**Interpopulation variation of behavioural and morphological traits that affect downstream displacement of the juvenile white-spotted charr *Salvelinus leucomaenis***

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**Abstract**

Downstream displacement, the passive downstream dispersal of riverine organisms, can generate evolutionary pressures that selectively remove susceptible individuals from upstream habitats. These evolutionary pressures may accumulate over time in fish populations situated upstream of a tall check dam that displaced fish are unable to swim over and can be diluted by the homing of displaced individuals in the absence of such barriers. Here, we conducted interpopulation comparisons between above-dam and unrestricted open-stream populations of the juvenile white-spotted charr *Salvelinus leucomaenis* to test the hypothesis that above-dam juveniles possess more advantageous traits that reduce downstream displacement than open-stream juveniles. We focused on sedentary behaviour and body depth, both of which are known to affect downstream displacement. Interpopulation comparisons revealed that juveniles from above-dam populations were consistently more sedentary than those from open-stream populations. On the other hand, there were no systematic differences in body depth between above-dam and open-stream populations. These results are consistent with the evolution of behaviours in above-dam populations that inhibit downstream displacement. However, several other factors could explain the results obtained, and further studies will be needed to confirm the presence of behavioural evolution in our study system.

**Keywords:**

behavioural evolution, isolated population, migration barrier, phenotype-dependent dispersal, salmonid

**1. Introduction**

Downstream displacement is a riverine phenomenon in which organisms are advected by water flow from their home river section to a downstream area. Water flows that cause downstream displacement can be divided into two types: flood flows (Meffe, 1984; Chapman & Kramer, 1991; Good et al., 2001; Sato, 2006; Weese et al., 2011; Yamada & Wada, 2021) and flows under ordinary river conditions (i.e., ordinary flows; Thiesmeier & Schuhmacher, 1990; Lechner et al., 2016; Nagel et al., 2021). Although flood flows can cause catastrophic downstream displacement (Meffe, 1984; Sato, 2006; Weese et al., 2011), occurrences of such downstream displacement are often trait-dependent in riverine fishes (Meffe, 1984; Chapman & Kramer, 1991; Good et al., 2001; Blondel et al., 2021; Yamada & Wada, 2021). For example, smaller individuals are more likely to be displaced by strong floods from their home river section in populations of the molly *Poecilia gillii* (Kner 1863) (Chapman & Kramer, 1991) and the Trinidadian guppy *Poecilia reticulata* Peters 1859 (Blondel et al., 2021). Downstream displacement due to ordinary flows can also remove individuals with vulnerable traits from upstream populations. For example, reduced use of low-current habitats in the stickleback *Gasterosteus aculeatus* (Linnaeus 1758) is correlated with increased downstream displacement under ordinary flow conditions (Jiang et al., 2015). Thus, downstream displacement can be a general evolutionary pressure that removes individuals with low resistance to flow-driven displacement from their home river reaches (Yamada & Wada, 2021).

Tall waterfalls and tall dams are strong barriers to upstream fish movement (Northcote, 2010; Zarri et al., 2022). These barriers could play an evolutionary role in creating and maintaining variation in many traits among local riverine populations because displaced fish cannot ascend the tall barrier and home to their original habitat (Northcote, 1981; Blondel et al., 2020; Yamada & Wada, 2021; reviewed by Northcote, 2010; Zarri et al., 2022). For instance, rainbow trout *Oncorhynchus mykiss* (Walbaum 1792) in above-dam streams in California have rapidly evolved freshwater residency in response to strong evolutionary pressures against seaward migration created by the presence of the dams (Pearse et al., 2014). The evolutionary pressure from downstream displacement might also accumulate in above-barrier populations and lead to the rise of functional traits that increase resistance to flood and/or ordinary flows. Yamada and Wada (2021) suggested that the juvenile amago salmon *Oncorhynchus masou ishikawae* (Jordan & McGregor 1925) evolved deep bodies, which enhance burst-swimming ability, to avoid downstream displacement during flooding. Blondel et al. (2020) speculated that high rheotaxis in *P. reticulata* might have evolved in above-waterfall habitats to allow individuals to remain in their habitats (see also Mohammed et al., 2012). In recent years, increasing attention has been paid to phenotypic shifts in upstream fish populations caused by the presence of migration barriers (Zarri et al., 2022). However, few studies have focused specifically on the evolutionary pressures of downstream displacement.

