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ORIGINAL ARTICLE

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American mink (*Neovison vison*) preying on hatchery and wild brown trout (*Salmo trutta*) juveniles in semi-natural streams

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Abstract

1. Predator–prey interactions are one of the main ecological factors influencing the structure of fish communities. The impact of wading and diving semi-aquatic predators on riverine fish populations is poorly known. We studied the effect of feral American mink predation on brown trout juveniles during winter in two experiments conducted in semi-natural streams (length 26 m, width 1.5 m).

2. In the first experiment, we compared the vulnerability of age-1+ hatchery (length 142 ± 16 mm, average ± *SD*) and wild (112 ± 8 mm) brown trout of similar genetic origin in sympatry and allopatry. In the second experiment we used age-0+ brown trout (79 ± 5 mm), increased habitat heterogeneity by addition of fine wood, and compared those to treatments without fine wood addition.

3. Hatchery fish were more vulnerable to mink predation than their wild counterpart, and the predation rate increased with increasing body size among the hatchery trout. Predation by mink on wild trout was higher in sympatric than in allopatric treatments suggesting that stocking of hatchery fish may increase predation on wild conspecifics. Increased habitat heterogeneity resulted in reduced predation rate.

4. The results show that a large size of hatchery fish in small streams was a negative trait, which was opposite to the mainstream observations of salmonid stockings made directly of feeding areas in lakes and oceans. Adding habitat heterogeneity was found important for habitat enhancements in streams with mammalian predators.

5. We highlight the importance of taking all the habitats during the life cycle of migratory fish into account in management decisions and carefully considering whether using hatchery fish to support wild populations in streams.

KEYWORDS
fish stocking, habitat heterogeneity, mesocarnivore, mink predation, semi-aquatic predator

1 | INTRODUCTION

Predation has both direct and indirect effects on the structure of fish communities (Allouche & Gaudin, 2001; Giam & Olden, 2016; Jackson et al., 2001). The direct effect of predation can be defined as mortality of prey species, which can be variably high and selective for many traits, such as prey size, other morphological characteristics and prey availability (He & Kitchell, 1990; Hoey & McCormick, 2004; Pinnegar et al., 2003). Responses to predation can lead to indirect interactions among prey species. These can be behavioural (Metcalfe et al., 1999; Vehanen, 2003) and physiological (Archard et al., 2012) adaptations or morphological changes (Svanbäck & Eklöv, 2006; Vinterstare et al., 2020).

Indirect predation effects include also changes in habitat selection, and it has been suggested that shallow areas are preferred by small fish, but avoided by large fish (Power, 1987; Schlosser, 1987; but see Sheaves, 2001). Small-sized fish are expected to take refuge in shallow areas to reduce predation risk from predatory fish, which are considered gape-limited predators (Mihalitsis & Bellwood, 2017; Nilsson & Brönmark, 2000). Thus, a larger body size of prey fish provides per se a shelter from predatory fishes (Hyvärinen & Vehanen, 2004). However, even if shallow areas create refuges against fish predators, fish can increase encounters with terrestrial piscivores, as wading and diving predators forage effectively in shallow water (Crowder et al., 1997; Power, 1987). Prey vulnerability to predation generally decreases as the environmental complexity increases (Beukers & Jones, 1997; Livernois et al., 2019; Nelson & Bonsdorff, 1990).

Whereas the effects of fish predation on salmonid fish populations are relatively well known, the effect of terrestrial mammalian predators is less clear. Pacific salmon (*Oncorhynchus* spp.) have been found to be an important resource for terrestrial wildlife through the allocation of nutrients to terrestrial predators (Hilderbrand et al., 2004; Levi et al., 2012, 2020). The most widely mentioned terrestrial predators on salmon are bears, but the range of vertebrate consumers includes various species, and also several avian foragers (Levi et al., 2015; Shardlow & Hyatt, 2013). Thus the migrating salmonids role to the ecosystem function can be high (Gende et al., 2002), even when iteroparous migratory species such as Atlantic salmon (*Salmo salar*) or brown trout (*Salmo trutta*) are considered (Enbom, 2015; Jonsson & Jonsson, 2003; also see Cairns, 2006). When large carnivores have been lost or are rare, smaller sized *mesocarnivores* play a larger role in the prey community structure (Roemer et al., 2009). In many European freshwater systems, the otter (*Lutra lutra*) and American mink (*Neovison vison*) play a key role as semi-aquatic predators (Holland et al., 2018). Both predators feed on fish, including salmonids, and otters are known to prey also on large salmonids (Carss et al., 1990), whereas mink, due their smaller body size, typically forage on smaller sized fish (Erlinge, 1969).

The American mink was introduced to Europe from North America for fur farming, and escaped minks have established naturally reproducing populations around Europe (Bonesi & Palazon, 2007). We have relatively limited knowledge about the impacts of this invasive species on its prey species, although several studies have indicated that it is a potential predator for a wide range of prey fauna (Bonesi & Palazon, 2007). Seasonal changes in the mink's diet originate from changes in the availability of specific prey categories, e.g. poikilothermic fish are an important part of the diet of the homeothermic mink especially in winter (Chibowski et al., 2019; Filip'echev et al., 2016; Gerell, 1967, 1969) due to lower water temperatures and the limited escape ability of fish at low temperatures (Huusko et al., 2007).

