Social behaviour of European grayling before and after flow peaks in restored and unrestored habitats

Johan Watz1 | David Aldvén2 | Antonis Apostolos Brouziotis1 | Niclas Carlsson1 | Eirini Karathanou1 | Kristine Lund-Bjørnås1 | Gustav Lundqvist2 | Martin Österling1 | John J. Piccolo1 | Olle Calles1

1River Ecology and Management Research Group RivEM, Department of Environmental and Life Sciences, Karlstad University, Karlstad, Sweden
2Vattenfall Research and Development, Älvkarleby Laboratory, Älvkarleby, Sweden

Correspondence
Johan Watz, River Ecology and Management Research Group RivEM, Department of Environmental and Life Sciences, Karlstad University, Sweden.
Email: johan.watz@kau.se

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Abstract
Cost-effective implementation of fish-friendly hydropower flow operation and habitat restoration measures require an understanding of their effects on fitness-related behaviours of stream fish. Here, we investigated how changes in flow and bottom structure influence the social behaviour of European grayling, using large experimental flumes (700 L s⁻¹), with and without added boulders (i.e., restored and unrestored habitat). Grayling increased their distance to nearest neighbour at the start of flow ramping up and after a flow peak compared to stable base flow. At the start of ramping up the flow, grayling made less position changes (movements >1 m) than at stable base flow and after a flow peak. In the unrestored habitat, the proportion of time grayling spent actively swimming was lower before a flow peak than it was both at the start of ramping up the flow and after the peak, an effect not found in the restored habitat. In addition, we compared two static flows, and habitat restoration mediated their effect on distance to nearest neighbour. Grayling in the restored habitat were positioned closer to each other in the low (~10 cm s⁻¹) than in the intermediate static flow (~40 cm s⁻¹), whereas in the unrestored habitat, grayling showed the opposite pattern. Moreover, grayling reduced their number of position changes in the intermediate static flow, which was reflected by a reduction in active swimming. Stomach analysis after the trials revealed that foraging success was higher in variable than in the stable flow treatment. These results show that flow magnitude, flow changes and instream structure play important roles in the behaviour of stream fishes.

KEYWORDS
foraging, hydropeaking, hydropower, movement, nearest neighbour, salmonid, structure, Thymallus
Ecosystem services from rivers are essential for human wellbeing. The infrastructure needed to provide these services (e.g., irrigation, electricity production and timber floating) have however had detrimental effects on biodiversity in many rivers (Dynesius & Nilsson, 1994). For instance, in regulated rivers, dams negatively affect migrating fish that may not reach habitats needed to complete their life cycles (van Puijenbroek, Buijse, Kraak, & Verdonschot, 2019) and create sub-optimal rearing and spawning habitats in terms of flow and structure that may reduce fish abundance (Hauer, Holzapfel, Leitner, & Graf, 2017). Mitigating measures targeted to improve riverine fish habitat often aim to restore natural flows and pristine bottom structures (Palmer, Menninger, & Bernhardt, 2010; Young, Cech, & Thompson, 2011). The effectiveness of these measures may rely on understanding the behavioural mechanisms of how complex interactions between flow and habitat influence fish distribution, growth and abundance.

Demands for electricity often vary with sub-daily fluctuations. Many hydropower plants store water in the reservoir when there is low demand and generate electricity by releasing water through the turbines when the demand is high. This operation causes a low base flow with periodic peaks with high flows, that is, hydropoeaking. Hydropoeaking has been suggested to have adverse effects on both river morphology (Moreira et al., 2019) and biota, including fish (Schmutz et al., 2015), which may experience risk of stranding, downstream displacement and reduced habitat quality (Young et al., 2011). Extreme high and low flows (and rapid transitions between them) drastically alter the hydraulic conditions, affecting behaviour and foraging success of drift-feeding fish (Miller & Judson, 2014; Scruton et al., 2005). How the hydraulic landscape changes with flow also depends on slope and physical structure of the riverbed, and the interaction between flow conditions and bottom structure complexity possibly shapes several important behavioural patterns in stream fish.

