

ORIGINAL ARTICLE

Growth and mortality of sympatric Atlantic salmon and brown trout fry in fluctuating and stable flows

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Abstract

Sub-daily fluctuations in streamflow may have adverse effects on the biota downstream of dams in hydropeaking-regulated rivers. Although the stranding of salmonid fry is one documented effect of hydropeaking, little is known about the species-specific behavioural and subsequent growth effects of sub-daily flow fluctuations. We investigated the effects of sub-daily flow fluctuation on growth, mortality and behaviour of sympatric Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) fry (29–34 mm) in a laboratory experiment. The fluctuating flow treatment negatively affected growth and increased mortality for trout but not for salmon. The level of aggressive behaviour was similar in the fluctuating- and stable-flow treatments. Within the fluctuating flow treatment, there was a trend that more fishes were visibly active above the substrate during low than high flow. These findings suggest that hydropeaking-induced flow fluctuations may affect fry of different salmonid species in different ways and that brown trout fry may be more vulnerable to hydropeaking effects than Atlantic salmon fry. It can therefore be important to consider the possibility of divergent reactions by different fish species under hydropeaking situations and to incorporate species-specific strategies to conserve culturally and economically relevant riverine fish species.

KEYWORDS

behaviour, hydropeaking, *Salmo salar*, *Salmo trutta*, survival

1 | INTRODUCTION

The growing demand for fossil-free energy makes hydroelectric power generation an important technology for flexible and renewable energy (Ashraf et al., 2018). Hydropower plants alter the natural flow regime of up- and downstream river reaches, however, with potential negative effects on aquatic organisms (Kuriqi et al., 2021; Poff et al., 1997). Particularly when electricity is generated to meet sub-daily fluctuations in energy demand, rapid changes in discharge downstream of hydropower plants can be extreme

(Carolli et al., 2015; Cushman, 1985); these hydropeaking flow regimes, which result in rapid changes in stream flow patterns, have been shown to severely affect riverine biota (Moreira et al., 2019; Smokorowski et al., 2011; Zimmerman et al., 2010). The ecological effects of hydropeaking on riverine organisms are linked to alterations in the natural river hydrology, morphology (e.g. river depth, width, velocity, riverbed material and grain size) and water quality (e.g. temperature and turbidity) (Charmasson & Zinke, 2011; Hauer et al., 2014). Specific to fish and their instream habitat, alterations in river depths, velocity and water temperature are the major sources

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of negative impacts on hydropeaking (Bakken et al., 2016; Burman et al., 2021; Nagrodski et al., 2012). These alterations influence, for instance, the density of drifting invertebrates, the risk of stranding, spawning conditions, behaviour, growth, reproduction and mortality (Moreira et al., 2019; Schülting et al., 2016; Young et al., 2011), with potential long-term effects on population development and community structure (Enders et al., 2017).

Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) occur sympatrically in many regulated rivers in northern Europe, and these two economically and ecologically important salmonid species have been studied in relation to hydropeaking for different life stages (e.g. eggs: Casas-Mulet et al., 2015, parr: Sauterleute et al., 2016, smolts: Alexandre & Palstra, 2017, spawners: Rocaspana, Aparicio, Alcazar, & Palau, 2016; Vollset et al., 2016). This body of literature, however, lacks information about how hydropeaking affects the newly emerged fry, which is surprising because this life stage is generally considered a critical period for survival, creating a bottleneck event for many salmonid populations (Elliott, 1990; Jonsson & Jonsson, 2011). The success of individual fry in surviving this critical period relies on them establishing the ability to develop energetically profitable foraging behaviours (Fausch, 1984), wherein fish balance the velocity-dependent costs of foraging against the gains of encountering more prey in faster water (Nislow et al., 1999; Piccolo et al., 2014). Sub-daily flow fluctuations such as those resulting from hydropeaking, therefore, might be expected to affect the growth and survival of fry by rapidly changing the fitness landscape by altering water velocities and flow patterns.