Lindstrom and Hubert (2004) concluded that mink predation might have a substantial effect on the winter mortality of salmonids in Wyoming mountain streams. Correspondingly, Heggenes and Borgstrøm (1988) suggested that mink predation may be a major cause of mortality in small streams, but the predation efficiency is likely to vary with stream characteristics. For example, in a structurally enhanced stream, where trout juveniles have better possibilities to find cover from predation compared to a stream with simplified habitat, mink predation was not an important source of mortality for brook trout (*Salvelinus fontinalis*) during summer (Burgess & Bider, 1980). Erlinge (1969) reported that mink largely fed on fish, but the majority of the fish diet consisted of non-salmonid fish, suggesting that brown trout could find hiding places from mink predation in a naturally complex river environment. Where mink are sympatric with otters, mink is a more generalised carnivore, and therefore switches diet opportunistically (Wise et al., 1981). Stream characteristics can affect mink predation efficiency, which has been observed, for example, when bears prey on salmonids (Andersson & Reynolds, 2018).

Despite, the concerns about the harmful effects to native fishes (Aas et al., 2018; Pister, 2001)), fish stocking is one of the most common methods to mitigate adverse effects on fish stocks (Cowx, 1994). Predation by feral predators, such as mink, is particularly concerning where fish stocking is used as management tool. Salmonids are a group of fishes with high socio and ecological value where fish stocking is used heavily for management and conservation (Aas et al., 2018; Armstrong, 2005; Krueger & May, 1991). Hatchery fish are typically raised to large sizes as larger fish have higher survival rates in the wild (the *bigger is better* hypothesis; Sogard, 1997). However, hatchery reared salmonids have lower survival rates in the wild compared to their wild counterparts or to fish raised in enriched environments (Einum & Fleming, 2001; Hyvärinen & Rodewald, 2013; Larocque et al., 2020). One major reason for lower survival in the wild is that stocked individuals have not been raised in environments that stimulate predator avoidance behaviours (Mes et al., 2019; Olla et al., 1998), and they are thus heavily preyed upon (Alioravainen et al., 2018; Berejikian, 1995; Einum & Fleming, 2001). Surprisingly, there are no published studies comparing whether hatchery fish are more vulnerable than wild fish to semi-aquatic mammalian predators, such as the American mink.

Habitat restoration is another mitigation tool to enhance the survival and reproduction of depleted fish stocks. The restoration of natural salmonid reproduction areas has recently gained more interest in fish management than more traditional hatchery fish

releases. Perhaps the most used technique is in-stream habitat restoration (Krall et al., 2019; Roni et al., 2008), which aims to re-establish channel complexity through the placement of structures (Nilsson et al., 2015; Vehanen et al., 2010). More complex habitat diversity is expected to increase the suitability of the habitat for juvenile salmonids, and provides more refuge from predators (Beukers & Jones, 1997; Höjesjö et al., 2014). Adding large or fine wood (FW) into the stream channel results in positive responses in the densities of juvenile salmonids (Louhi et al., 2016; Nagayama & Nakamura, 2010; Roni et al., 2015), and wood can also function as cover from predators. However, there is an ongoing debate about how successful the in-stream restoration efforts have been, and what are the most influential measures behind successful in-stream restorations (Krall et al., 2019; Marttila et al., 2019; Nilsson et al., 2015; Stewart et al., 2009; Taylor et al., 2019).

In this study, we present the results of two experiments run in semi-natural streams to test the hypotheses that: (1) hatchery fish are more vulnerable to predation from the semi-aquatic predator, American mink, than wild fish; (2) a larger body size protects fish from mink predation; and (3) habitat complexity in the form of FW protects fish from mink predation. Even if the original aims for the experiments were different (see below), the design of the experiments allowed us to study the effects of the unexpected mink predation on juvenile brown trout.

2 | METHODS

This study assessed the mortality of brown trout juveniles from mink predation in stream channels at the Kainuu Fisheries Research Station (Natural Resources Institute Finland, http://www.kfrs.fi/en/frontpage/, 64°30′N, 27°10′E). In the experiments, several months after the experimental start, we noticed tracks of feral minks in the snow in the experimental stream area, and it became obvious that the minks had preyed on the experimental fish in both experiments. Thus mink predation took place unexpectedly, and we were able to study its effect on brown trout juveniles in these experimental setups. The first experiment was designed to study the long-term patterns in the strength of competition between hatchery and wild brown trout (Huusko & Vehanen, 2011), and the second experiment was designed to examine growth effects on brown trout with and without wood addition (Enefalk et al., 2019). The detailed descriptions of study designs are given for Experiment 1 by Huusko and Vehanen (2011) and for Experiment 2 by Enefalk et al. (2019) and are only summarised here.

2.1 | Semi-natural streams

We conducted the experiments in six 26 m long and 1.5 m wide outdoor artificial stream channels. In the first experiment, we used three of the six stream channels, and in the second experiment, we used all six channels. The bottom of the streambed consisted of natural material, a 10–15 cm layer of gravel and pebbles (15–40 mm in diameter). Each stream was divided into three 8.5-m long sections (upstream–middle–downstream) with wire mesh panels (mesh size 10 mm [Experiment 1] or 6 mm [Experiment 2]). All channels shared the same water source drained from the nearby Lake Kivesjärvi, thus having the same temperature regime. Experiment 1 took place from 30th August to 8th November 2006, and experiment 2 from 17th August 2013 to 24th February 2014. During Experiment 1, water temperature decreased from 17.0 to 2.1°C, while during experiment 2, it decreased from 17.1 to 1.1°C. The stream channels supported benthic invertebrate communities similar to those present in a nearby stream in terms of both species composition and densities (Korsu et al., 2009; Vehanen, 2006). Thus, trout were feeding on natural food during the experiments.