Increased structural complexity can be accomplished by placing objects (e.g., boulders and wood) in the river (Friberg et al., 2016). Where little instream structure remain, for example, in rivers dredged for timber floating, measures to increase physical bottom complexity has been shown to increase fish abundance and macroinvertebrate diversity (Louhi, Vehanen, Huusko, Mäki-Petäys, & Muotka, 2016; Pilotto, Nilsson, Polvi, & McKie, 2018). A major explanation for these positive effects is that structural complexity results in an instream riverscape with a wide range of heterogeneously distributed microhabitats with varying water velocities and depths, providing opportunities for individuals to perform key fitness-related behaviours, such as feeding, hiding and mating (White, Giannico, & Li, 2014). The magnitude of the effects, however, may be site and species specific. For example, in a study by Hellström, Palm, Brodin, Rivinoja, and Carlstein (2019), European grayling (Thymallus thymallus), a stream salmonid that often form tight social groups (Greenberg, Svendsen, & Harby, 1996; Hart et al., 2014), was not affected by a streambed restoration designed for increasing the abundance of other salmonid fish species.

The abilities to recognize conspecifics and discriminate amongst individuals are important for social animals. Many fish species have these abilities (Ward & Hart, 2003). European grayling are more exploratory with familiar partners than with non-familiar ones (Hart et al., 2014), and in Arctic char (Salvelinus alpinus) the ability to recognize familiar individuals makes it possible to form stable group hierarchies, which increases food intake (Höjesjö, Johnsson, Petersson, & Järvi, 1998) and has fitness consequences (Seppä, Laurila, Peuhkuri, Piironen, & Lower, 2001). The combined effects of the propensity to stay near conspecifics and exploratory behaviour of individual group members determine foraging performance, energetic costs of swimming and predator avoidance (Hart et al., 2014; Jolles, Boogert, Sridhar, Couliz, & Manica, 2017). Thus, sociability may play a key role in the growth, survival and population dynamics of fishes such as juvenile salmonids, which form strong dominance hierarchies. Grayling in groups may display both interference and exploitative competition (Hughes, 1992; Salonen & Peuhkuri, 2006), but may also benefit from foraging with familiar ones (Hart et al., 2014) and attack dilution (Ward & Webster, 2016). In cohesive groups, individuals may access information regarding resource abundance and quality, as well as the presence of predation threats. This information is potentially costly to gather alone, and its accessibility is possibly related to spatial distance to the other group members and the configuration of the physical environment (Ward & Webster, 2016). In a dynamic environment where the distribution of resources is difficult to predict, the benefits from collecting information from group members should be less beneficial.

In this study, we examined the sociability (in terms of group cohesion measured by mean distance to nearest neighbour within groups), position changes (i.e. movements >1 m) and proportion of time spent actively swimming of juvenile European grayling in large experimental flumes with and without added boulders (representing restored and unrestored instream habitats). We compared these behaviours before, at the start of and after flow peaks (in a simulated hydropoeaking flow regime) and, in addition, in two static water velocities. We predicted that a rapid increase in flow followed by a decrease to base flow (i.e., experiencing a flow peak) would lead to less cohesive groups (i.e., longer distances to nearest neighbour), more position changes and increased active swimming, particularly in the restored habitat, because the energetically favourable positions (e.g., low water velocity near areas with high velocity; Piccolo & Watz, 2018) would vary spatially and temporarily with flow. Furthermore, we predicted that there should be a negative relationship between movement and water velocity when comparing the two static flows, because drift-feeding fish tend to leave their stationary positions and switch to active search foraging at low water velocities (Grant & Noakes, 1987).
testing sections, in which we constructed two test arenas (Figure 1). Steel mesh demarcated the upstream and downstream ends of the arenas which measured 15 × 1.5 m, and we covered the bottom with coarse gravel (diameter = 2–10 cm). The flumes were filled with water from the nearby river Dalälven, and water temperature ranged from 19.0 to 20.7 °C. Four electronically controlled pumps (Flygt N3202, Xylem Inc, USA) created adjustable circulatory flow, and water depth could be adjusted at the downstream ends of the arenas (Figure 1). Over each arena, we mounted eight video cameras (GoPro Hero 5, GoPro Inc, USA), which enabled us to monitor and film the entire area of the arenas. Light intensity over the arenas was 10 lx during trials. We added 47 boulders (diameter 18–53 cm; Figure 1) to one of the test arenas, creating a diverse bottom structure. This and the arena without boulders are hereafter referred to as the restored and the unrestored habitat treatment, respectively.