The white-spotted charr *Salvelinus leucomaenis* (Pallas 1814) is a common riverine salmonid fish in northern Japan. It establishes populations in river sections above tall artificial check dams (i.e., above-dam populations) in addition to unrestricted open river sections (i.e., open-stream populations) (Morita et al., 2000; Morita & Yamamoto, 2001; Yamada et al., 2019; Hasegawa et al., 2020). In this study, we compare ancestral open-stream populations against their derivative above-dam populations. We focus our analysis on juveniles, which are likely subject to stronger evolutionary pressure from downstream displacement than adults because of their less-developed swimming ability (Lechner et al., 2016).

We chose to compare sedentary behaviour and body depth among juvenile *S. leucomaenis* from open-stream and above-dam populations. Sedentary behaviour might help flow-sensitive animals avoid downstream displacement because more active fish have a higher risk of accidentally encountering fast currents (Lechner et al., 2016; see also Brittain & Eikeland, 1988; Naman et al., 2016). Deep bodies could also reduce downstream displacement because greater body depth is associated with enhanced transient burst swimming performance (Taylor & McPhail, 1985a; Domenici et al., 2008; Bolnick et al., 2009; see also Webb, 1984), which could aid escape from fast currents (Yamada & Wada, 2021). The aim of our study is to examine whether juvenile white-spotted charr inhabiting above-dam and open-stream habitats differ in behavioural and morphological traits that affect downstream displacement and to discuss the potential impacts of evolutionary pressures associated with downstream displacement.

**2. Materials and methods**

*2.1 Subject fish*

We used a hand net to sample juveniles from above-dam and open-stream populations in southern Hokkaido, Japan (Figure 1; Table 1). Basic environmental data for each study station (Stn.) are summarized in Table 1. The dam at Stn. 1 was constructed 30 years before the survey year, and the dam at Stn. 3 was constructed 45 years before the survey year (Table 1). Assuming a generation length of *S. leucomaenis* of 3.73 years (see Yamamoto et al., 2006), we estimated that 8 and 12 generations had elapsed after dam construction at Stns. 1 and 3, respectively. Juveniles were sampled from Stn. 1 (an above-dam population) on 23 May 2019, Stn. 2 (an open-stream population) on 26 May 2019, Stn. 3 (an above-dam population) on 28 May 2019, and Stn. 4 (an open-stream population) on 2 June 2019 (Figure 1). The number of fish sampled at each station were: Stn. 1, 34; Stn. 2, 35; Stn. 3, 33; and Stn. 4: 36. Four fish, for which video and still images were not recorded, were discarded from the analysis and are not included in the above counts. No reservoirs were located at either of the above-dam stations.

*2.2 Behavioural observations and morphological measurements*

Collected juveniles were transported to a thermostatic chamber (5 °C) in our laboratory on the Hakodate campus of Hokkaido University (Figure 1) and were kept in a small holding tank (30 × 18 × 24 cm, water depth 10 cm) until the next procedure. Each juvenile was individually placed in an observation tank (60 × 20 × 25 cm; Figure 2) in the thermostatic chamber. The observation side of the tank was covered with a grey sheet to ensure that the juveniles would not be disturbed by researchers. Water in the observation tank was circulated by using a submersible pump (e-ROKA PF701, GEX Co., Ltd., Osaka, Japan) at a flow rate of 0.16 L/s (Figure 2).

Juvenile behaviours were recorded by using a digital camera (TG-4, Olympus Co., Ltd., Tokyo, Japan). We focused on station-holding (SH) as a metric of sedentary behaviour. We defined SH as a fish resting on the bottom of the observation tank during a period of inactivity (Yamada and Wada, 2023). After an acclimation period of 60 s following introduction to the observation tank, we observed the juveniles for 540 s and recorded the seconds during which SH occurred. These times were then summed to determine the total time spent on SH for each individual. Although the repeatability of the behaviour was not examined, we expect propensity for SH in the observation tank to reflect behaviour in the wild, based on the following studies on the genus *Salvelinus*. Biro and Ridgway (2008) observed that sedentary juvenile brook trout *Salvelinus fontinalis* (Mitchill 1814) remained sedentary for several days in the field. Wilson and McLaughlin (2007) found that juvenile *S. fontinalis* that were sedentary in the field were also sedentary in an experimental tank and tended to stay at the bottom of the tank.