2.2 | Brown trout

Brown trout juveniles from the same adfluvial brown trout stock were used in both experiments, and originated from the Kuusinkijoki River, north-eastern Finland. The river has its own wild genetically divergent, lake-migrating brown trout stock (Huusko et al., 1990; Lemopoulos et al., 2018). This brown trout stock has been maintained for stocking purposes in the state fish hatcheries in Finland.

The hatchery brown trout juveniles used in Experiment 1 were hatched and reared using normal procedures on the Kuusamo Fish Farm, a state hatchery about 300 km from the experimental site. The brown trout were the first-generation progeny of wild parents from the Kuusinkijoki River. The average rearing density in 4-m^2 indoor ponds was 3 kg/m^2. During rearing, the fish were fed with artificial food pellets. The wild counterparts for the hatchery fish, also aged 1+, were caught using electrofishing methods from the Raatekoski Rapid (66°23′88.8″N, 29°67′41.1″E) in the Kuusinkijoki River. Directly after capture, we transported both the hatchery-reared and wild fish to the study site in separate oxygenated containers. For recovery, we placed the fish in separate holding tanks with a low water flow (velocity 0.02–0.10 m/s) for 48 hr, and during this time, we provided no food. Thereafter the fish were anaesthetised with clove oil, measured (total length, mm and mass, g), and tagged with passive integrated transponder (PIT) tags (HDX Oregon RFID, Portland, USA, tag size 23 mm × 3.65 mm, weight 0.6 g) in their body cavities for individual recognition. After the fish had recovered from tagging and behaved normally, they were randomly placed into the different stream sections according to the study design.

The brown trout used in the Experiment 2 were produced in the same hatchery, Kuusamo Fish Farm, and originated from wild parents from the Kuusinkijoki River. We transferred the brown trout to the experimental site already in their late yolk-sac phase in early June 2014. Altogether, 175 age-0+ individuals were placed into each of the six channels used in the experiment. In the channels we did not feed the fish, instead they started to feed on natural food. After two months, we collected all fish by multi-pass sampling with a DC electro shocker. The flow in the channels was reduced to a low level

and carefully searched to make sure no fish were left in the channels. The collected brown trout were kept in a holding tank (3.5 m², water volume 1.4 m³, and flow 1.5 L/s). From the tank, 360 fish were randomly selected, anaesthetised with clove oil, measured (fork length, mm and weight, g), and tagged with a PIT tag (HDX Oregon RFID, tag size 12 mm × 2.15 mm, weight 0.1 g), and then placed into the stream sections according to the study design.

2.3 | Study design

In Experiment 1, all channels had a similar discharge regime, 43.7 ± 7.1 L/s (average ± 1 SD). Each study section comprised an upstream riffle and a downstream pool section. The water velocity in the riffle part of each section ranged between 20–60 cm/s (depth 15–25 cm, mean substrate diameter 15 cm) and in the pool 0–20 cm/s (25–35 cm, 4 cm, respectively). We used a substitutive experimental design as such a design is useful for drawing conclusions for wider contexts (Vehanen et al., 2009; Weber & Fausch, 2003, 2005; Yamamoto et al., 2008). The design included three treatments, with three replicates, in randomly selected sections: (1) 10 wild brown trout (WBT); (2) five WBT and five hatchery-reared brown trout (HBT); and (3) 10 HBT, resulting in trout densities of 0.78 ind. m⁻² in each stream section (Figure 1). The fish densities used in the experiment were comparable to average field densities of age-1+ brown trout in natural trout streams in northern Finland (Korsu et al., 2007). The length of the WBT at the beginning of the experiment was 112 ± 8 mm (average ± SD, n = 45) and their mass was 13.9 ± 3.0 g, and for HBT the corresponding values were 142 ± 16 mm (n = 45) and 33.7 ± 12.1 g, respectively. Thus, the hatchery trout were larger than the wild trout, with the result that the fish biomasses in the treatment areas were different. However,
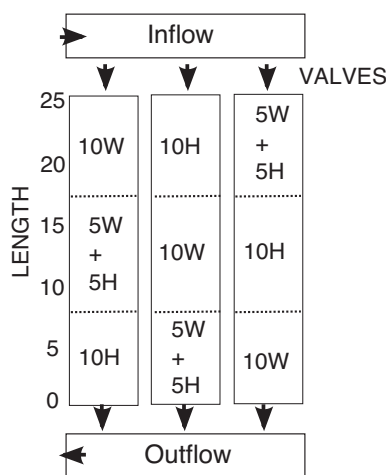
the aim was to follow the standard stocking procedure in which hatchery brown trout are added to support wild stocks. This meant that no changes in the rearing procedures, for example, by restricting feeding or selecting small-sized hatchery fish to result in matching sizes, were applied for the hatchery fish.