The fish used in the experiment were two-summers-old hatchery-reared European grayling (n = 160, mean wet mass and length ± SD (standard deviation) = 35 ± 14 g and 171 ± 19 mm), first-generation from wild parents (Bröderna Olssons fiskodling, Vallsta, Sweden). There may be behavioural differences between wild and hatchery-reared European grayling (Horká et al., 2015), but these changed behaviours in hatchery-reared fish can be subtle (Turek et al., 2010) and sometimes both increase and decrease compared to wild conspecifics, for example aggression levels (Salonen & Peuhkuri, 2004, 2006). The grayling were transported from the hatchery to the laboratory on September 12, 2019 and were acclimated to experimental conditions in two circular tanks (diameter = 3 m, depth = 1 m) for 9 days before the first trial. The tanks contained water from the same source as the test arenas, that is, the nearby river Dalälven.

2.2 | Experimental protocol

Before a trial, four grayling were hand netted at random from their holding tanks and released to each of the two experimental arenas. As the grayling had been reared in the hatchery and kept in the laboratory together, we concluded that the individuals were familiar (sensu Hart et al., 2014). Grayling have previously been shown display normal social behaviour shortly after being translocated to a new environment (Hart et al., 2014; Hughes, 1992). We therefore assumed that the grayling in our study readily associated after being transferred into the experimental arenas. We used two flow treatments: (1) a variable (simulating hydropeaking using a high and a low flow with transitions between them) and (2) a stable intermediate (a magnitude between the hydropeaking high and low) flow regime (Figure 2). We randomized the order of the flow regime treatments and performed 10 replicate trials for each combination of flow and habitat restoration treatments in a 2 × 2 design.

Water velocity was measured at 25, 50 and 75% of the width along 15 transects (one every m) at 60% of the depth (i.e., the depth-averaged velocity). In the trials with the steady flow regime, water depth was 35 cm and mean water velocity (±SD) in the restored and the unrestored arenas were 40.4 (±9.8) and 44.6 (±5.4) cm s⁻¹, respectively. The corresponding values at the low base flow during the hydropeaking regime were 24 cm depth and 8.4 (±3.0) and 14.4 (±2.3) cm s⁻¹, and at the maximum flow (during flow peaks) they were 56 cm depth and 78.4 (±14.8) and 82.8 (±4.1) cm s⁻¹. In the restored habitat, velocities were thus more heterogeneous and on average slightly lower.

A trial lasted 120 min, and the experimental arenas were filmed for 3 min every 12 min (starting at 12 min). This design resulted in nine films (1–9) of grayling in a steady intermediate flow for the treatment with the stable flow regime. For the hydropeaking flow regime (with two flow peaks), the design resulted in one film (1) at low stable base flow (before the first flow peak) and two films (2 and 6) at the start of ramping up the flow (3 and 7), right after peak flow was reached (4 and 8), at the start of ramping down the flow and (5 and 9) right after base flow was reached, respectively (Figure 2). During the first 3 min when ramping up of the flow (Films 2 and 6), grayling experienced a threefold increase in water velocities and depth increased by approximately 50%.

FIGURE 1  To the left, diagram of the experimental flumes used in the experiment (note: this figure is not to scale). To the right, 3D visualizations of the flumes with (restored; upper) and without (boulder; lower)
We concluded that whether grayling were fed during the first or the second potential feeding time had little effects on the results, and thus we pooled the data from the two feeding regimes (Figure 2). The order of the feeding regimes was selected at random to ensure that the two feeding events occurred at different times during each trial. We used two-way analysis of variance (ANOVA) to analyse the effects of flow changes and habitat treatment (the latter analysis was based on data collected before feeding, that is, from film 1). For the analysis within the experimental arenas, we defined the response variable distance to nearest neighbour as the mean number of movements within a group, where a movement corresponded to movements longer than those made by position-holding juvenile salmonids to capture prey or fending of competitors (Gowan & Fausch, 2002). Each grayling could hence make between zero and four position changes between the five observations. We monitored fine-scale movements during 30 s (between 00:30 and 01:00 in the films). In the 3 min periods that included food being introduced, these 30 s occurred before feeding. We defined active swimming as the time grayling were not holding a fixed position. In the statistical analyses of active swimming and position changes, we used arcsine square-root-transformed proportions.

