± 0.32 body lengths) than at IWF (1.18 ± 0.28 body lengths), regardless of the time of day (Table 1, Figure 2). Fish attacked prey at similar rates under LWF (0.28 ± 0.06) and IWF (0.21 ± 0.06) and during the day and the night (Table 1). Arctic charr also attacked prey at a faster rate on the second day after a switch to LWF (Table 2, Figure 3).

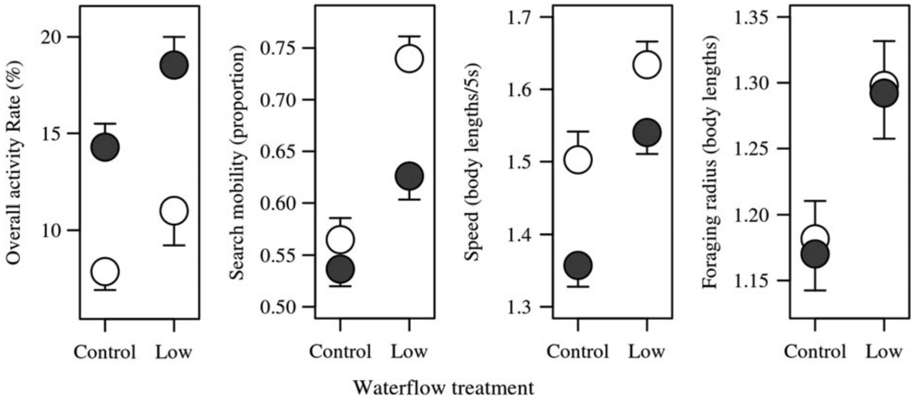

FIGURE 2 Activity and foraging mode (mean ± standard error) of age 1+ Arctic charr during the water flow manipulation phase at stable and intermediate water flow and low water flow, during the day (06:00 to 18:00, white symbols) and the night (21:00 to 03:00, grey symbols)

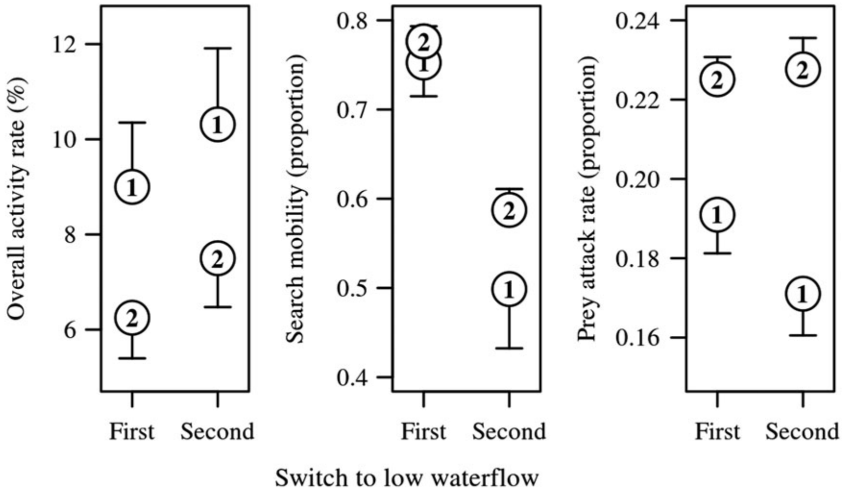

FIGURE 3 Activity and foraging mode (mean ± standard error) of age 1+ Arctic charr during the first (Symbol 1) and the second day (Symbol 2) after the first and second switch to low water flow

4 | DISCUSSION

Fluctuating water flow affected several components of Arctic charr behaviour. In stable water flow, activity rates were comparable with previous studies on Arctic charr in cold streams (Fingerle et al., 2016; Larranaga & Steingrímsson, 2015). In fluctuating water flow, however, fish increased their activity drastically during low flow periods but ceased activity almost completely during high flow. In lotic environments, Arctic charr typically use slow habitats (Heggenes & Saltveit, 2007; Tunney & Steingrímsson, 2012; but see Fingerle et al., 2016), so it is not surprising that they restricted their activity to periods of LWF. Activity peaks followed switches to LWF conditions. This may be due to hunger after 2 days without activity at HWF, although we observed the same phenomenon after a switch from stable conditions. It could result from a brief increase in food availability caused by the flow manipulation, but this is unlikely because activity remained high for several hours and foraging rates were higher on the second day after the switch to LWF. Other potential factors may include fish remaining alert following a sharp decrease in water levels (Larranaga & Steingrímsson, 2015) or active competition for newly available habitat (Keenleyside & Yamamoto, 1962). Our data cannot conclude firmly on the origin of those peaks.

