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Winter Behavior of Juvenile Brown Trout in a Changing Climate: How Do Light and Ice Cover Affect Encounters with Instream Predators?

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Abstract: During winter, stream fishes are vulnerable to semi-aquatic predators like mammals and birds and reduce encounters by being active in darkness or under surface ice. Less is known about the behavior of fishes towards instream piscivorous fishes. Here, we examined how surface ice and light affected the anti-predator behavior of juvenile brown trout (*Salmo trutta* Linnaeus, 1758) in relation to piscivorous burbot (*Lota lota* Linnaeus, 1758) and northern pike (*Esox lucius* Linnaeus, 1758) at 4 °C in experimental flumes. Trout had lower foraging and swimming activity and spent more time sheltering when predators were present than when absent. In daylight, trout's swimming activity was not affected by predators, whereas in darkness trout were less active when predators were present. Trout consumed more drifting prey during the day when ice was present, and they positioned themselves further upstream when under ice cover, regardless of light conditions. Trout stayed closer to conspecifics under ice, but only in the presence of pike. Piscivorous fishes thus constitute an essential part of the predatory landscape of juvenile trout in winter, and thus loss of ice cover caused by climate warming will likely affect trout's interactions with predators.

Keywords: anti-predator; global changer; diel behavior; foraging; piscivores; predators

Key Contribution: Most studies involving predation on fishes in northern temperate streams in winter have focused on prey behavior in relation to semi-aquatic predators like mammals and birds. Here, we show that the prey also modify their behavior in the presence of instream piscivorous fishes and how this interaction is affected by surface ice cover and light.

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Citation: Filipsson, K.; Åsman, V.; Greenberg, L.; Österling, M.; Watz, J.; Bergman, E. Winter Behavior of Juvenile Brown Trout in a Changing Climate: How Do Light and Ice Cover Affect Encounters with Instream Predators? *Fishes* **2023**, *8*, 521. https://doi.org/10.3390/fishes8100521

Academic Editor: Assaf Barki

Received: 14 September 2023
Revised: 13 October 2023
Accepted: 16 October 2023
Published: 20 October 2023

1. Introduction

The global climate is gradually becoming warmer [1], with the magnitude of the effect dependent on location and time of year. In most northern latitudes, it is expected that temperature increases will be more pronounced during winter than during summer [2]. Hence, the effects of global warming during winter may be profound and have direct and indirect effects on organisms [3–5]. In aquatic systems situated in northern latitudes, the effects of warmer winters on the physical environment have already been documented. Warmer winters have resulted in reduced snow and ice cover, both temporally and spatially, as well as erratic ice cover formation and breakup throughout winter [6–10]. Surface ice cover is thought to protect ectothermic fish from many endothermic predators, and thus ongoing and expected further reductions of the period with intact surface ice cover may have negative effects for fish.

Many juvenile salmonids overwinter in streams and rivers, where they are vulnerable to predation [11–13]. Semi-aquatic predators, such as mammals and birds, both endotherms, are some of the main winter predators of stream salmonids [11,13]. As poikilotherms, salmonids and most other fishes have reduced predator detection and escape capabilities during winter, as a result of constrained physiological performance at low temperatures [14–17]. This thermal effect makes fish relatively easy to catch for these endothermic predators. In addition, the abundance of terrestrial prey, *e.g.*, reptiles, amphibians and insects, for semi-aquatic predators is generally low in winter, whereas fish provide a reliable food source.

Mammals and birds that prey on fish in winter are mainly active during daylight hours. Stream fishes can therefore reduce their risk of being preyed upon if they reduce their diurnal activity. During the day, juvenile salmonids seek shelter within dead wood, beaver dams, crevices in the streambed or along undercut streambanks [18–21]. Stream fishes are often nocturnal in winter as long as there is enough invertebrate prey to meet their energetic needs. In fact, this relationship between food availability and diel activity is not only evident during winter but in other seasons as well [22]. However, in winter, fish have low metabolic rates in cold water, and therefore a reduced need to forage. Therefore, fish often remain inactive during the day in winter, and this is not only true for salmonids [23–25], but also other stream fishes such as minnows and galaxiids [26,27].

Surface ice cover reduces the risk that stream fishes succumb to predation by mammals and birds [28]. Overwintering fish often have higher growth and survival rates when surface ice cover is present than when it is absent [12,29–34]. Ice cover leads to larger energy reserves, as fish increase the time they spend foraging and are less vigilant to predators [30,33,35]. Stream salmonids are active both in darkness and in daylight when surface ice cover is present [34,36]. In a winter field experiment, juvenile brown trout (*Salmo trutta* Linnaeus, 1758) in stream sections covered with simulated surface ice cover had higher growth rates, were more active and used more of the width of the stream during the day than trout in exposed stream sections. Instead, trout in exposed sections remained inactive and sheltered along the streambanks during the day [34]. Juvenile brown trout have also been shown to allocate more time to foraging and territoriality in winter when under ice cover [36,37]. Similarly, field studies of bull (*Salvelinus confluentus* Suckley, 1859) and cutthroat (*Oncorhynchus clarkii* Richardson, 1836) trout show that these fishes spend less time sheltering among instream structures if surface ice cover is present [38]. Salmonids also exhibit reduced stress levels when surface ice cover is present, which has been quantified as reductions in oxygen consumption [39], cortisol levels, opercular beat rate and lighter body coloration [36,40]. Surface ice cover thus plays a major role in behavioral trade-offs between foraging and predator avoidance of juvenile salmonids in winter [41,42].