Linear mixed models (LMM) were used in the statistical analyses of distance to nearest neighbour, position changes and active swimming. Effects of flow changes and habitat treatment were assessed by using data from grayling exposed to the hydropeaking treatment only, and we examined their behaviour at the start of ramping up from low base flow (Films 2 and 6) and after reaching low base flow after ramping down (Films 5 and 9), and compared these with those from the initial stable base flow (Film 1). The repeated measurements on grayling groups within the hydropeaking treatment were taken into account in the analyses by specifying the covariance matrix as compound symmetry. These analyses, therefore, had three levels of the within-subject factor (stable, ramping up and after ramping down) and two levels of the between-subjects factor (restored and unrestored habitat).

To assess the isolated effects of static flows (low from the initial state in the variable flow regime vs. intermediate stable flow regime) and habitat treatment, we only used the first film in each trial, that is, before the first flow peak in the hydropeaking flow regime (Figure 2). We used two-way analysis of variance (ANOVA) to analyse distance to nearest neighbour, position changes and active swimming, using two levels of each factor (low and intermediate static flow; restored and unrestored habitat).

We concluded that whether grayling were fed during the first or the second potential feeding time had little effects on the results, and thus we pooled the data from the two feeding regimes (Figure 2) for the analyses of flow changes x habitat treatment and static flow x habitat treatment (the latter analysis was based on data collected before feeding, that is, from film 1). For the analysis within the

2.3 Data analysis

From each analysed film (duration = 3 min), we observed and recorded the positions of the four grayling at the following five times (mm:ss): 00:30, 01:00, 01:30, 02:00 and 02:30. For films in which all four grayling were observed at all five times (71% of the films), we calculated the distance to nearest neighbour (resolution = 0.1 m) for each fish by using reference points on the bottom to relate true distances. In the analyses of sociability, we defined the response variable position changes as the mean number of movements within a group, where a movement was recorded when an individual no longer was observable in the same video screen as 30 s before. These movements were >1 m, which corresponds to movements longer than those made by position-holding juvenile salmonids to capture prey or fending of competitors (Gowan & Fausch, 2002). Each grayling could hence make between zero and four position changes between the five observations. We monitored fine-scale movements during 30 s (between 00:30 and 01:00 in the films). In the 3 min periods that included food being introduced, these 30 s occurred before feeding. We defined active swimming as the time grayling were not holding a fixed position. In the statistical analyses of active swimming and position changes, we used arcsine square-root-transformed proportions.

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variable flow regime, this conclusion was based on an analysis showing that feeding (Regime A vs. B) had no effects on distance to nearest neighbour regardless of habitat restoration treatment, both at the first (ANOVA, feeding regime $F_{1,25} = 0.09$, $p = .77$, feeding regime $\times$ habitat interaction $F_{2,25} = 0.56$, $p = .58$) or at the second potential feeding occasion (ANOVA, feeding regime $F_{1,22} = 0.33$, $p = .57$, feeding regime $\times$ habitat interaction $F_{2,22} = 0.65$, $p = .53$). Similarly, there were no such effects on position changes or active swimming at the first (ANOVA, feeding regime $F_{1,22} = 0.33$ and $<0.01$, $p = .48$ and .97, feeding regime $\times$ habitat interaction $F_{2,22} = 0.53$ and 0.68, $p = .60$ and .52) or the second potential feeding occasion (ANOVA, feeding regime $F_{1,22} = 0.01$ and 0.71, $p = .93$ and .41, feeding regime $\times$ habitat interaction $F_{2,22} = 0.71$ and 0.48, $p = .51$ and .63).

In an additional check to verify that potential effects of flow changes were not confounded by an effect of time, we compared distance to nearest neighbour and position changes between the films (1, 2, 5, 6 and 9) in the stable flow regime. There was no effect of film on distance to nearest neighbour (LMM, $F_{4,26.7} = 1.44$, $p = .25$) or on position changes (LMM, $F_{4,76} = 1.84$, $p = .13$), indicating that time had no major impact on the results. We did not collect data on active swimming from Films 2–9 in the unrestored habitat.

We analysed differences in food intake between flow regimes (steady vs. variable) and habitat treatments (restored vs. unrestored) with a two-way ANOVA, using the mean number of captured chironomids for each group of grayling as the response variable. All statistical analyses were performed in SPSS Statistics 25 (IBM, Armonk, USA).