After behavioural observation, the left side of each juvenile was photographed by using a digital camera (TG-4, Olympus Co., Ltd.) fixed to a photographing platform. We used these photographs to measure body depth at three locations along the body (Figure 3) as well as fork length (FL; an index of body size) in millimetres by using image analysis software (ImageJ, National Institutes of Health, Bethesda, MD, USA). Because body size affects the downstream displacement of small fishes (Jowett & Richardson, 1989; Chapman & Kramer, 1991; Weese et al., 2011), we treated FL as a covariate for interpopulation comparisons. These laboratory experiments were conducted 1–2 days after sampling (i.e., Stn. 1, 24 May; Stn. 2, 27 May; Stn. 3, 29 May; Stn. 4, 3 and 4 June). All individuals were returned to their original habitat after these procedures.

*2.3 Data analyses*

We used R version 4.1.0 (R Core Team, 2021) for all statistical analyses. Means of FL were analysed by using analysis of variance without assuming equal variances (i.e., Welch’s ANOVA). A post-hoc comparison among all populations was then conducted by using the Games–Howell test for data with unequal variances. We used the function *posthocTGH* in the package “userfriendlyscience” version 0.7.2 (Peters, 2018) for the Games–Howell test.

To compare body depth among populations, a principal component analysis was performed for the three body depth measurements (Figure 3) by using the pooled data of all populations. As a result, we obtained a first principal component (PC1) explaining 99.4% of the total variance and considered this to be the aggregate value of body depth. We then calculated a linear regression of the PC1 on FL from the pooled data of all populations. Residuals were then calculated from the regression result (i.e., PC1 residual) and treated as an indicator of relative body depth. Larger values of PC1 residuals indicate greater body depth. Mean PC1 residuals were compared among all populations by using the same analysis as for FL (i.e., Games–Howell post-hoc test after Welch’s ANOVA).

A generalized linear model (GLM) was also constructed to evaluate differences in SH among all populations. The response variable was the proportion of the total observation time (540 s) taken up by SH (hereafter, the “SH proportion”). The explanatory variables were population type (above-dam = 1, open-stream = 0), FL, and an interaction term. A quasi-binomial error distribution with a logit link function was used to avoid overdispersion. The statistical significance of the explanatory variables was tested by using analysis of deviance based on the *F* value by using the function *Anova* in the package “car” (Fox & Weisberg, 2019).

*2.4 Ethical statement*

Fish were collected in a manner that did not violate the fisheries regulations of Hokkaido Prefecture; therefore, no permission was required from the local government. The Hokkaido University Animal Experiment Committee, to which the authors belong, does not require approval for research plans using fish. Therefore, this study did not receive an approval number from the committee. However, we took care to minimize contact with fish and avoid unnatural experimental treatments and devised ways to reduce stress on the experimental fish.

**3. Results**

A total of 138 data points were obtained from the four stations. There was a significant difference in FL among the populations (Welch’s ANOVA, *F*3, 73.69 = 85.86, *P* < 0.001). Means and standard deviations of FL at each station were as follows: Stn. 1, 35.30 ± 3.63 mm; Stn. 2, 41.75 ± 4.13 mm; Stn. 3, 32.67 ± 2.57 mm; and Stn. 4, 42.77 ± 3.22 mm. Games–Howell tests revealed that FL was largest at Stn. 2 and Stn. 4, followed by Stn. 1, and was smallest at Stn. 3 (Table 2; Figure 4). These results indicate that FL was smaller in the above-dam populations (Stns. 1 and 3) than in the open-stream populations (Stns. 2 and 4), and that there were also differences in FL among the above-dam populations (Figure 4).

The PC1 residual (an index of body depth) differed significantly among populations (Welch’s ANOVA, *F*3, 74.23 = 20.56, *P* < 0.001), but differences between above-dam and open-stream populations were inconsistent. Games–Howell tests revealed that juvenile body depth was greatest at Stns. 4 and 1, followed by Stn. 3, and smallest at Stn. 2 (Table 2; Figure 4).