Salmonids of age 1+ are mostly nocturnal, although extensive variation exists among and within species (Breau, Weir, & Grant, 2007; Imre & Boisclair, 2004). Fish that use contrasting current velocities may also distribute their activity differently over the 24-hr cycle (Imre & Boisclair, 2004). In our study, fish were active later at night under LWF (23:27) than under IWF (21:20). This could indicate higher predation risk of fish during the day at LWF, which is consistent with experimental studies suggesting that stream fishes are more conspicuous to diurnal predators at low water level (Lonzarich & Quinn, 1995), and with observations of fish using fast and slow habitats during the day and the night, respectively (Polacek & James, 2003). More generally, this suggests that perceived predation risk is an important factor limiting the food intake of salmonids in streams, which may be exacerbated in hydropeaking environments.

As expected, fish were more mobile, swam faster during prey search and attacked prey at longer distances under LWF than IWF (Grant & Noakes, 1988; Tunney & Steingrímsson, 2012). Slow-running waters typically result in lower food availability (Nislow et al., 1998) and energetic costs (Hill & Grossman, 1993), both of which favour mobility (Grant & Noakes, 1987; Tunney & Steingrímsson, 2012). Arctic charr attacked prey at similar rates under LWF and IWF, which probably mirrors their use of larger foraging areas (see also Gunnarsson & Steingrímsson, 2011). Overall, these results combined with activity rates suggest that energy expenditure and intake should not differ much between stable and fluctuating conditions. We expected Arctic charr to be less mobile at night than during the day, which was confirmed in this study (search mobility and speed, but not foraging radius) and was consistent across levels of water flow. Importantly, these changes occurred even under conditions where nights are short and relatively bright (high latitude, summertime), so adjustments of diel activity patterns may be even stronger when light varies more between day and night

Fish attacked prey more frequently on the second day after a switch to LWF, which could result from lower activity on that day as fewer individuals competed for food. Our results are based on 2-day fluctuations in water flow and suggest that salmonids may require time to adjust their behaviour (activity, mobility, and prey attack rates). For instance, Keenleyside and Yamamoto (1962) concluded that the establishment of defended territories by Atlantic salmon *Salmo salar* took a minimum of 12 hr after fish were moved to a new environment (aquarium). Although the duration of low and high flow periods varies considerably across studies (21 days of low flow in Riley et al., 2009, 12-hr periods of low and high flow in Scruton et al., 2005), few if any monitor changes in behaviour at short temporal scales after a fast change of habitat availability. If the frequency of hydropeaking events exceeds the time needed for salmonids to adjust their behaviour, this could be an additional source of perturbation affecting individual fitness (Murchie et al., 2008).

Earlier studies are equivocal on the effect of water flow fluctuations on growth, as some suggest that fish may grow slower (Flodmark et al., 2004; Puffer et al., 2015; Weyers, Jennings, & Freeman, 2003), faster (Finch, Pine, & Limburg, 2015), or at similar rate (Flodmark, Forseth, L'Abée-Lund, & Vøllestad, 2006; Korman & Campana, 2009; Puffer, Berg, Huusko, Vehanen, & Einum, 2017) in altered flow. Our results indicate that stream fishes compensate for low food intake under unfavourable conditions by adjusting their activity and foraging mode, that is, more activity and mobility under LWF, and the costs associated with such adjustments should be low. This may explain why hydropeaking has minor influence on the growth of stream-dwelling fish (Puffer et al., 2017), but rather affects other aspects of fitness, for example, mortality through stranding or predation (Young et al., 2011). Although caution needs to be taken because fish were confined in stream enclosures and could not display mid to long-scale movements, data on the foraging behaviour of salmonids could shed new light on the fitness of stream fishes in hydropeaking environments.

Our results suggest that fluctuating water flow can have a drastic effect on the activity patterns and foraging mode of juvenile salmonids. Importantly, there is strong variation in habitat selection and diel activity patterns among salmonids (Armstrong et al., 2003; Reebs, 2002) and among cohorts (Armstrong et al., 2003; Bradford & Higgins, 2001). Hence, similar experiments with different fish could produce opposite results, for example, if they prefer faster currents (e.g., Atlantic salmon), or are diurnal (e.g., young-of-the-year). In conclusion, this study demonstrates that behavioural adjustments are important for stream fish populations living in rapidly changing and unpredictable environments like regulated rivers with hydropeaking.

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