In this study, we assessed the effects of short-term flow fluctuations on the growth, mortality and behaviour of sympatric Atlantic salmon and brown trout (hereafter salmon and trout) fry (30–40 mm) in a laboratory experiment. The term flow fluctuation used in our study refers to variation in water velocities while keeping water depth constant throughout the experiment. We predicted that both salmon and trout fry would grow and survive better in a stable, constant flow (without hydropeaking) versus in fluctuating flow (simulating hydropeaking conditions). We investigated potential mechanisms for this expected pattern in relation to fish activity and aggression. We hypothesised that there would be fewer active fish in fluctuating versus in stable flow treatments, due to increased swimming costs in fluctuating flows. We consequently hypothesised that reduced fish activity in a fluctuating flow would result in fewer aggressive interactions in fluctuating versus a stable flow treatment.

2 | METHODS

We used salmon and trout fry reared from eggs collected from wild spawning adults returning to River Klarälven, Sweden (the ecology of these populations is described in detail in Piccolo et al., 2012). The study was performed at the stream aquarium facility at Karlstad University, Sweden, during May–June, 2021. The fishes were kept in holding tanks at 11°C and fed maintenance rations (3% of fish body mass per day) until translocation to the test arenas in 80 L

aquaria. We used 160 randomly selected individuals of each species for the experiment. Each aquarium was uniformly stocked with a total of 20 fry (10 salmon and 10 trout). We measured fish wet mass and total length at the start of the experiment (mean \pm SD, salmon: mass = 0.19 ± 0.02 g, length = 29.6 ± 1.0 mm; trout: mass = 0.27 ± 0.04 g, length = 32.4 ± 1.6 mm). Within each species, mean size and coefficient of variation (CV) in size did not differ between the two flow treatments (salmon: length, mass, CV_{length} and CV_{mass}, $t_{14} = 0.92, 0.37, 0.71$ and $0.24, p > .05$, trout: length, mass, CV_{length} and CV_{mass}, $t_{14} = 0.6, 1.69, 1.14$ and $0.72, p > .05$).

We equipped 16 aquaria (length \times width \times height = $75 \times 40 \times 40$ cm) with canister filters (1000 L/h Eheim, GmbH & Co. KG, Deizisau, Germany) and chillers (Hailea HC-300A, HC-150A, Hailea Group Co., Ltd, Guangdong, China; TECO TK150, TK2000 and RA200, TECO, Ravenna, Italy). The mean water temperature in the aquaria was $11.1 \pm 0.4^\circ\text{C}$. Water intakes were covered with nylon cloth to prevent fish and food from being sucked into the filter system, and we covered the bottom with 10 L of coarse stone substrate (diameter = 30–80 mm). Each aquarium was filled with 80 L filtered, copper-free water buffered with 0.1 g L^{-1} NaCl and 0.1 g L^{-1} Na₂CO₃. Mean (\pm SD) pH, light intensity and conductivity, measured throughout the experiment were pH 8.18 ± 0.18 , $1647 \pm 209 \text{ lx}$ and $415.1 \pm 15.2 \text{ }\mu\text{S cm}^{-1}$. There was no difference in temperature, light intensity, water conductivity or pH between the treatments (Mann–Whitney U tests, $p > .05$). Lights were turned on at 04:30 and off at 21:30 each day corresponding to the time of sunrise and sunset in Karlstad, Sweden in late May.

Two flow treatments were used in the experiment: stable flow (SF) where water velocity was kept constant and fluctuating flow (FF) where water velocity was varied periodically to mimic outflow from a peaking hydropower plant. Each of the 16 aquaria was assigned to one of these two treatments at random. To control the flow, we used two types of internal pumps: WM-101 and WM-1 (Boyu Wave-Maker, Boyu Group, Guangdong, China). For aquaria with SF, we used a WM-101 pump constantly running to create a stable flow, whereas aquaria with FF were equipped with a WM-1 pump that was turned on and off at intervals using a timer (creating high flow at 07:00–13:00 and 16:00–21:00 and low flow at all other times). The mean water velocity (\pm 1 SD) in front of the pump outlet in aquaria with FF was too low to be measured at low flow and $0.11 \pm 0.02 \text{ ms}^{-1}$ at high flow, whereas in aquaria with SF, the mean water velocity in front of the pump outlet was $0.05 \pm 0.01 \text{ ms}^{-1}$. These velocities are within the range of those experienced by salmonid fry in river margins of hydropeaking rivers (Korman & Campana, 2009).

