CHARR III



# Effects of water depth and structural complexity on survival and settlement of white-spotted charr (*Salvelinus leucomaenis*)

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**Abstract** Both climate change and dam operations are affecting water levels in river systems worldwide and their influence can be especially drastic in upper streams, where juvenile salmonids hatch and grow. However, efficient means of mitigating such influence on salmonid populations have not been developed, at least not in a practical manner throughout the world. In this study, we investigated effects of declining water levels and structural complexity on populations of age-0 white-spotted charr (*Salvelinus leucomaenis*) in

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tank and pond experiments. Survival of the charr was lower in the shallow tanks (15 cm water depth) than in the deeper ones. Similarly, more fish survived in the tanks with artificial structures (cobbles with Ringlong tape) compared to those without them. The grey heron (*Ardea cinerea*) was the most frequently observed predator during the tank experiment, and settlement of fish in the shallow ponds increased when artificial structures were provided. These results suggest that declining water levels and the loss of structural complexity may lead to a decrease in populations of white-spotted charr by increasing predation risk and interference competition.

**Keywords** Water level  $\cdot$  Predation risk  $\cdot$  Climate change  $\cdot$  Dam  $\cdot$  Grey heron *Ardea cinerea*  $\cdot$  Artificial structure

# Introduction

During the 21st century, the average global temperature is projected to increase by 2.6–4.8°C (IPCC, 2014 (scenario RCP8.5)). In regions that receive most precipitation as snow, increased temperatures may lead to earlier runoff in winter, and reduced flows after spring (Barnett et al., 2005). Therefore, climatechange induced intensification of the hydrologic cycle is further expected to increase the number and frequency of droughts (Dai, 2011). However, another potentially major cause for declining water levels is operation of dams that result in conditions that mimic droughts (Magoulick & Kobza, 2003). Therefore, problems induced by declining water levels already exist today and should not be ignored or simply relegated for future consideration.

Most age-0 salmonids use shallow areas at river edges of small tributaries as habitats (Kennedy & Strange, 1982; Johnson & Kucera, 1985; Moore & Gregory, 1988; Nagoshi et al., 1988; Kubota et al., 2001; Hasegawa & Maekawa, 2009). Therefore, declining water levels, caused by reducing river flows, could damage populations of salmonids in small tributaries, due to a reduction in or complete disappearance of their habitats. This may leads to streamdwelling salmonids exhibiting strong interference interactions while defending their territories through interspecific and intraspecific competition (Fausch & White, 1986; Nakano, 1995a, b; Hasegawa et al., 2004).

For many freshwater fishes, riparian predators (predatory birds and mammals that wade or dive) and piscivorous fishes are important predators. These predators use different water depths for predation: piscivorous fishes in deeper water and riparian predators in shallower water (Power, 1987; Harvey & Stewart, 1991). Therefore, declining water levels, as an indirect effect, are expected to increase predation risk by birds and mammals, especially for age-0 salmonids, which use shallow areas as their main habitat. However, when it comes to salmonids, studies that evaluate the effects of predation by birds and mammals as an indirect effect of declining water levels are extremely rare. Such a scenario is thus still mainly speculation.

The effects of declining water levels on the populations of fish will depend not only on water depth, but also on other physical factors, such as habitat complexity. Fish population density generally increases with increasing habitat complexity (Kalleberg, 1958; Dolinsek et al., 2007; Finstad et al., 2007) which can be explained by: an overall increase in the number of territories (Gowan & Fausch, 1996); enhanced productivity (Harmon et al., 1986; Sundbaum & Näslund, 1998); protection from predators (Beukers & Jones, 1997; Finke & Denno, 2006); or competitors (Jarman, 1974; Coulston & Maughan, 1983). Therefore, in order to evaluate the effects of

declining water levels properly, it is necessary to understand the relationship between water depth, structural complexity and the population of fish.