## RESULTS

### 3.1 Effects of changing flow and habitat restoration

Grayling that experienced a flow peak (both at the start of ramping up flow and after a flow peak) had longer distance to the nearest neighbour (means ± SEM [standard error of mean] = 1.73 ± 0.13 and 1.84 ± 0.16 m) than those during the initial stable low base flow (mean ± SEM = 1.14 ± 0.16 m) (LMM $F_{2,75.4} = 4.44$, $p = .02$). There was little effect of habitat restoration (LMM, $F_{1,22.3} = 3.89$, $p = .06$) and no effect of the interaction between flow and habitat treatment on distance to the nearest neighbour (LMM, $F_{2,75.4} = 1.12$, $p = .33$; Figure 3a).

Pairwise post hoc comparisons showed that distances to nearest neighbour at the start of ramping up and after ramping down were longer than that during the low stable base flow ($p < .05$), but not different from each other ($p = .58$). Grayling made fewer position changes during the start of ramping up than at the initial stable flow.

**FIGURE 3** Boxplots of (a) mean distance to nearest neighbour, (b) mean position changes and (c) mean active swimming of groups of European grayling (*Thymallus thymallus*) in experimental flumes with (restored) and without (unrestored) boulders added in three flow treatments: (i) low, stable base flow, (ii) at the start of ramping up from and (iii) after ramping down to base flow.
and after ramping down to base flow (mean movements ± SEM = 0.56 ± 0.08 vs. 1.16 ± 0.22 and 1.11 ± 0.14) (LMM, $F_{2,76} = 5.52, p = .01$; pairwise post hoc comparisons $p_{\text{ramping up vs. stable and ramping up vs. after ramping down}} < .01, p_{\text{stable vs. after ramping down}} = .71$).

There was no effect of habitat treatment (LMM, $F_{1,19.6} = 0.44, p = .52$) or of the interaction between flow and habitat treatment on position changes (LMM, $F_{2,76} = 2.46, p = .09$; Figure 3b). In the analysis of active swimming, there were no main effects of flow (LMM, $F_{1,76} = 0.75, p = .48$) or habitat (LMM, $F_{1,19.6} = 1.95, p = .18$). There was a significant interaction effect between flow and habitat treatment (LMM, $F_{2,76} = 3.36, p = .04$), showing that grayling in the unrestored habitat treatment increased their active swimming when experiencing a ramping up of the flow or after ramping down, whereas grayling in the restored habitat did not (Figure 3c).

### 3.2 Effects of static flow and habitat restoration

Grayling in the restored habitat treatment had longer distance to nearest neighbour in the low than in the intermediate static flow (mean distances ± SEM = 1.50 ± 0.21 vs. 0.59 ± 0.12 m). In the unrestored habitat, grayling showed the opposite effect and had shorter distance to nearest neighbour in the low than in the intermediate static flow (0.79 ± 0.18 vs. 1.04 ± 0.25 m). This contrasting pattern was revealed by a significant interaction effect between static flow and habitat treatment (ANOVA, main effects of static flow $F_{1,28} = 2.28, p = .14$ and habitat $F_{1,28} = 0.37, p = .55$; static flow × habitat interaction effect $F_{1,28} = 6.93, p = .01$; Figure 4a). Grayling made more position changes in the low than in the intermediate stable flow (mean movements ± SEM = 1.16 ± 0.22 vs. 0.13 ± 0.08) (ANOVA, $F_{1,36} = 30.08, p < .001$). Habitat restoration or the interaction between static flow and habitat restoration had no effect on position changes (ANOVA, $F_{1,36} = 2.08$ and 0.77, $p = .16$ and .39, respectively; Figure 4b). Grayling had higher active swimming in the restored than the unrestored habitat (mean proportion ± SEM = 0.38 ± 0.07 vs. 0.25 ± 0.05) (ANOVA, $F_{1,36} = 52.47, p < .001$) and in the low than in the intermediate static flow (0.52 ± 0.06 vs. 0.11 ± 0.02) (ANOVA, $F_{1,36} = 7.02, p = .012$). There was no interaction effect between static flow and habitat treatment on active swimming (ANOVA, $F_{1,36} = 1.25, p = .27$; Figure 4c).