Fish were subjected to the experiment for 5 weeks. We fed the fishes twice per day (half of the daily food ration at 10:15 and the other half at 13:15). During the last two weeks of the experiment, we collected video footage of each aquarium immediately after feeding for two 30 min sequences: one at low and one at high flow for the FF treatment, and twice at stable flow for the SF treatment. We analysed the videos by counting the number of active, visibly swimming fish at ten time points (each minute between minutes 15 and 25, with the first 15 min as an acclimation period), using the mean

number of visible fish for further analysis. In addition, we counted the number of aggressive interactions (chases and nips) in each aquarium for 2 min (from minute 15 to 17). Due to the small size of the fry, we could not differentiate between the species in the video recordings, thus all behavioural measurements for each aquarium were for both species combined. At the end of the experiment, all the fishes in each aquarium were identified to species, weighed (wet mass), measured (total length) and counted (to record mortalities).

The small size of the fish precluded any form of individual marking, thus we did not keep track of individual fish. We therefore based our calculations of growth on the mean mass at the start and end of the experiment for each aquarium and species. We calculated the mean instantaneous growth rate (g) for each aquarium as

$$g = (\ln(M_{\text{end}}) - \ln(M_{\text{start}})) / \Delta t$$

where M_{end} and M_{start} are the mean masses at the end and the start of the experiment and Δt is the total number of days the experiment lasted. Specific growth rate (SGR; % per day; Crane et al., 2020) was calculated as

$$\text{SGR} = 100 \times (e^g - 1).$$

We also calculated CV for the individual body masses for each species and aquarium at the end of the experiment.

To examine the effects of flow treatment on fish behaviour (number of visibly active swimming fish and aggressive interactions), we used the mean values from the two video films from each aquarium (i.e. for SF the mean of two films with the same stable flow; for FF the mean from high and low flow conditions). In addition, we analysed the effects of low vs high flow within the FF treatment, basing this analysis on eight replicated aquaria only.

All response variables except mortality were normally distributed (Shapiro–Wilk's tests, $p > .05$), and variances between treatments were similar (Levene's tests, $p > .05$). We analysed the effects of flow treatment for the two species separately on SGR and CV using Student's t -tests and on mortality using Mann–Whitney's U -tests. For the behavioural analyses, we used Student's t -tests to compare the number of visible fishes and aggressions between flow treatments, whereas paired t -tests were used to compare the effects of high vs low flow within the FF treatment. All statistical analyses were performed using SPSS 28 (IMB, Armonk, USA).

3 | RESULTS

On average, trout and salmon grew $2.92\% \pm 0.08\%$ and $2.27\% \pm 0.07\%$ day⁻¹ respectively. Trout fry grew significantly better in SF ($3.08\% \pm 0.10\%$ day⁻¹) than in FF ($2.76\% \pm 0.10\%$ day⁻¹) ($t_{14} = 2.32$, $p = .04$, Cohen's $d = 1.16$), whereas flow treatment had no effect on salmon growth (SF: $2.28\% \pm 0.11$; FF: $2.26\% \pm 0.09\%$ day⁻¹; $t_{14} = 0.20$, $p = .84$, Cohen's $d = 0.10$) (Figure 1a). At the end of the experiment, the variability in trout mass (CV) was significantly