To evaluate effects of predation by riparian animals, species of predator animals and their behavior must be investigated in an environment that allows for free movement of all parties involved. However, the number of studies on this subject is limited, mainly because of difficulties in identifying species of predatory animals and observing their behaviors directly. These studies are further complicated by the fact that many predators exhibit complex behaviors, such as regular movements from one area to another for feeding and nesting (Collis et al., 2002), movements in response to changes in prey densities (Kushlan, 1976; Gawlik & Crozier, 2007), and movements in response to human disturbances (Klein, 1993). Recent developments in camera trapping technologies (fixed cameras with infrared sensors) provide us an opportunity to collect information on the behavior of predators in the wild (Silveira et al., 2003; Wegge et al., 2004). This study focuses on the relationship between water depth and predation risk of age-0 white-spotted charr (Salvelinus leucomaenis), by using outdoor tanks together with camera trapping, to evaluate effects of declining water levels on survival of salmonids. Additionally, for the purposes of developing techniques to counter the effects of declining water levels, this study also focuses on evaluating benefits of providing artificial structures as habitats for fish to mitigate predation risk and interference competition.

#### Materials and methods

## Test fish

Test fish used in experiments were age-0 F1 offspring of wild white-spotted charr from the Yanagisawa River in Tochigi Prefecture, Japan (approximately  $36^{\circ}44'$ N,  $139^{\circ}24'$ E). Fish were reared in four rearing tanks (50 cm wide × 120 cm long × 20 cm deep, water supply of 18 l/min) according to standard hatchery procedures as directed by National Research Institute of Fisheries Science (NRIFS) facility at Nikko. Test fish were age-0, 50–65 mm in fork length and 1.05–2.9 g in body weight, roughly similar in body size to age-0 stocked charr in Japan (Nakamura and Iida, 2009). Before the start of the study, fish were fed daily food rations (commercial trout pellets) equal to 1.5-2.0% of their estimated body weight.

# Tank experiment

We conducted tank experiments with 960 fish (in total) in four Fiber-Reinforced Plastic (FRP) circular tanks (120-cm in diameter, 50 cm high) at the riverside of the Jigoku-gawa River at NRIFS in Nikko in a forested and grassy area from 23 June to 29 August 2017. Each tank had a thin layer of natural gravel (particle size 2-7-cm in diameter) substrate and nine 15-cm cobbles, placed at the bottom as shelters. Each tank had a circular fence (10-cm high in an mounted around the tank circumference and an additional 8-cm in length at an angle over the tank) with green artificial leaves installed (Miyamoto et al. 2018 for more details), to provide fish with cover and prevent them from jumping out but leaving the center of the tank exposed from above. Furthermore, each tank had a camera (Trophy Cam HD, Bushnell, Overland Park, KS, USA) to monitor the whole tank from its side. Cover and gravel substrate allowed the charr to show nearnatural behavior, by providing options to hide or escape (Miyamoto, 2016a), thus minimizing experimental stress. Thirty fish were placed in each tank. The density was relatively high for salmonid fry, but was within the range observed in nature (Korsu et al., 2010). During the study, fish were fed daily food rations (commercial trout pellets were scattered all over the tank) equal to 1.0-2.0% of total body weight of all fish present at the time of feeding in a particular tank. Spring water was introduced into each tank at a rate of 6 l/min; water temperature of the tanks was  $10.4 \pm 0.5^{\circ}$ C (mean  $\pm$  SD) during the experiments.

To evaluate the relationship between water depth and predation risk in a first tank experiment, four different water depths (15, 25, 35, and 45) were maintained by bedding the bottoms of each tank differently with bags of gravel and then putting a layer of gravel on top of the bags. Each tank's water depth was changed randomly at the beginning of every trial. Fish that survived were removed and counted separately for each tank every 4 days at the end of each trial, which was replicated four times. To identify predator animals, photograph taken by the four cameras were evaluated (described below) at the end of each experiment.