### 3.3 Food capture

We found 98% of the ingested chironomids (assessed by dissection) by stomach pumping the grayling. Individual grayling ($n = 160$) captured between 0 and 73 chironomids during a trial (mean ± SD = 23 ± 16). Only four grayling did not capture any chironomids. The mean number of captured chironomids was higher for groups in the variable than in the stable flow treatment (means ± SEM = 29.4 ± 2.7 vs. 15.7 ± 1.5) (ANOVA, main effect of flow regime $F_{1,36} = 21.24, p < .01$, main effect of habitat $F_{1,36} = 3.79, p = .06$, flow regime × habitat interaction effect $F_{1,36} = 1.29, p = .26$; Figure 5).
In natural rivers, graylings often occur both alone, defending a drifting feeding position, and in small groups (Greenberg et al., 1996; Hughes & Boll, 1990), indicating that the outcome of both competitive and cooperative interactions play important roles in these species. We show that changes in flow affects the social behaviour of juvenile European grayling. Grayling positioned themselves closer to each other (i.e., shorter distance to nearest neighbour) before a flow peak than at ramping up the flow and after a flow peak, indicating that hydropoaching may disrupt sociability in shoaling fish (Garner, 1997), with effects on for example, risk-taking and anti-predator performance (Pitcher, 1986). Flow magnitude also influenced the distance to nearest neighbour, but the direction of the effect depended on the habitat. In the restored habitat with complex instream structure, distance to nearest neighbour was shorter (i.e., more cohesive group structure) in the low than in the intermediate static flow, whereas the opposite pattern was found for the unrestored habitat. Mäki-Petäys, Vehanen, and Muotka (2000) found a similar interaction effects for small (3–4 g), young-of-the-year grayling in summer (but not in winter) conditions, indicating that this effect may be general for several life stages but not during all seasons. Possibly, grayling depend on information from conspecifics to find food and optimize its intake (which should be most important during the growth season) and to reduce energetic cost associated with swimming. At low flow condition, information about food availability and predation threats could have been more valuable than at high flows. The boulders in the restored habitat probably blocked vision, which influenced grayling to reduce their distance to nearest neighbour to be able to see each other. At high flows, the interaction between flow and structure possibly created many good foraging locations (low velocity positions near fast water), and social foraging might have been replaced by station holding to some extent, which increased distance.

Dynamic flows may also affect the movement patterns of riverine fishes (Liao, 2007). For example, Scruton et al. (2003) showed that brook trout (Salvelinus fontinalis) move more during up- and downramping of the flow than at both high and low steady flow, whereas studies on brown trout (Salmo trutta) and Atlantic salmon (Salmo salar) regarding this behaviour show conflicting results (e.g., Berland et al., 2004; Bunt, Cooke, Katopodis, & McKinley, 1999; Scruton et al., 2008). In contrast to our predictions, grayling reacted by reducing their position changes (i.e., movements longer than 1 m) during upramping of the flow. Grayling did, however, increase their active swimming (also including short-scale movement) when they experienced changing flows compared to an initial stable flow, but this effect was found only in the unrestored habitat. A general interpretation may be that both flow changes and magnitude influenced movement, but in opposite directions (high variability leading to increased movement and high magnitude leading to a reduction). Furthermore, it is possible that the reaction to dynamic flows are species and life stage specific, and that different aggression levels and propensities to social foraging may influence effects on movement.

When comparing two static flows, we observed fewer position changes and less active swimming in the intermediate than in the low flow, results that are similar to previous observations (e.g., Grant & Noakes, 1988; Hasegawa & Yamamoto, 2010). This effect of flow corroborates drift-foraging theory that predicts a feeding mode shift from a sit-and-wait tactic to active searching at low velocities (Harvey & Railsback, 2014; Larrañaga, Valdimarsson, Linnansaari, & Steinbringsson, 2018). Active swimming was also lower in the unrestored than in the restored habitat. Grayling were never positioned over the boulders, and a complex habitat that partially obstructs vision possibly increases the need for small-scale movements to keep track of the positions of conspecifics visually and to adjust social behaviour.