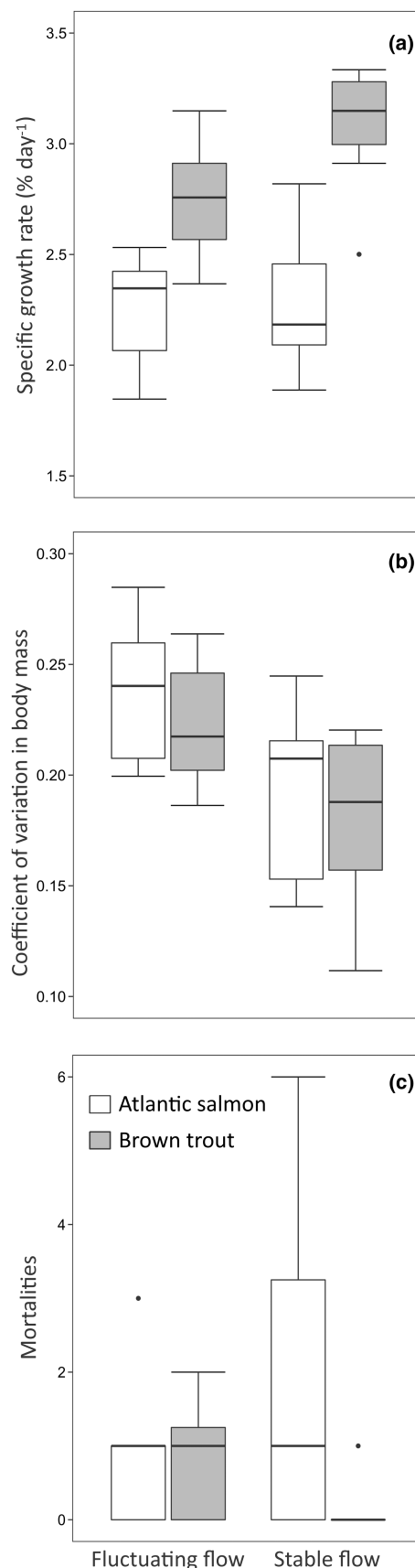


FIGURE 1 Mean (± 1 SE) (a) specific growth rate, (b) coefficient of variation in body mass and (c) mortality rate for Atlantic salmon and brown fry trout under fluctuating and stable flow treatments ($n = 8$) in aquaria during one month.

higher in FF (0.23 ± 0.01) than in SF (0.18 ± 0.01) ($t_{14} = 2.64$, $p = .02$, Cohen's $d = 1.32$). Flow treatment did not affect the variability in salmon mass (SF: 0.21 ± 0.02 ; FF: 0.24 ± 0.11 ; $t_{14} = 0.99$, $p = .34$, Cohen's $d = 0.49$) (Figure 1b).

In total, 22 salmon (7 in FF and 15 in SF) and 8 (7 in FF and 1 in SF) trout died during the experiment. Median mortality rates (25%–75% quartile) for salmon was 10 (0–10) % in FF and 10 (0–37.5) % in SF. The corresponding values for trout were 1 (0–17.5) and 0 (0–0) % respectively. Flow treatment had no statistical significant effect on the median mortality rate of salmon ($U = 26$, $Z = 0.66$, $p = .51$). Conversely, trout had higher mortality rate in aquaria with the FF than in the SF treatment ($U = 15$, $Z = 2.07$, $p = .04$; Figure 1c).

We observed a maximum of 14 visible fishes actively swimming in one analysed video frame. There was no difference in the number of visible fishes between the flow treatments (means \pm SE = 8.97 ± 0.74 and 7.67 ± 0.35 for SF and FF respectively; $t_{14} = 1.59$, $p = .14$, Cohen's $d = 0.79$) (Figure 2a). Furthermore, flow treatment had no effect on the number of observed aggressions (8.38 ± 1.52 and 6.5 ± 1.3 for SF and FF, $t_{14} = 0.94$, $p = .36$, Cohen's $d = 0.47$) (Figure 2b). Within the FF treatment, there was a nonsignificant trend that more fishes were visible in the low flow (mean \pm SE = 8.1 ± 0.32) than in the high flow (7.2 ± 0.47) ($t_7 = 2.20$, $p = .06$, Cohen's $d = 0.78$) (Figure 3a). Moreover, aggression did not differ between high and low flow within the FF treatment ($t_7 = 0.94$, $p = .38$, Cohen's $d = 0.33$) (Figure 3b).