During the study period, we located the fish seven times with intervals of 7–14 days over the course of the study at noon by slowly moving a customised portable PIT antennae (Texas Instruments TIRIS S-2000; Linnansaari et al., 2007) about 20 cm above the water surface in the upstream direction. When a fish was located, we marked its individual code on a map.

In Experiment 2, the discharge regime in all channels was 59.0 ± 5 L/s (mean ± 1 SD). Three gravel deflectors (triangle shaped, with a side length of 0.5 m) were placed into each section protruding from the water surface. These deflectors shaped the water flow into meandering patterns. Two bricks with an arch underside (height 4 cm) were placed in each section to provide additional sheltering sites for fish. The water depth was 16.1 ± 1.2 cm in treatment areas with additions of FW, and 16.3 ± 1.2 in control sections without wood additions. The water velocities were 24.4 ± 2.6 cm/s and 24.9 ± 2.1 cm/s, respectively. The study design was similar to a stratified random design (Figure 2). There were three channel sections in each of the six channels, for a total of 18 sections. According to the study design, equal numbers of sections were assigned to treatment areas with FW added, and control with no wood added (Figure 2). The FW load used in the study equalled 50 m³ of wood/ha of the stream bottom surface (Enefalk et al., 2019). About 1 m long (Ø = 1 cm) willow sticks (Salix sp.) were collected in early June. The sticks were tied in bundles of 25–26 sticks and were waterlogged for 2 months before use in the experiment. In Experiment 2, eight waterlogged willow stick bundles were placed in the upstream area of the FW treatment sections and the rest of the sections (length 6.5 m) remained free-flowing. Each channel section was stocked with 20 brown trout. The fork length of the brown trout individuals in the FW treatment section was 78 ± 5 mm (mean ± 1 SD) and mass 5.5 ± 1.1 g, and correspondingly 79 ± 5 mm and 5.5 ± 1.1 g in the controls. Again, the fish density in the Experiment 2 was selected to be within the range of natural densities of juvenile brown trout in streams in Scandinavia (Korsu et al., 2009).

Similarly to Experiment 1, the daytime distribution of brown trout in the channel sections was determined by slowly moving a customised portable PIT antenna (Texas Instruments TIRIS S-2000; Linnansaari et al., 2007), approximately 20 cm above the water surface. During the study period, in September, October, and December, brown trout were captured by electrofishing, counted, and measured for length and mass for growth and survival responses, and returned back to the channels.

2.4 | The mink and mink predation

After 10 weeks from the start of Experiment 1, at the onset of winter in November 2006, we noticed tracks of feral minks in the

FIGURE 1 Schematic presentation of the study design in three semi-natural streams in Experiment 1. Treatment positions for the substitute design in the channels are indicated by the letters. 10W = 10 wild brown trout, 10H = 10 hatchery brown trout, and 5W + 5H = five wild brown trout and five hatchery brown trout in stream sections separated by wire mesh panels
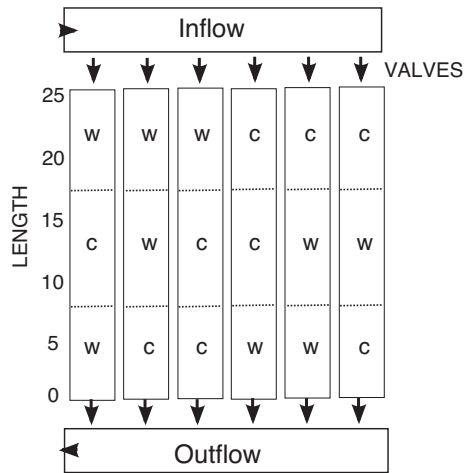
FIGURE 2 Schematic presentation of the study design in three semi-natural streams in Experiment 2. Treatment positions for the design in the channels are indicated by the letters. W, fine wood addition; C, control, no wood added. 20 brown trout were in each stream section separated by wire mesh panels

experimental stream area. After checking the channels, it became obvious that the minks had preyed on the brown trout in all the streams and sections. A wire mesh fence surrounds the area of the experimental streams and it is unclear which route the minks used to access the stream channel area. The snow cover in the area was about 20 cm deep, and the stream sections had border ice of 20–40 cm in width. From the mink tracks, we could estimate that two minks had visited the experimental area several times in early November. The mink had collected the brown trout they had killed into piles under the border ice of the streams in sites with a very shallow water depth, probably as food storage. Many of them were not eaten at all or were only partly eaten. We collected the dead fish and electrofished the ones remaining alive, measured their total length and mass, and recorded the individual PIT tag codes. PIT tags from the channels and the surrounding area were also located with the customised portable reader. Altogether, we found 17 tags (nine HBT and eight WBT tags) loose and signalling from the channel bottom. Before the mink invasion, only two out of 90 fish had lost their tags (during the positioning of the brown trout at the end of October, fish found alive but tags were recovered from the bottom), thus the tags in the bottom could be classified as eaten by mink.