A second tank experiment investigated the relationship between structural complexity and predation risk. This experiment used four FRP circular tanks with 15 cm water depth. To create artificial structures as cover for the fish, individual cobbles were covered in twelve 30 cm strings of biodegradable Ringlong tape (made from polylactic acid by Tokokosen Inc., Japan) tied in place with flaxen rope (Online Appendix 1). For this experiment, two tanks lacked artificial structures (hereafter referred to as control tanks) and two tanks had artificial structures (hereafter referred to as AS tanks). Cobbles with Ringlong tape were used only in the AS tanks, while regular cobbles (without tape) were used in control tanks. Tanks were positioned in a configuration alternating between AS and control tanks (AS, control, AS, control). This configuration was reversed at the beginning of each trial (AS, control, AS, control to control, AS, control, AS). Furthermore, fish that survived were removed and counted separately for each tank every 4 days at the end of each trial, along with the number of photographs of potential predators taken by the motion sensor cameras (described in the section below). No cameras failed during the study, and all the photographs taken during the study captured images of at least one living animal representing a potential predator. This trial was replicated four times.

#### Pond experiment

The pond experiment was conducted in order to evaluate the effects of structural complexity on settlement of charr. This experiment was conducted using 960 fish (in total) in four concrete outdoor ponds (3.6 m long, 1.0 m wide, 80 cm high, 15 cm deep) covered with black greenhouse shading nets (with light transmittance at 50% to prevent direct sunlight and extrinsic stimuli) at NRIFS in Nikko from 24 July to 10 August 2017. In this experiment, two fish trap boxes (52 cm long, 52 cm wide, 36 cm high) were set at the upper (water pipe) and lower (drain) ends of each pond at a distance of 2.5 m.

During the study, stocked fish were fed with thawed bloodworms equal to around 1.0% of the total body weight of all fish (calculated at the beginning of each trial). The area (2.5 m long, 1.0 m wide, 15 cm deep) between the two fish traps was designated as the experimental area. In the experimental area, cobbles (about 15 cm in diameter) were arranged in a grid of three columns and five rows (15 cobbles for each pond), where the distance between each row was about 30 cm and the distance between each column was about 20 cm. Cobbles with Ringlong tape, made the same way as in the second tank experiment, were used only in two AS ponds, while regular cobbles (without tape) were used in two control ponds. Ponds were positioned in a configuration alternating between AS and control tanks (AS, control, AS, control). This configuration was reversed at the beginning of each trial (AS, control, AS, control to control, AS, control, AS). Each trial was conducted for 3 days, and the trial was replicated four times. Before the experiment was started, mean current velocity in the center of each experimental area was adjusted to be in the range of 4.2 to 5.8 cm/s, similar to habitats occupied by whitespotted charr fry (Ueno et al., 2009).

To evaluate normal fish behavior, fish were first acclimated to experimental areas of ponds, so 60 fish were stocked per experimental area (240 fish in total) at the beginning of each trial, and both fish traps in each pond were opened after a 3-h waiting period. At the end of each trial, fish traps were closed quickly and inconspicuously by shutting entrances of upper and lower traps simultaneously. Subsequently, the number of fish in traps at the end of each trial was counted separately for upper and lower traps. Finally, the number of fish that stayed in the experimental area was counted separately for each pond using a backpack electrofishing unit (model 12-A POW Electrofisher, 300 V, Smith-Root, Vancouver, WA, USA).

## Camera traps

To assess day-time and night-time predator encounters, potential predators were recorded using motionsensitive and infrared sensor cameras (Trophy Cam HD, Bushnell, Overland Park, KS, USA) for tank experiments. Each camera was mounted on a wooden stake about 50 cm above the water's surface. Cameras were triggered with a passive infrared motion sensor and were set to wait 15 s after an initial trigger before attempting to detect additional triggers. To identify predators and estimate the frequency of their appearances at the study site, all photographs containing potential predators were inspected, sorted, and counted. For photographs of two or more animals, the species, number, and number of photographs were recorded. In addition, the number of predators capturing or eating fish was counted and identified. For the first tank experiment, to estimate the relationship between water depth and predator behavior, the number of predators inside tanks was counted separately for each tank.