4 | DISCUSSION

The present study investigates the effects of short-term fluctuations in flow per se on growth, mortality and behaviour of salmon and trout fry, omitting the effects of changing water levels and stranding. We found that fluctuating flows had negative effects on the growth and mortality of brown trout fry but not Atlantic salmon fry. These results suggest that hydropowering-induced flow fluctuations may affect the growth and mortality of salmonid fry through behavioural mechanisms in addition to possible stranding or scouring effects. Moreover, flow fluctuations may affect fry of different salmonid species in different ways; in our study, salmon fry seemed to cope better with sub-daily flow fluctuations than trout fry.

Studies that have examined the effects of fluctuating flow on salmonid fry growth are almost completely lacking although growth is commonly used as a proxy for fitness in juvenile salmonids (e.g. Martin-Smith & Armstrong, 2002, and references therein). Korman and Campana (2009) showed that growth rates (as measured by otolith increments) of rainbow trout (*Onchorynchus mykiss*) fry (20–30mm) were greater during periods with steady than with fluctuating flows from hydropowering: our results for brown trout corroborate these findings. There are relatively more studies focusing on the growth of parr in hydropowering flow regimes; the results of these studies are ambiguous, however. For example, Puffer et al. (2015) reported lower growth of Atlantic salmon parr (70–90mm) in hydropowering than in stable flow conditions during summer. In a later