In Experiment 2, we observed mink tracks for the first time in the experimental stream area in late January 2014. The snow cover was about 10 cm deep, and from the mink tracks on the snow, it was judged that three individuals had visited the area. During the next 2 weeks, we checked mink tracks and blood patches in the snow all weekdays, and estimated that the minks were preying on brown trout in the experimental channels. To protect the fisheries station's experimental activities, a local hunter trapped and removed one mink. Following the detection of mink predation, we electrofished the flumes for brown trout on 24 February and 6 May 2014. On both occasions, we recorded their PIT tag codes, fork length and mass. Fish that were present in the flumes up until the last electrofishing

in December but were not recorded during these two electrofishing occasions were classified as preyed upon by mink. This is an over-estimation of the predation rate as it also includes other natural mortality. The natural mortality outside mink predation (see Results, Experiment 2 for exact numbers) was, however, relatively low. For example, out of the fish that were detected in the October electrofishing sampling (319 trout), 8.5% (27 trout) were not detected alive in later samplings, and thus had died by natural causes between October and December. There was no statistical difference in numbers of dead fish between treatments (FW/no FW, 12/15 trout, chi square test, $\chi^2 = 0.333$, $df = 1$, $p = 0.564$). Thus, the natural mortality outside the mink predation was low, and there was no difference between treatments. Because we could not individually identify out of PIT-tagged trout the fish that were preyed upon by mink from the fish that had died from other sources of natural mortality, we used total mortality as a measure of mink predation mortality in our analyses.

2.5 | Data analysis

Substitutive comparisons (see Weber & Fausch, 2003) in Experiment 1 were made between allopatric treatments (i.e. either wild or hatchery fish separately in each section) and sympatric treatments (i.e. both wild and hatchery fish in each section) using a t-test. The significance level used in the analyses was 0.05. The response variables were survival (%), the size of fish (length in mm) killed by mink and surviving, respectively. The survival was also compared between allopatric treatments. In the Experiment 2, the survival (%) of brown trout in channels with and without FW was analysed using a mixed ANOVA model. The treatments (FW addition, control with no wood addition) were used as fixed factors and the experimental channels (1–6) as random factors. The possible size selectivity of mink predation was examined using a mixed ANOVA approach using the size of the fish (killed by mink or those that survived) as response variables and experimental channels as random factors. Statistical analyses were done using Systat 13 and SPSS 25 statistical software programs.

3 | RESULTS

3.1 | Experiment 1

Out of 87 brown trout, 58.6% or 51 fish (38 HBT and 13 WBT) were killed by mink. Three fish (two HBT and one WBT) were lost: their fate could not be identified as they or their tags were not found in the flumes or in their surroundings inside the wire mesh fence bordering the area.

There was a significant difference in survival of allopatric WBT and HBT ($t_3 = 6.918$, $p < 0.002$, Figure 3) such that the HBT had a survival of 10.4%, which was clearly lower than the 83.3% for the WBT. The survival of the sympatric WBT (46.7%) was significantly lower than the survival of the allopatric WBT ($t_3 = 3.317$, $p = 0.029$).

For HBT, there was no treatment effect on the survival ($t_3 = 0.336$, $p = 0.754$),

Both in the sympatric and allopatric treatments the average length of HBT fish (measured in October before mink invasion) that had been preyed on were significantly greater than that of the surviving fish (Figure 4, allopatry: $t_3 = -7.816$, $p = 0.004$; sympatry: $t_3 = -2.567$, $p = 0.0083$). No similar effects were found for the WBT in allopatry ($t_3 = 0.386$, $p = 0.719$) and in sympatry mink seem to prey on larger WBT individuals, but the difference was insignificant ($t_3 = -1.822$, $p = 0.142$, Figure 4a).

3.2 | Experiment 2

After the mink visits in February 2014, in total 56.6% of the trout in the FW sections, and 35.7% in control sections were found alive, compared to the trout numbers present in early December. The
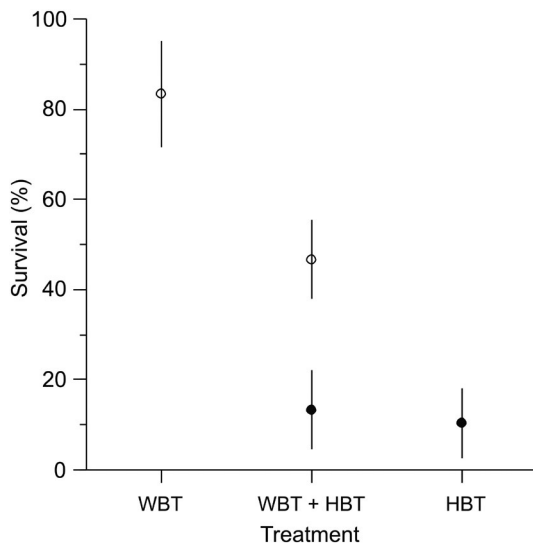