## Statistical analyses

Effects of water depth and structural complexity on populations of charr were evaluated using a generalized linear mixed model (GLMM), with individual trials and tanks or ponds as random factors. Significance of explanatory variables was evaluated using a likelihood-ratio test.

To evaluate effects of water depth on predation risk of charr in the first tank experiment, a GLMM was fitted with a binomial distribution. The model was described as  $logit(p) = a + b_1$ Water depth category +  $S_i$ , with p = probability of survival, a = regression constant,  $b_1$  = regression coefficient, and  $S_i$  = study period (i.e., first, second, third and fourth trial). Water depth represented the water depth of each outdoor tank (i.e., 15, 25, 35, or 45). Post-hoc comparisons of all possible combinations of paired comparisons between numbers of surviving fish from each tank were made using the Games–Howell test.

For evaluating effects of water depth on the number of photographs showing the primary predator species in the first tank experiment, a GLMM was fitted with a Poisson distribution. The model describes the following:  $log(n) = a + b_1$ Water depth category +  $S_i$ , with n = the number of photographs of the primary predator animal appearing around or in tanks, a = regression constant,  $b_1 =$  regression coefficient, and  $S_i =$  the study periods. Post-hoc comparisons of all possible combinations of paired comparisons between the numbers of photographs showing the primary predator for each tank were made using the Games–Howell test.

To evaluate effects of structural complexity on predation risk in the second tank experiment, a GLMM was fitted with a binomial distribution. The model describes the following:  $logit(p) = a + b_1$ Structure category +  $S_i$  +  $T_j$ , with p = the probability of survival, a = regression constant,  $b_1$  = regression coefficient,  $S_i$  = study period, and  $T_j$  = tank. Structure category represents the AS and control tank. Posthoc comparisons of all possible combinations of paired comparisons between the numbers of surviving fish from each tank were made using the Games-Howell test.

To evaluate effects of structural complexity on the number of photographs showing the primary predator species in the second tank experiment, a GLMM was fitted with a Poisson distribution. The model describes the following:  $log(n) = a + b_1$ Structure category  $+ S_i + T_i$ , with n = the number of photographs showing the primary predator species appearing around or in the tanks, a = regression constant,  $b_1$  = regression coefficient,  $S_i$  = study period, and  $T_{\rm j}$  = tank. Structure category represents the AS and control tank. Post-hoc comparisons of all possible combinations of paired comparisons between the numbers of photographs showing the primary predator for each tank were made using the Games-Howell test.

To evaluate effects of structural complexity on the number of charr that settled in the experimental area during the pond experiment, a GLMM was fitted with a binomial distribution. The model describes the following:  $logit(q) = a + b_1$ Structural complexity category  $+ S_1 + T_j$ , with q = the probability of charr settling within the experimental area, a = regression constant,  $b_1$  = regression coefficient,  $S_i$  = study period, and  $T_j$  = tank. Structure category represents the AS and control tank.

To evaluate migration of charr into fish traps in the pond experiment, a GLMM was fitted with a binomial distribution. The model describes the following:  $logit(n) = a + b_1$ Structure category  $+ b_2$ Trap category  $+ S_i + T_j$ , with n = the probability of charr migrating to the fish traps, a = regression constant,  $b_i$  = regression coefficient,  $S_i$  = study period, and  $T_j$  = tank. Structure category represents the AS and control tank. Trap category represents the location of a fish trap (i.e., upper and lower area). All statistical analyses were performed using the lme4 package for R ver. 3.4.3 for Windows (www.r-project.org).