In boreal regions, burbot (*Lota lota* Linnaeus, 1758) [43,44], northern pike (*Esox lucius* Linnaeus, 1758) [45,46] and salmonids [47] prey on juvenile salmonids in winter. As predicted, juvenile salmonids exhibit vigilance and anti-predator behaviors in the presence of these predators. Juvenile brown trout are both less active and increase the time they spend sheltering in winter when burbot are nearby [20,21]. Enefalk et al. [20] found that trout sheltered less within the streambed and more among dead wood when a burbot was present. This behavioral change has been interpreted as a response to the benthic burrowing lifestyle of burbot. Filipsson et al. [21] found that juvenile trout maintained positions further away from burbot in darkness, and in daylight trout sheltered under overhead cover. It thus seems plausible that the risk of predation from piscivorous fish is most pronounced in darkness (at night or under surface ice cover) when diurnal mammals and birds are less successful at foraging for fish.

Climate warming and altered ice regimes are likely to have major consequences for the winter ecology of stream salmonids. The aim of this study was to examine the anti-predator behavior of an overwintering juvenile salmonid in the presence and absence of surface ice cover. We observed the behavior of juvenile brown trout in an experimental setting in darkness and in daylight, both with and without artificial surface ice cover present. We studied the trout in the presence of either burbot or northern pike or in the absence of predators. We chose these two predatory fish species as they are sympatric with overwintering juvenile brown trout. In addition, burbot is active at low temperatures and mainly in darkness [48], whereas pike is a visual predator that has reduced physiological performance at winter temperatures [49]. We predicted that trout would exhibit antipredator behaviors in the presence of burbot and pike. We also predicted that trout would become more active and forage more when under ice cover, at least in daylight, when the risk of predation from semi-aquatic, endothermic predators should be low, even though predatory fish should still pose a threat.

2. Materials and Methods

2.1. Study Fish

We captured 76 juvenile brown trout (12 yearlings and 64 one-year-old fish) in late September 2020, by electrofishing in the forest stream, Barlingshultsälven, Sweden (59°31.356′ N 12°18.728′ E). The fish were subsequently transported to the aquarium facility at Karlstad University and kept in four 200 L aquaria (~20 trout in each aquarium). Trout were acclimated to aquarium conditions for approximately 4 months before the experiment commenced. Water in the aquaria was constantly filtered (EHEIM 2217 Classic canister filter; Eheim GmbH & Co KG; sourced from Karlstad, Sweden) and cooled (Teco TK 2000, Teco, sourced from Fornace Zarattini, Italy), and 25% of the water in each aquarium was changed once a week. The water temperature in all aquaria was initially maintained at 11 °C, the temperature in the Barlingshultsälven when trout were captured. After one week of acclimatization, we reduced the water temperature by 1 °C/week, until temperatures reached 4 °C in the beginning of December. Photoperiod followed natural daylight cycles. During the acclimatization period, we fed trout approximately 1% of their body mass three times a week with thawed, previously frozen, red chironomid larvae. At the beginning of the experiment, the mean wet mass ± SD of the trout was 10.02 ± 4.66 g (min–max = 2.67–23.17 g). The mean total length ± SD was 109 ± 19 mm (min–max = 71–151 mm).

One burbot and one pike were used as predators. The burbot (53 cm and 1064 g) was captured using net cages during winter 2019 and was kept in a 4000 L flume until the start of this experiment. The pike (53 cm and 1179 g) was captured by angling in early October 2020 and kept in a second 4000 L flume. Burbot and pike were captured at the same location, at the mouth of the River Klarälven, close to Lake Vänern, Sweden (59°21.905′ N 13°33.075′ E). Light conditions and the water temperature regime for these fish followed the same protocol as for the brown trout. One week prior to starting the experiment, both burbot and pike were fed two thawed, previously frozen, 5 g brown trout.