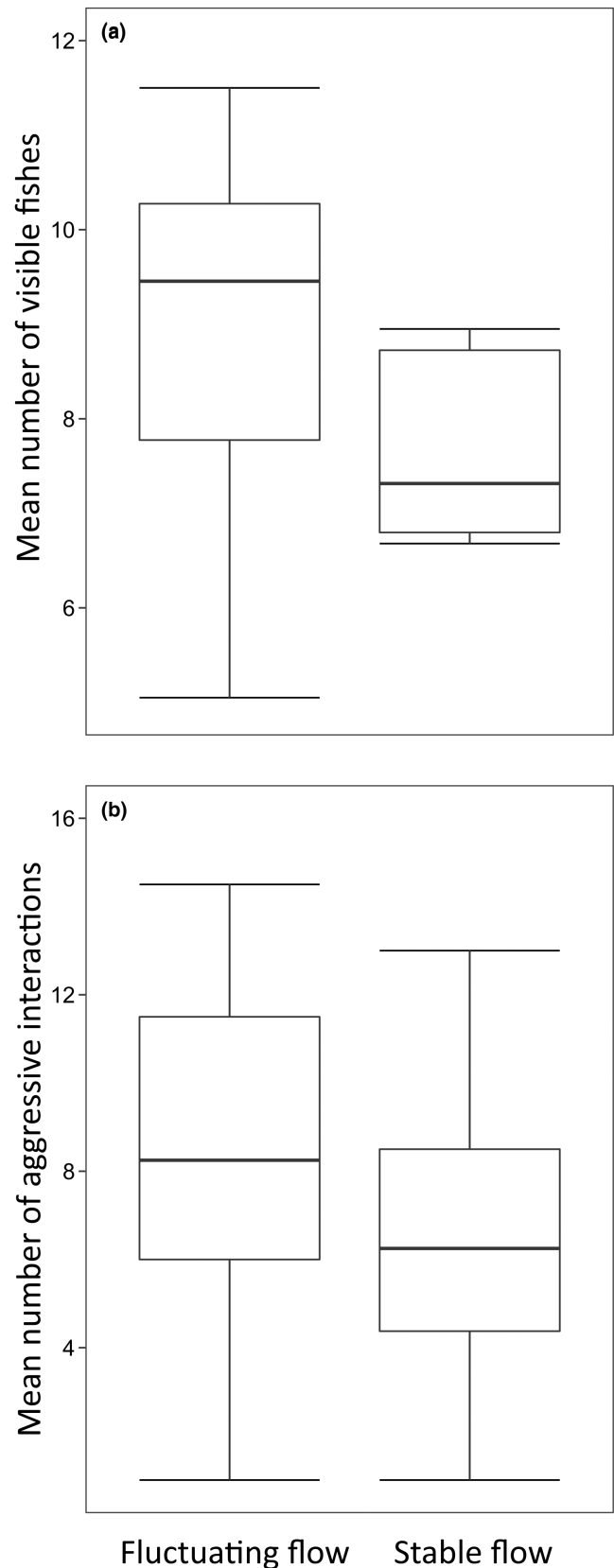


FIGURE 2 Mean (\pm SE) (a) number of visible fish above the substrate and (b) mean number of aggressive interactions between fry (Atlantic salmon and brown trout) under fluctuating and stable flow treatments ($n = 8$).

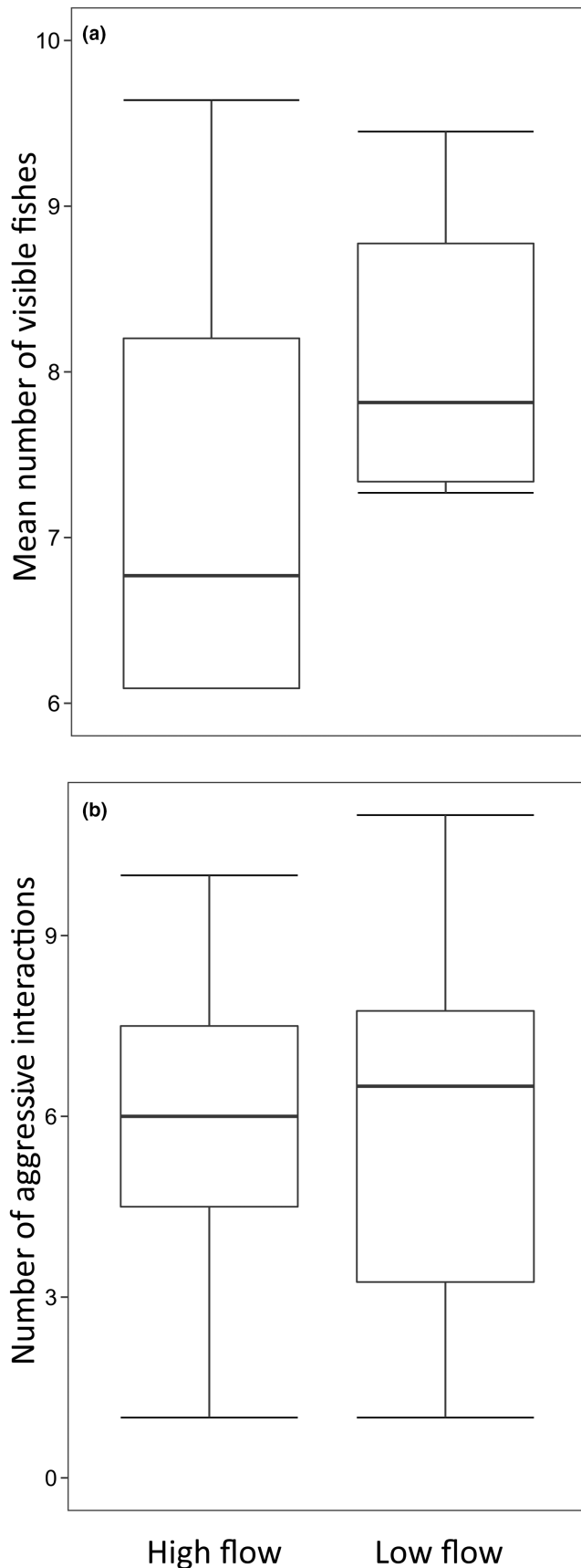


FIGURE 3 Mean (± 1 SE) (a) number of visible fish above substrate and (b) number of aggressive interactions between fry (Atlantic salmon and brown trout) at high and low flows ($n = 8$).