## Results

In the first tank experiment, mean fork length of the charr was  $57.9 \pm 3.9$  (mean  $\pm$  SD) mm, and mean body weight was  $1.86 \pm 0.4$  g. The GLMM confirmed a significant effect of water depth on the probability of survival (Table 1). The number of surviving fish for the 15 cm water depth tank was significantly lower than for the other three water depth

tanks (Games–Howell test; 15 cm vs. 25 cm, t = 17.58, P < 0.001; 15 cm vs. 35 cm, t = 18.36, P < 0.001; 15 cm vs. 45 cm, t = 18.36, P < 0.001) (Fig. 1a).

Cameras captured photographs of grey heron (Ardea cinerea), raccoon dog (Nyctereutes procyonoides), and sika deer (Cervus nippon) during the first tank experiment. Of 255 photographs containing potential predators, 222 photographs (87.1%) contained grey heron, 31 photographs contained sika deer, and 2 photographs contained raccoon dog. No photographs included two or more individual animals. Grey heron were holding fish in their beaks in 42 photographs. Predators were inside tanks in 49 photographs with all of the grey heron inside the 15 cm water depth tank. The GLMM detected a significant effect of water depth on the number of photographs containing the grey heron (Table 1). The number of photographs containing grey heron in and/or around a tank was significantly greater for the 15 cm water depth tank than for the other 3 water depth tanks (the Games–Howell test; 15 cm vs. 25 cm, t = 4.51, P < 0.05; 15 cm vs. 35 cm, t = 4.30, P < 0.05; 15 cm vs. 45 cm, t = 4.57, P < 0.05) (Fig. 1b).

In the second tank experiment, mean fork length of the charr was 58.9  $\pm$  4.0 (mean  $\pm$  SD) mm, and mean body weight was  $1.92 \pm 0.4$  g. The GLMM identified a significant effect of structure on the probability of survival (Table 2). The number of prey that survived was higher for the AS tanks (Fig. 1c). Cameras captured grey heron, Asiatic black bear (Ursus thibetanus), grey wagtail (Motacilla cinerea), and sika deer during the second tank experiment. Of 1260 photographs containing potential predators, 1247 photographs (99.0%) contained grey heron, 3 photographs contained Asiatic black bear, 5 photographs contained grey wagtail, and 5 photographs contained sika deer. No photographs contained two or more individual animals. Grey heron were holding fish in their beaks in 68 photographs. The GLMM identified a significant effect of structure on the number of photographs containing the grey heron (Table 2), and the number of photographs containing grey heron was slightly higher for the AS tanks (Fig. 1d).

In pond tests, mean fork length of the charr was  $59.1 \pm 3.7$  (mean  $\pm$  SD) mm, and mean body weight was  $1.84 \pm 0.4$  g. The GLMM identified a significant effect of structure on the probability of settlement in an experimental area (Table 3); the number of fish that

-			-			
	Variable	G2	df	Coefficient	SE	Р
(a) <sup>a</sup>	Water depth category <sup>b</sup>	124.7	3	0 to 6.619	0.728 to 0.836	< 0.001
	Constant			- 2.363	0.471	
(b) <sup>c</sup>	Water depth category <sup>d</sup>	171.1	3	- 2.197 to 0	0.208 to 0.255	< 0.001
	Constant			3.548	0.247	

**Table 1** Results of a generalized linear mixed model: effects of the water depth category (i.e., 15, 25, 35, and 45) on charr probability of survival (a) and on the number of photographs containing grey heron (b) (G2, the likelihood-ratio statistic)

<sup>a</sup>Standard deviations of the random effects: 0.641 for trials

<sup>b</sup>Coefficient value: 0 for 15 cm, 6.203 for 25 cm, 6.619 for 35 cm and 45 cm; standard error (SE): 0.728 for 25 cm, 0.836 for 35 cm and 45 cm

<sup>c</sup>Standard deviations of the random effects: 0.462 for trials

 $^{d}$ Coefficient value: 0 for 15 cm, -1.812 for 25 cm, -1.735 for 35 cm, -2.197 for 45 cm; standard error (SE): 0.215 for 25 cm, 0.208 for 35 cm, 0.255 for 45 cm

settled in the experimental area was higher for the AS ponds (Fig. 2). Evaluating migration of charr into fish traps, the GLMM did not identify a significant effect of the trap category (upper or lower) on the probability of charr migrating to traps (Table 3).