FIGURE 3 Average survival (± 1 *SE*) of brown trout from mink predation in the outdoor semi-natural streams in Experiment 1. Black symbols indicate hatchery-reared brown trout (HBT), the open symbols indicate wild brown trout (WBT). $N = 3$ for each treatment, error bars represent standard error of the mean
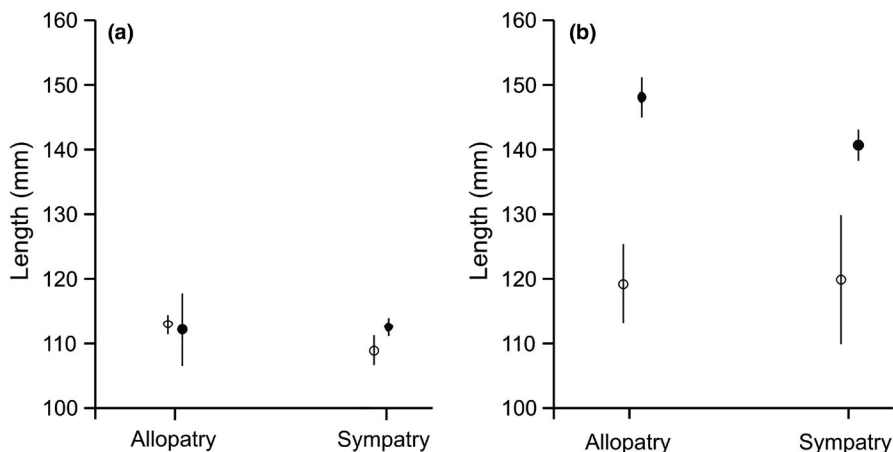
survival of the brown trout was significantly higher in the treatment areas with FW addition compared to control treatment areas with no wood addition ($F = 10.570$, $df = 1$, $p = 0.023$, Figure 5a), but there was no effect of channel ($F = 1.830$, $df = 5$, $p = 0.262$) or treatment-channel interaction ($F = 1.603$, $df = 5$, $p = 0.290$). Neither did the minks select brown trout of any particular size (fish lengths based on December 2013 measurements of pit-tagged fish, $F = 2.402$, $df = 1$, $p = 0.182$). In treatment areas where the habitat complexity was increased by adding FW smaller trout seemed to survive better, but this was insignificant (Figure 5b). The channel factor ($F = 0.358$, $df = 5$, $p = 0.858$) and the treatment-channel interaction ($F = 1.563$, $df = 5$, $p = 0.171$) were insignificant.

4 | DISCUSSION

Our study showed that the predation by mink can cause high mortality among juvenile salmonids in small streams. In addition, we found that the mortality of wild brown trout was significantly higher when in sympatry with hatchery trout than it was in allopatric wild trout treatments. Thus, presence of hatchery fish can increase the predation effect from mink on wild brown trout juveniles. High predation by feral mink should be considered in management actions when restoring and conserving salmonid populations in small streams. Increased habitat complexity by FW in our small streams decreased the mortality of brown trout juveniles from predation by mink, as our hypothesis was, and increasing habitat complexity can be used to decrease mink predation. We found considerably lower survival rates in hatchery brown trout than in wild trout of the same genetic origin, which is in accordance with earlier findings that hatchery fish are more vulnerable to predation than wild fish (Einum & Fleming, 2001). It also confirms our hypothesis that hatchery brown trout are more vulnerable to mink predation than wild brown trout. Among the hatchery brown trout under mink predation pressure, smaller trout individuals survived better than larger individuals, which suggests that stocking of large-sized juveniles in small streams might not be beneficial. The result of large trout surviving poorer was the opposite to our hypothesis that large body size protects

FIGURE 4 The average total length (± 1 *SE*) of brown trout that survived (open symbols) and that were preyed on by mink (black symbols) in the Experiment 1 in semi-natural streams. (a) Wild brown trout, (b) hatchery-reared brown trout. Allopatry: fish of one origin present, sympatry: both fish origins present. $N = 3$ for each treatment, error bars represent standard error of the mean

FIGURE 5 (a) Survival (%) of brown trout in two treatment areas with the addition of small wood and a control (no wood addition), in Experiment 2 in semi-natural streams. *N* = 9 for both treatments. (b) Size (fork length in mm) of brown trout that were preyed on and those that survived in both treatments. Box plots: box length shows the range within which the central 50% of the values fall, vertical line marks the median, asterisks are outliers
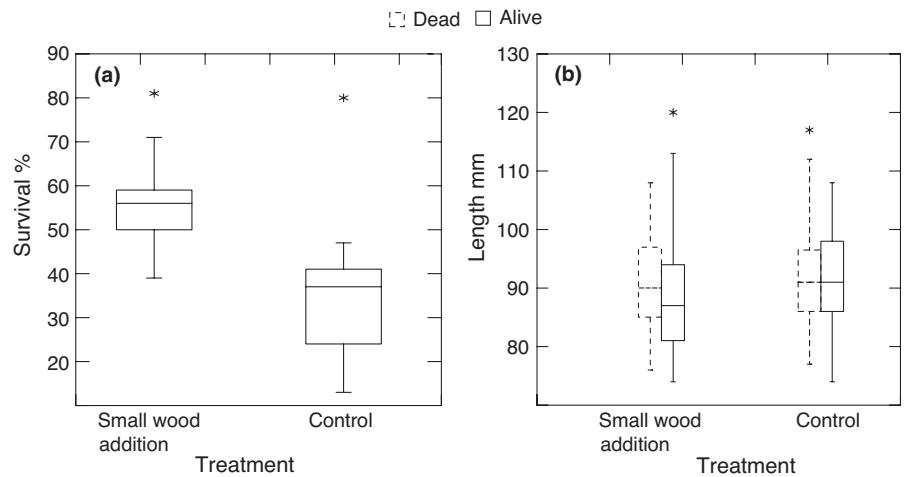
from mink predation, but in this study we cannot rule out a different outcome in a different habitat.