Grayling caught more prey in the variable than in the stable flow regime. The foraging success in water velocities experienced by our grayling during the low base flow in the variable flow regime (~10 cm s$^{-1}$) has been shown to be nearly 100% in other studies (Bozeman & Grossman, 2018; Watz, Piccolo, Bergman, & Greenberg, 2014). On the other hand, during the other feeding (which occurred at peak flow), high water velocities (~80 cm s$^{-1}$) should have resulted in few captures, because foraging success at these velocities is low (Bozeman & Grossman, 2018). In the stable flow regime, water velocities were ~40–50 cm s$^{-1}$, and at these velocities grayling have been shown to capture roughly 50% of the prey (Bozeman & Grossman, 2018). Hence, grayling in our study were either feeding twice in intermediate water velocities resulting in an intermediate prey capture ability or once in velocities with low and high velocities resulting in high and low abilities, respectively. Therefore, the effect of velocity on foraging ability may not explain the difference in food capture between the flow treatments, and the difference may instead
have been caused by different times the prey was present in the test arena at different flows.

Grayling (of similar size as those in our study) presented with many prey simultaneously have a relatively short handling time (<2 s; Watz, Bergman, Piccolo, & Greenberg, 2014), and the bursts of prey at the low base flow should therefore have resulted in many captures. In a regulated river, if there is enough food resources available also at low flows, it is possible that fish will use this resource more efficiently than at higher flows. Indeed, in the Noguera Pallaresa River, hydropeaking did not have negative effects on the feeding behaviour of brown trout (S. trutta), and instead led to increased food consumption (Rocaspana, Aparicio, Vinyoles, & Palau, 2016). Finch, Pine II, and Limburg (2015) found that Humpback hub (Gila cypha) in the Colorado River had lower growth rates during periods of steady natural flow than during fluctuating hydropeaking operation, and that this result was consistent across multiple years and seasons. Contrastingly, compared to stable flow, a simulated hydropeaking flow regime reduced growth of Atlantic salmon (S. salar) during summer (but not during winter) in experimental stream channels (Puffer et al., 2015). It is difficult to predict how our findings in terms of altered social behaviour, movement, activity and food intake may translate into growth of European grayling in regulated rivers, and further field studies are warranted (Hellström et al., 2019).

Flow and physical structure interact to create stream fish habitat, and restoration projects often aim to increase microhabitat heterogeneity. Most studies investigating the effects of river restoration on stream fish populations have focused mainly on salmonid species other than grayling, and these studies demonstrate that structural complexity and a natural flow regime generally increase salmonid abundance (Louhi et al., 2016; Marttila et al., 2019). The few published studies on grayling report, however, an ambiguous effect on grayling (e.g., Hellström et al., 2019; Vehanen, Huusko, Yrjänä, Lahti, & Mäki-Petäys, 2003). Our results indicate that grayling can adjust their social behaviour in response to local flow conditions (both magnitude and changes) and the level of physical complexity. Grayling can establish dominance hierarchies (Hughes, 1992; Hughes & Dill, 1990), but do not defend their feeding territories as strongly as other juvenile salmonids, and may forage in groups (Greenberg et al., 1996). We suggest that in rivers with a dynamic flow regime, instream structure may not be as important for grayling as it is for other (more territorial) salmonids. In fast and relatively stable water velocities, grayling may in contrast depend on defending fixed foraging positions, which requires structure.

We showed that the social behaviour of a riverine fish is influenced by ramping up and down the flow (conditions experienced by fishes in for example, regulated rivers with a hydropeaking flow regime), and that the effects of flow may depend on the bottom structure. Generalising results from flume experiment to effects on populations in natural systems must be done with caution, and the influence of changing flows on growth may be to some extent season and site specific. In contrast to many other laboratory studies, however, we used large flumes (15 m) and water velocities (up to ~1 m s⁻¹) that stream salmonids may well experience in nature. The results presented here were based on 120 min and two flow peaks, and for stream fish populations that experience hydropeaking every day for extensive periods, the effects of changing flow on behaviour may affect survival rates and thus population dynamics.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Johan Watz https://orcid.org/0000-0002-4417-6636
Kristine Lund-Bjørnás https://orcid.org/0000-0003-3576-7538
Martin Österling https://orcid.org/0000-0001-6758-5857
John J. Piccolo https://orcid.org/0000-0002-2633-4178
Olle Calles https://orcid.org/0000-0002-8738-8815

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