#### Discussion

Results of this study indicate that predation risk of juvenile salmonids from predatory terrestrial animals increases when water level declines. Additionally, increasing structural complexity can mitigate predation risk and possibly interference competition as a countermeasure for declining water levels.

The results indicate that, at least in our experimental setting, grey heron can significantly reduce salmonid populations by consuming a large quantity of juvenile fish. This is consistent with our previous studies, in which grey heron exerted high predation pressure on fish in shallow water (Miyamoto, 2016a; Miyamoto et al., 2018). Water depth can strongly influence wading birds' selection of foraging habitats (Master et al., 2005; Gawlik and Crozier, 2007). The length of the grey heron's legs restricts the maximum depth in which it can stand and hunt for food to 17 cm (Ntiamoa-Baidu et al., 1998), thereby limiting their habitat range for hunting. Therefore, the 15 cm water depth tank was the only condition where grey heron were easily able to hunt for food. Furthermore, grey heron was only photographed inside the 15 cm water depth tank, and the number of photographs showing grey heron around or inside a tank was greatest for this experimental area. These studies collectively suggest that declining water levels due to reducing river flows could increase the predation risk of charr by avian predators in small streams.

Results of the second tank experiment showed that artificial structures can be used as a method of mitigating the predation risk of charr. Generally speaking, salmonids, including the white-spotted charr, avoid predators by using shelter and concealing themselves among gravel (Miyamoto, Miyamoto, 2016a, b). Therefore, fish could have avoided predator attacks if they had noticed their predators in time, even inside control tanks, by using cobbles, gravel, and shade as shelter. However, only a few fish survived each trial in control tanks. This result implies that charr had difficulty avoiding grey heron, perhaps because the grey heron is an ambush predator that usually stands still in an upright position while waiting for fish (Tojo, 1996). Therefore, the charr subject to predation were most likely caught by grey heron before noticing its predator. On the other hand, water birds, such as the grey heron and kingfisher, are obstructed in their hunting of fish by wind ruffled (Sawara et al., 1990), turbid waters (White, 1936; Cezilly, 1992), and submerged aquatic vegetation (Lantz et al., 2011). These results collectively support the possibility that artificial structures may reduce predation risk by obstructing the view of potential predators. Furthermore, the number of photographs showing grey heron around or inside a tank was slightly higher for AS tanks than control tanks, thereby showing that the number of visits was not a factor in the survival of charr. All of this might indicate that



**Fig. 1** Box plots illustrating **a** the number of surviving charr for each of the four water depth tanks, **b** the number of photographs containing grey heron for each of the four water depth tanks, **c** the number of surviving charr for the control tanks and the

grey heron had much less success and needed to expend more time and energy hunting in an AS tank than in a control tank, possibly because artificial structures obstructed its view.

Results of the pond experiment suggest that structural complexity was one of the determining factors for settlement of charr. Physical habitat lessens the intensity of interference competition by reducing

artificial structure tanks, and  $\mathbf{d}$  the number of photographs containing grey heron for the control tanks and the artificial structure tanks

visual contacts between competitors (Eason & Stamps, 1992). Physical habitat may reduce the intensity of intraspecific competition between salmonids (Höjesjö et al., 2004; Yamamoto et al. 2008; Hasegawa and Yamamoto, 2009) because they are visually oriented species (Imre et al., 2002). Therefore, reduced intraspecific interference during territory disputes in our pond experiment by artificial structures could be