study, the same authors (Puffer et al., 2017) examined the influence of hydropeaking on the growth of Atlantic salmon parr (60–80 mm) in relation to intra- and interspecific competition with brown trout, and they reported no statistically significant effect of hydropeaking or the competition regime. There was, however, a trend in reduced growth in hydropeaking compared to stable flow conditions (Puffer et al., 2017). We studied the fry life stage and found no effects of hydropeaking on the growth and mortality of salmon. Flodmark et al. (2006) reported that daily flow fluctuations in a regulated river did not affect the behaviour and growth rate of brown trout parr (158–170 mm). Contrastingly, we found a significant reduction in the growth rate of trout fry in fluctuating flows. The discrepancy between the findings in our study and those of Flodmark et al. (2006) and Puffer et al. (2015, 2017) may be related to different life stages studied (i.e. parr vs. fry). Furthermore, increased growth in hydropeaking rivers has also been demonstrated. Kelly et al. (2017) reported improved brook trout (*Salvelinus fontinalis*) parr growth in a hydropeaking river compared to a nearby river with a natural flow, and the discussed potential mechanism were differences in density of food resources, foraging success, reduced fishing pressure and presence of invasive species, all of which were likely affected by hydropeaking. The same pattern of high growth in a hydropeaking river has been reported for juvenile (Flodmark et al., 2004) and adult (Rocaspana, Aparicio, Vinyoles, & Palau, 2016) brown trout. Likewise, several studies on the growth of nonsalmonid species in relation to hydropeaking have reported positive effects (e.g. *Cottus cognatus*: Bond et al., 2016; Bond & Jones, 2015; Kelly et al., 2016, *Gila cypha*: Finch et al., 2015), whereas others reported no effects (*Luciobarbus bocagei*: Oliveira et al., 2020; *Micropterus henshalli* and *Micropterus coosae*: Earley & Sammons, 2018).

Our experiment showed that fluctuating flow did not affect the number of aggressive interactions among sympatric salmon and trout fry, but there was a trend that more fishes were visible swimming above the substrate in the stable versus in fluctuating flow treatments. The fluctuating flow treatment created higher flow velocities, but these velocities were below the critical limit for downstream displacement of salmonid fry (Heggenes & Traaen, 1988). Perhaps reduced foraging success (e.g. Piccolo et al., 2008) and net energetic profitability (Nislow et al., 1999), led to more fry seeking velocity shelter in the substrate. High flow velocities can reduce the inter- and intra-specific aggression behaviour of young-of-the-year juvenile salmonid either due to increased energy cost for territorial defence (Grant & Noakes, 1988) or for holding positions against the water current (Vehanen et al., 2000), but we could not find any changes in aggression in relation to flow. On the other hand, low flows may induce a shift in foraging modes (Gibson, 1978; Grant & Noakes, 1988; Watz et al., 2012), increasing active search feeding and reducing sit-and-wait foraging. Fry may experience reduced drift-foraging even in the relatively low velocities in our experiment (Nislow et al., 1999), which may have resulted in a low net rate of energy intake (Piccolo & Watz, 2018) in our experiment, with effects on growth and mortality of brown trout. Possibly, the salmon with a morphology adapted to higher

velocities (e.g. elongated body and large pectoral fins) than trout could partly explain why salmon was not as negatively affected by the fluctuating flows.

The mortality rates of juvenile salmonids under fluctuating flow conditions have previously been related to stranding (Casas-Mulet et al., 2016; Moreira et al., 2019; Nagrodski et al., 2012; Young et al., 2011). For example, high amplitude and frequencies of hydropeaking-induced flow fluctuation on Storåne River in Norway led to low survival of brown trout (Saltveit et al., 2020), and Korman et al. (2011) showed that occurrences of flow fluctuations with high amplitude shortly after the time of peak emergence of rainbow trout (*Oncorhynchus mykiss*) fry controlled their abundance. In our study, however, we focused on the effects of hydropeaking on mortality not related to stranding. Instead, the different mortality rates of brown trout between stable and fluctuating flow treatments appeared to be linked to energy spent on swimming (Puffer et al., 2015), interactions with con- and hetero-specifics (Puffer et al., 2017) and food acquisition (Bond & Jones, 2015). Our results suggest that brown trout fry may survive better in steady than in fluctuating flow conditions. Atlantic salmon had a higher overall mortality rate than trout, but the rate was not affected much by flow treatment.