4.1 | Mortality of hatchery and wild brown trout

High mortality from mink predation was found in the experimental channels, built to simulate small natural streams. Similarly to our results, minks have been observed to prey effectively on brown trout juveniles in corresponding environments in small natural streams (Heggenes & Borgstrøm, 1988; Lindstrom & Hubert, 2004). When together with hatchery trout, wild trout were preyed on more than in treatments when only wild trout were present. This indicates that the occurrence of hatchery fish might increase predation pressure, thereby exposing wild conspecifics to a higher predation risk. Earlier research has shown that large releases can attract predators and thereby reducing the production of wild populations (Nickelson, 2003; Van Alen, 2000), or that the larger size of hatchery salmonids increase predation because they are in the predators' preferred size range (Nelson et al., 2019). Both minks and otters are known to use hatchery fish as a food resource by visiting fish farms for prey (Manikowska-Ślepowrońska et al., 2016), and otters also use salmonid-rich streams of stocked salmonids during the winter (Jacobsen, 2005; Ludwig et al., 2002). We suggest that hatchery brown trout, when stocked among the wild trout, can increase predation from semi-aquatic predators, thus increasing the predation mortality also among wild fish, as we observed in semi-natural streams.

Higher predation on hatchery fish may be the result of behavioural differences. Predator-naïve hatchery fish have not developed the same predator avoidance behaviours as wild fish (Mes et al., 2019; Olla et al., 1998). Although predator-naïve brown trout are able to develop antipredator behaviour, it commonly occurs when they sense faeces from minks that have been feeding on their conspecifics (Rosell et al., 2013). During the winter, brown trout juveniles shift to deeper water or use more cover to avoid predation (Huusko et al., 2007). We did not observe any significant differences in habitat use; both the wild and hatchery trout used mostly the flowing

stream habitat (see Enefalk et al., 2019; Huusko & Vehanen, 2011). Our results support the earlier results that hatchery fish are more vulnerable to predation than wild fish (Einum & Fleming, 2001), also in the case with a semi-aquatic predator.

4.2 | The effect of body size

We hypothesised that larger brown trout would be less preyed upon by mink, which was contradicted by our results. Instead, we found higher predation rates on larger brown trout. Generally, larger fish individuals both in marine (Sogard, 1997; Vehanen et al., 1993) and freshwater lake environments (Hesthagen & Johnsen, 1992; O'Grady, 1984; Vehanen, 1998) avoid predation better compared to smaller individuals when the main predation pressure stems from piscivorous, gape-limited, fish predators. The bigger is better hypothesis, i.e. that fish with a larger body size have higher survival than smaller individuals, has led managers to use of large hatchery juveniles for stocking in streams and rivers (Harvey et al., 2016; Nelson et al., 2019). These stocked hatchery juveniles are typically considerably larger than their wild conspecifics at the same age. Although a large body size is beneficial against gape-limited predators in the sea or lake environments, our results from small streams show that a smaller body size could be beneficial when coping with wading and diving non–gape-limited predators. In streams, small body size has been found to be an advantage over larger individuals in terms of survival in brown trout (Carlson et al., 2008) and cutthroat trout (*Oncorhynchus clarkii*) (Uthe et al.,2016) juveniles. Also, for bird predation, enhanced survival of smaller individuals has been observed in rare cases among salmonids (Sogard, 1997). Therefore, the generality of the bigger is better hypothesis could be questioned.

Size-selective mortality may also have prolonged consequences for salmonids (Russell et al., 2012; Sogard, 1997). Specifically, mortality during different life stages of salmonids are not independent of each other, i.e. characteristics carried over from their juvenile phase in rivers may be important determinants of their survival during their growth phase also in marine or freshwater environments (Russell et al., 2012). To maximise adult returns of declining Atlantic salmon

stocks, restoration efforts should focus on the freshwater life-stages to maximise the number and the size of emigrating smolts (Gregory et al., 2019). In shallow water in coastal marine environments, however, otters select larger fish for prey from the prevailing fish community (Cote et al., 2008). It is obvious that the effect of body size on the vulnerability to predation is dependent on the environment and the predator or mix of predators (Livernois et al., 2019), which should be taken into account in management. In shallow water with wading and diving non–gape-limited predators, a large body size of juvenile brown trout was a disadvantage.

4.3 | Habitat heterogeneity and predation mortality

As hypothesised, we observed that the mortality from mink predation was lower in treatment areas where FW was added to the streams. FW adds heterogeneity to the habitat by providing shelter for juvenile fish. Before the mink entered our semi-natural streams, Enefalk et al. (2019) had found that brown trout aggregated among wood bundles, whereas fish in the control sections the fish were more evenly distributed, and that the growth rate was significantly lower in treatment areas with wood addition than without wood addition. Here, we found (Experiment 2) brown trout juveniles were willing to use the cover from the wood addition, possibly to increase survival from predation, even at the cost of slower growth. Similar results have been observed for chub (*Squalius cephalus*), that was observed to grow significantly less under bird predation threat, and the authors argued that the increased use of cover led to costs in terms of lost feeding opportunities but to benefits in terms of predator avoidance (Allouche & Gaudin, 2001). The smaller body can also be viewed as a benefit in terms of lowered predation rates, as diving non–gape-limited predators seem to prefer larger prey.