A GLM for SH proportion detected a significant effect of the interaction between FL and population (*F*3, 130= 4.088, *P* = 0.008; Table 3), meaning that the slope of the relationship between SH proportion and juvenile size differed among populations. The relationship between FL and SH proportion was consistent among above-dam populations: smaller individuals exhibited a lower SH proportion. In open-stream populations, there was a positive relationship between SH proportion and FL at Stn. 4, but a weakly negative relationship at Stn. 2 (Table 3; Figure 5). SH proportions were higher for above-dam populations than for open-stream populations for almost the entire range of FL (Table 3; Figure 5).

**4. Discussion**

Our results reveal interpopulation variations in the morphological traits of juvenile *S. leucomaenis*. Juveniles from above-dam populations had smaller FL than those from open-stream populations. This difference could have been caused by the absence of anadromous individuals in the above-dam populations (see Morita et al., 2000; Northcote, 2010). Anadromous salmonids tend to produce larger eggs than residents, which can grow into larger offspring during the early juvenile phase (e.g., Jonsson & Jonsson, 1999; Liberoff et al., 2014). For instance, young-of-the-year juvenile *O. mykiss* from anadromous mothers are larger than those from resident mothers (Liberoff et al., 2014). The absence of this maternal effect from anadromous individuals could explain the small juvenile sizes observed in above-dam populations.

The observed differences in FL could also be attributed to the relatively low water temperatures in above-dam habitats, which are often located at high elevations. In salmonids, low temperature delays egg hatching and suppresses juvenile growth (Jonsson et al., 2005; Finstad & Jonsson, 2012). In turn, slow growth rates could result in small juvenile sizes in high-elevation habitats (Kennedy et al., 2003). However, there was a significant difference in FL between Stn. 2 (an open-stream population) and Stn. 3 (an above-dam population), even though the two stations are at almost the same elevation. Similarly, among the above-dam populations, juveniles from Stn. 1 were larger than those from Stn. 3, even though Stn. 1 is located at a higher elevation. These results indirectly suggest that the differences in FL between above-dam and open-stream populations were more likely to have been caused by differences in life history type than by differences in temperature.

In contrast to our results for FL, we found no evidence of systematic differences in body depth between the two habitat types. Although some interpopulation variations in body depth were detected, the differences were not consistent between above-dam and open-stream populations; the deepest body depths were observed at Stn. 4 (an open-stream population) and Stn. 1 (an above-dam population), intermediate values were observed at Stn. 3 (an above-dam population), and the shallowest body depths were observed at Stn. 2 (an open-stream population). The differences observed among open-stream populations might reflect differences in the seaward-migration distance from each station. For salmonid juveniles, deep bodies enhance transient burst swimming performance, but shallow bodies (which have low drag) increase swimming stamina during long-distance migrations (Taylor & McPhail, 1985a). Inland populations, therefore, often have shallower bodies than coastal populations because of the long migration distances required to reach the sea (Taylor & McPhail, 1985b). This could explain the shallow bodies of juveniles from Stn. 2, which is far removed from the sea. The slightly shallower bodies of juveniles from Stn. 3 (the station with the smallest body size overall) than those collected from Stns. 1 and 4 could reflect underdevelopment in body shape.

Our results show clear interpopulation variations in SH proportion. The slope of the regression of FL against SH proportion differed substantially between above-dam and open-stream populations. Small fish consistently had higher SH proportion than large fish in the above-dam populations; however, this trend was inconsistent in the open-stream populations. Small fish are generally at high risk of downstream displacement owing to their poor swimming ability (Jowett & Richardson, 1989; Chapman & Kramer, 1991; Blondel et al., 2021), thus the relationship observed in the above-dam populations would more effectively reduce downstream displacement. Additionally, the SH proportions of above-dam populations were higher than those of open-stream populations across almost the entire estimated range of FLs. These results support our initial hypothesis that juveniles with higher propensities for SH can avoid downstream displacement and hence persist in above-dam habitats.