The salmonid fry life stage is a vulnerable period because they face a high risk of displacement and mortality from predation and competition over scarce food resources and suitable habitats (Millidine et al., 2018; Nislow & Armstrong, 2012). Hydropeaking may exacerbate their vulnerability by further increasing the risk of mortality through stranding (Nagrodski et al., 2012), downstream drifting (Irvine, 1986; Saltveit et al., 1995) and increased energy expenditures (Korman et al., 2011; Korman & Campana, 2009; Scruton et al., 2003). Although the salmonid fry life stage is considered a critical period (Elliott, 1990), most studies examining the effects of hydropeaking on salmonids are conducted on parr. Conducting more research on fry will likely improve our understanding of how flow regimes affect population dynamics; our results provide evidence that flow fluctuations may affect growth and mortality directly in addition to the effects of stranding, which needs to be considered when assessing the critical period of fry in hydropeaking-regulated rivers.

The negative effects of fluctuating flow on the trout fry in our experiment could be related to decreased foraging success and increased energy expenditure; salmon fry did not experience these effects. A better understanding of species-specific foraging abilities of fry under fluctuating flows would provide valuable inputs for ecological population models, particularly for individual-based models (IBM, e.g. inSTREAM, Railsback et al., 2009). Such IBMs can be valuable tools for examining the consequences of alternative scenarios related to physical restoration projects and different flow regimes, for instance, how salmonid populations are affected by sub-daily fluctuations (Hajiesmaeili et al., 2022; Railsback et al., 2021). Further development of these IBMs may also benefit from species-specific parameters (e.g. Bjørnås et al., 2021), and our results highlight that even fry of congeneric species differ in their responses to hydropeaking flows.

Our study was limited to analysing the effects of one flow regime that might simulate, for example, the flow changes near the river margin downstream of a hydropeaking powerplant. The velocities experienced by fry in such habitats may be dynamic and with other velocities and bottom structures than those used in our study, the results might have been different. We did not simulate changes in depth, because our focus was specifically on how altering water velocity (and turbulence) would affect fry. In a hydropeaking river, dynamic flow would alter velocity as well as depth and water temperature (i.e. thermopeaking). Studies that test multiple combinations of flow and temperature regimes and field studies would perhaps be needed to assess the combined effects accurately of hydropeaking on growth and survival. We did not simulate alterations in the thermal regime. The effects of temperature on foraging behaviour (Watz, Bergman, et al., 2014; Watz, Piccolo, et al., 2014) may, however, play an important role at sites affected by thermopeaking, and studies that investigate potential interaction effects between fluctuating flows and temperature may be warranted. Nevertheless, we showed that two species that are considered to occupy relatively similar niches may indeed react differently to fluctuating flows, and this difference may make co-existence possible, perhaps by condition-specific competition (Watz et al., 2019). Since we could not identify fish species in the video analyses, it was not possible to assess inter- vs. intraspecific competition. Therefore, we do not know if the effects of flow fluctuations on trout growth and survival were caused directly by the flow treatment or indirectly by condition-specific competition with salmon.

Atlantic salmon and brown trout occur sympatrically in many northern rivers. When those rivers are subjected to hydropeaking, flow fluctuations may affect these species in different ways. Stranding may affect population development negatively, and we have shown that velocity fluctuations may cause additional direct negative effects on the growth and survival rates of fry. Also, we showed that trout were more negatively affected than salmon. The study thereby highlights the need for life stage- and species-specific considerations to conserve culturally and economically important riverine fish species (Liu et al., 2019; Watz et al., 2022).

AUTHOR CONTRIBUTIONS

LA, JJP and JW conceived and designed the study. LA, MH and JW carried out the laboratory work. LA and MH took care of the fish and collected the data. LA and JW analysed the data. LA, JJP and JW planned the structure of the drafted paper. LA wrote the first draft of the article. All co-authors provided manuscript edits.

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CONFLICT OF INTEREST

The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study is available upon request from the corresponding author.

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