Understanding the relationships among habitat preferences and how these affect predation can be complex and challenging. Habitat preferences differ between size classes of brown trout juveniles. For example, larger juveniles prefer deeper water and coarser substrate during winter compared to smaller size class (Mäki-Petäys et al., 1997). Also, larger salmonids prefer to shelter among larger wood (Langford et al., 2012). It may be that the habitat in our research units in semi-natural streams, consisting of FW material, upstream riffle, and a downstream pool section, were more suited for small-sized hatchery trout. We acknowledge that our inferences may not extend to larger rivers with larger wood and more diverse habitat. Habitat complexity strongly affects predation rates due to the availability of preferred refuges (Beukers & Jones, 1997; Nelson & Bonsdorff, 1990). In successful restoration projects, it is important to have knowledge about the habitat preferences of native species as to create useful refuge habitats (Billman et al., 2013). Restoration is specifically important for migrating salmonids, that have complex life cycles involving different habitats, and are thus especially vulnerable for habitat changes (Vagg & Hepworth, 2006). In an example of habitat improvement, both crayfish (*Cambarus bartoni*) and brook trout (*Salvelinus fontinalis*) production increased, but the

mink population only exploited the crayfish population (Burgess & Bider, 1980). This implied that crayfish were easier catch for mink, whereas trout were capable of taking advantage of the increased complexity to avoid mink predation also during summer period. In another example otters were found to prey on hatchery brown trout in one stream, but not in another, due to different fish community composition in the two streams (Jacobsen, 2005). This supports the idea that wading/diving predators adapt their foraging to local conditions. As mink predation efficiency seems to vary with habitat characteristics (Heggenes & Borgstrøm, 1988), prey populations might benefit from habitat restoration. Overall, these results highlight the complexity of predator–prey interactions and pinpoint the need to follow up fish populations in newly restored habitats, to ensure that the target species benefits from the restoration.

Additionally, habitat preferences vary seasonally as fish typically shift to low velocity areas in the winter (Huusko et al., 2007). In juvenile salmonids, these changes in habitat use typically are observed at micro- to mesohabitat scale as they prefer lower water velocity areas within riffles, such as streambank areas or larger cover substrate, or emigrate relatively short distances to pools (Cunjak, 1996). These changes in preferred habitats have been related to the need to conserve energy at low water temperatures, but also to obtain shelter from endothermic predators and piscivorous fish (Valdimarson & Metcalfe, 1998). Thus, it is possible that overwinter survival of salmonids increases if fish has a possibility to move between habitats or in search of preferred pool areas (Elso & Greenberg, 2001). If suitable winter habitats are not present, brown trout can demonstrate greater movements (Huusko et al., 2007), presumably to seek more suitable habitat. Larger scale movements between summer habitat in lakes and winter habitat in rivers to avoid predation are also common in fishes (Skov et al., 2013). While our semi-natural streams consisted of pool and riffle habitat, juvenile brown trout could not emigrate outside this area. Therefore, the movements of fish were more limited than in a natural stream, and this could have intensified the predation intensity from the mink. However, the physical habitat (water depth and velocity) in our semi-natural streams was within the preferred range of brown trout juveniles during winter in the region (Mäki-Petäys et al., 1997).

4.4 | Fish stocking to support wild populations in streams

Stocking of hatchery fish is a globally used method to support weakening fish stocks (Cowx, 1994). Fish stocking can increase the densities of fish, but there is strong evidence of negative ecological effects on wild populations (Aas et al., 2018; Huusko et al., 2018; Uusi-Heikkilä et al., 2018). For managers, an important decision is whether or not to use hatchery fish to support wild populations. Our results suggested that stocking hatchery fish among wild trout could increase the predation pressure from terrestrial predators, such as mink. The brown trout used in our study, both hatchery and wild juveniles, originated from one of the last remaining viable

naturally reproducing adfluvial brown trout stocks in Finland, and the status of this stock is considered endangered due to anthropogenic impacts (Huusko et al., 1990, 2018). As this is a worldwide trend where migrating salmonids, both anadromous and adfluvial, are considered vulnerable (Freyhof, 2014; Hyvärinen et al., 2019; Ricciardi & Rasmussen, 1999), it is essential to understand the consequences of hatchery releases in all habitats and all life cycles.

5 | CONCLUSIONS

Our study has management implications specifically in small streams, which are important for brown trout (Jonsson et al., 2001; Sutela et al., 2020; Vehanen et al., 2020). Survival during the juvenile stages is highly important for the growth of the brown trout populations (Elliott, 1994), and predation is one of the main drivers of fish community structure (Gebrekiros, 2016). Our results illustrate the importance of considering how the needs differ between life stages of migrating salmonids in terms of suitable habitat conditions for feeding and predator avoidance. Second, before supporting wild salmonid stocks with hatchery juveniles, the characteristics of hatchery fish, such as the hatchery background, should be considered. For example, occurrence of hatchery fish may increase predation on wild fish and a large individual size is not necessarily beneficial in small streams. Third, we encourage increasing the habitat heterogeneity, for example by adding wood to streams, in restoration and habitat enhancement efforts, as this is likely to reduce predation from wading and diving predators, such as feral American mink. In addition to restoration of habitat complexity, other management actions should be considered to mitigate the predation effect of feral mink. These could include eradication (removing all feral mink from a limited area), control (keeping mink numbers low) by trapping or hunting or prevention of further escapes of feral mink (Bonesi & Palazon, 2007).

DATA AVAILABILITY STATEMENT
Data are available from the authors upon reasonable request.

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