Our results for SH are consistent with the contention of a previous study that *S. leucomaenis* juveniles from above-dam populations are genetically less likely to move downstream. Morita and Yamamoto (2001) transplanted wild *S. leucomaenis* juveniles collected above and below a dam to an above-dam habitat where fish were absent. They found that juveniles from above the dam moved a shorter distance downstream than those from below the dam, even under the same environmental conditions. In salmonid juveniles, freezing behaviour (which resembles SH in that individuals remain immobile on the substrate) is often suggested to have a genetic basis (e.g., Kortet et al., 2014; Ågren et al., 2019). Ågren et al. (2019) examined the heredity of personality traits in the juvenile brown trout *Salmo trutta* (Linnaeus 1758) and concluded that the personality axis represented by freezing behaviour has a genetic basis. Therefore, the higher SH proportions among above-dam juveniles observed in this study may explain the low tendency of above-dam juveniles for downstream movement observed by Morita and Yamamoto (2001).

Although the interpopulation variations in SH proportion observed in our study are consistent with our evolutionary hypothesis, we are unable to rule out other ecological mechanisms. For example, for *S. leucomaenis* inhabiting our study region, juvenile densities are several times higher in open-stream populations, in which anadromous individuals produce a large number of offspring, than in above-dam populations consisting solely of resident individuals (Morita et al., 2000, 2009). The lower SH proportions observed among open-stream juveniles could reflect increased intraspecific competition in these high-density populations, which might necessitate an increase in growth-related behavioural activity. This explanation is consistent with the result that small open-stream juveniles were as active as (Stn. 2) or more active than (Stn. 4) large sympatric juveniles because the high activity of small juveniles would be indicative of a need for compensatory growth. Overall, caution should be exercised in interpreting our results.

Unfortunately, our results are insufficient to accept our evolutionary hypothesis because of the many unmeasured environmental factors that could have caused the observed interpopulation variations. However, given the recent global focus on the evolutionary pressures exerted on above-barrier fish populations (Zarri et al., 2022) and on evolutionary mechanisms associated with phenotype-dependent dispersal (Davis & Stamps, 2004; Edelaar et al., 2008; Shine et al., 2011; Edelaar & Bolnick, 2012), we believe that further examination of our hypotheses is worthwhile. Additional work is needed to quantify the importance of evolutionary pressures from downstream displacement.

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**Data availability**

Data are available from the authors upon reasonable request.

**Conflict of interest**

The authors declare that they have no conflicts of interest.

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**Table 1.** Summary of environmental conditions and dam characteristics for all study stations. Elevations were determined as the average of the lowest and highest elevation of each study station, as recorded by using a handheld GPS (eTrex 20XJ, Garmin Ltd., Olathe, KS, USA). Slopes were calculated from the difference in elevation between the lowermost and uppermost reaches of each study station (*d*) and the length of the study station (*l*), as follows: slope (%) = 100 × *d* / (*l*2 – *d*2)0.5. The length of the stations was measured as the distance along the stream from the lowermost to the uppermost part of the station. River widths were measured at 5-m intervals from the downstream end of each study station and are reported as means ± standard deviations. Dams were located immediately downstream of Stns. 1 and 3. Dam width indicates the width of the water passage above the dam, and dam height indicates the vertical drop height of the dam. Years of construction of the dams at Stns. 1 and 3 are drawn from Yamamoto et al. (2006) and the year listed on the dam itself, respectively. All data were collected in the field in early June 2022.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Stations | Elevation (m) | River width (m) | Slope (%) | Dam width (m) | Dam height (m) | Dam construction year |
| 1 (above-dam) | 132.00 | 4.53 ± 1.45 | 2.65 | 9.86 | 2.48 | 1989 |
| 2 (open-stream) | 98.00 | 1.68 ± 0.56 | 5.57 | - | - | - |
| 3 (above-dam) | 97.30 | 1.85 ± 0.73 | 13.05 | 4.05 | 5.12 | 1974 |
| 4 (open-stream) | 10.95 | 2.59 ± 0.98 | 3.73 | - | - | - |