G2 Р Variable df Coefficient SE  $(a)^a$ Structure category<sup>b</sup> 97.77 0 to 2.813 0.285 1 < 0.001Constant -2.5160.403 Structure category<sup>d</sup>  $(b)^{c}$ 30.29 1 0 to 0.315 0.057 < 0.001Constant 3.925 0.337

**Table 2** Results of a generalized linear mixed model: effects of the structure category (control tank/artificial structure tank) on charr

 probability of survival (a) and on the number of photographs containing grey heron (b) (G2, the likelihood-ratio statistic)

<sup>a</sup>Standard deviations of the random effects: 0.395 for trials, 0.010 for tanks

<sup>b</sup>Coefficient value: 0 for control tank, 2.813 for artificial structure tank; standard error (SE): 0.285 for artificial structure tank <sup>c</sup>Standard deviations of the random effects: 0.445 for trials, 0 for tanks

<sup>d</sup>Coefficient value: 0 for control tank, 0.315 for artificial structure tank; standard error (SE): 0.057 for artificial structure tank

**Table 3** Results of a generalized linear mixed model: effects of the structure category (control pond/artificial structure pond) on charr probability of settlement in an experimental area

(a) and on charr probability of migrating to the fish traps (b) (G2, the likelihood-ratio statistic)

	Variable	G2	df	Coefficient	SE	Р
(a) <sup>a</sup>	Structure category <sup>b</sup>	116.7	1	0 to 2.339	0.217	< 0.001
	Constant			- 2.771	0.265	
(b) <sup>c</sup>	Structure category <sup>d</sup>	55.61	1	- 0.712 to 0	0.096	< 0.001
	Trap category <sup>e</sup>	0.326	1	0 to 0.054	0.095	0.568
	Constant			- 0.865	0.085	

<sup>a</sup>Standard deviations of the random effects: 0.287 for trials, 0.214 for ponds

<sup>b</sup>Coefficient value: 0 for control pond, 2.339 for artificial structure pond; standard error (SE): 0.217 for artificial structure pond <sup>c</sup>Standard deviations of the random effects: 0 for trials, 0 for ponds

<sup>d</sup>Coefficient value: 0 for control pond, -0.712 for artificial structure pond; standard error (SE): 0.096 for artificial structure pond <sup>e</sup>Coefficient value: 0 for upper area, 0.054 for lower area; standard error (SE): 0.095 for lower area



Fig. 2 Box plots illustrating the number of charr settled in the experimental area for the control and artificial structure ponds

the reason that AS ponds had a greater number of settled charr than control tanks. On the other hand, structural complexity may be essential for the charr when choosing habitat, irrespective of interference interactions, because they rely on structure to avoid predation more than do other salmonids (Miyamoto, 2016b). In any case, the results of our study show that structural complexity is strongly related to settlement of charr, which should be considered as an important factor when discussing conservation of fish and ways of improving their living environment. In addition to the previously discussed interference interactions, the reasons why fish migrated into traps might in principle include rheotaxis and current velocity (e.g., charr being swept away by the flow). However, because the location of the fish traps (upper and lower) was not significantly related to migration of fish, rheotaxis and current velocity were not likely to be the main reasons why fish migrated into traps.

## Conclusion

Our results suggest that providing artificial structure may be an effective way to reduce predation risk by avian predators, and thereby lead to an increase in the number of charr settled in their habitat. These results imply that habitat loss caused by floods and river engineering works may lead to decreasing fish populations, mainly due to increased avian predation risk and decreased habitat. Therefore, to retain suitable habitat for fish, maintaining and restoring original habitat by providing necessary materials (e.g., rocks, logs, and water plants) is required. However, if such management is impossible or floods are frequent, providing artificial structures could be considered as an effective way to conserve and enhance salmonid populations in small tributaries. Additionally, our results suggest that artificial structures could mitigate against a decrease in fish populations caused by the declining water levels. Therefore, developing techniques to mitigate effects of declining water levels and disappearing habitat will eventually be crucial in the ongoing struggle to conserve and propagate fish against the effects of global warming and dam operation.

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