**Table 2.** Summary of Games–Howell post-hoc comparisons of fork length and PC1 residual (an index of body depth) among study stations. Larger PC1 residuals indicate greater body depth. Significant *P*-values are shown in bold.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Combination of comparisons | Difference | df | *t* | *P* |
| Fork length |  |  |  |  |
| Station 2 (OP) – Station 1 (AD) | 6.45 | 66.4 | 6.90 | **<0.001** |
| Station 3 (AD) – Station 1 (AD) | –2.63 | 59.6 | 3.43 | **0.006** |
| Station 4 (OP) – Station 1 (AD) | 7.48 | 65.9 | 9.10 | **<0.001** |
| Station 3 (AD) – Station 2 (OP) | –9.09 | 57.4 | 10.96 | **<0.001** |
| Station 4 (OP) – Station 2 (OP) | 1.02 | 64.3 | 1.16 | 0.654 |
| Station 4 (OP) – Station 3 (AD) | 10.11 | 65.8 | 14.46 | **<0.001** |
|  |  |  |  |  |
| PC1 residual (an index of body depth) |  |  |  |  |
| Station 2 (OP) – Station 1 (AD) | –0.388 | 67.0 | 6.10 | **<0.001** |
| Station 3 (AD) – Station 1 (AD) | –0.186 | 63.7 | 2.74 | **0.039** |
| Station 4 (OP) – Station 1 (AD) | 0.098 | 67.5 | 1.45 | 0.476 |
| Station 3 (AD) – Station 2 (OP) | 0.202 | 64.5 | 2.98 | **0.021** |
| Station 4 (OP) – Station 2 (OP) | 0.485 | 68.3 | 7.18 | **<0.001** |
| Station 4 (OP) – Station 3 (AD) | 0.283 | 66.8 | 3.95 | **0.001** |

OP, open-stream population; AD, above-dam population.

**Table 3.** Summary of a generalized linear model with a quasi-binomial error distribution used to analyse interpopulation variations in the proportion of time spent on station holding. Significant *P*-values are shown in bold.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Variable | | Estimate | SE | Num df | Den df | *F* | *P* |
| Intercept | | 12.84 | 4.67 |  |  |  |  |
| Fork length | | –0.30 | 0.12 | 1 | 130 | 7.680 | **0.006** |
| Station | Station 2 | –11.95 | 5.26 | 3 | 130 | 5.246 | **0.002** |
| Station 3 | –3.76 | 6.28 |
| Station 4 | –19.75 | 6.22 |
| Interaction | Station 2 × Fork length | 0.29 | 0.14 | 3 | 130 | 4.088 | **0.008** |
| Station 3 × Fork length | 0.07 | 0.18 |
| Station 4 × Fork length | 0.44 | 0.16 |
|  |  |  |  |  |  |  |  |
| Dispersion parameter | | 0.48 |  |  |  |  |  |

Num df, Numerator degrees of freedom; Den df, Denominator degrees of freedom.

**Figure legends**

**Figure 1.** Map of study stations (Stns.) including check dams. Open arrows indicate the direction of river flow, and black bars show the check dams. For simplicity, only the most downstream check dams are shown for non-surveyed tributaries.

**Figure 2.** Schematic cross-sectional **(a)** and overhead **(b)** views of the observation tank. For simplicity, the grey sheet on the observation side of the tank has been omitted from the illustration.

**Figure 3.** Morphological measurements of the juvenile white-spotted charr *Salvelinus leucomaenis*. The three measurements of body depth were aggregated into a single variable (PC1) by using principal component analysis.

**Figure 4.** Box plots of fork lengths **(a)** and PC1 residuals (an index of body depth) **(b)** of juvenile white-spotted charr *Salvelinus leucomaenis* from above-dam (black) and open-stream (grey) populations. PC1 residuals were calculated from a linear regression model estimated from pooled data of all individuals (i.e., PC1 = 0.308 × FL – 11.764, *n* = 138). Larger PC1 residuals indicate greater body depth. Whiskers indicate maximum and minimum values of non-outlier data. The top and bottom edges of each box indicate first and third quartiles, the thick black lines show the median, and grey dots show raw data. Station types are indicated in parentheses as open-stream (OP) or above-dam (AD). Letters indicate homogenous subsets at the *P* < 0.05 level based on Games–Howell post-hoc comparisons.

**Figure 5.** Comparison of the proportion of observed seconds spent on station-holding (SH) by juvenile white-spotted charr *Salvelinus leucomaenis* from above-dam (black) and open-stream (grey) populations during 540 s of observation in an experimental tank. The *y*-axis indicates the total time spent on SH (s) / observation time (540 s). In both panels, lines show estimated generalized linear models with a quasi-binomial error distribution and a logit link function for above-dam populations (dashed, Stn. 1; solid, Stn. 3) and open-stream populations (dashed, Stn. 2; solid, Stn. 4). Station types are indicated in parentheses as open-stream (OP) or above-dam (AD).

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**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**



**Figure 5**