2.2. Experimental Design

This experiment was conducted in the mid-sections of three 7-meter-long stream flumes (Figure 1). Glass windows on one side of the flumes enabled observations of fish during the behavioral trials. We demarcated the sections of the flumes used for the experiment with stainless steel mesh screens (mesh size 5.35 mm, thread 1 mm, 71% open area). Two experimental arenas were constructed in each flume, separated by green plastic net screens (mesh size 5.35 mm, thread 1 mm, 71% open area) attached to wood frames (95 cm wide and 60 cm high). Upstream and downstream arenas had areas of 95 × 50 cm and 95 × 130 cm, respectively. Burbot and pike were kept in the upstream sections, and placed there 48 h before the experiment started. The third flume was kept completely free from burbot and pike and functioned as a predator-free control. Downstream arenas served as experimental arenas for the trout. The water depth in all the flumes was 25 cm, and the average water velocity was 5 cm/s. Water temperature was kept constant at 4 ± 0.1 °C throughout the experiment, and the substrate consisted of 5–20 mm gravel. In the middle of each trout arena, we put one large stone (~10 × 5 × 3 cm) to provide a focal point for the trout when foraging. We also attached a measuring scale to the flume's glass panel, with tick marks to enable measurements of the upstream-downstream position of the trout.

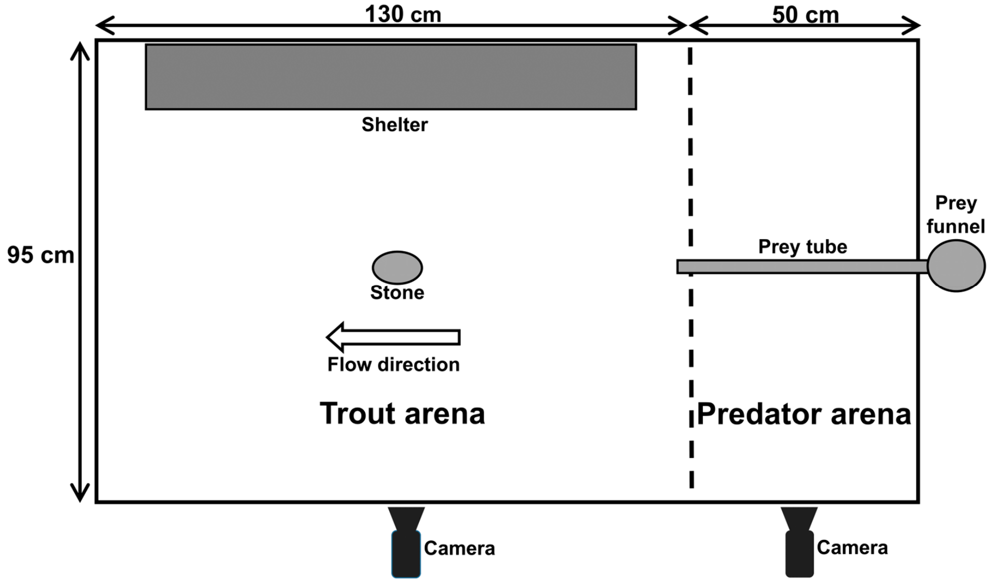

Figure 1. Birds-eye view of the experimental setup. Predators, i.e., burbot or pike, were kept in enclosed predator arenas upstream of the brown trout. We used net screens to separate trout from the predators. A plastic sheet 10 cm above the substrate provided overhead shelter for the trout, and a stone in the middle of the trout arenas provided a focal point when trout were foraging. Red chironomid larvae were used as food for the trout and were delivered to the trout through a funnel and tube, which entered the trout arenas through an opening in the net in the middle of the cross-section at 5 cm water depth. No predators were present in the control treatment.

We constructed one large shelter for the trout per stream by attaching a thin black opaque plastic sheet (975 × 190 × 5 mm) to three concrete blocks (10 × 16 × 3 cm). Four iron legs (7 cm) supported each concrete block. We positioned the concrete blocks at each end and in the middle of the shelters. The shelter structure was placed in an upstream-downstream direction along the side opposite the glass panels (Figure 1). Ice cover was simulated by using transparent multiwall polycarbonate boards (six layers, 30 mm thick in total, hereafter these plastic boards are referred to as ice cover), cut to fit snugly over the entire surface of the middle section of the stream flume. The ends of the boards were covered with duct tape to prevent water from entering the walled chambers, and thus ensuring that the boards would float on the water surface. The boards (ice cover) reduced illuminance by ~200 lx.

We conducted the experiment in January 2021. Prior to each trial, we removed six trout from the holding aquaria and sorted them into three size-matched pairs. Trout were anesthetized (benzocaine, 0.1 g/L), weighed and measured before the trials. Size differences within each pair did not exceed 15 mm or 3 g and trout sizes did not differ between the three predator treatments (One-way ANOVA, $p > 0.8$ for both wet mass and total length). We placed one pair of trout into each of the three flumes. Thereafter, trout were left in the flumes overnight for *c.* 12 h before observations of fish started. Trout were not fed during the 48 h prior to the experimental trials. During the experiment, we kept the light regime at 17 h darkness and 7 h daylight, which reflects the natural daylight cycle for January in the area from which the trout originated. Trout spent *c.* 20 h in the stream flumes during each experimental trial.

During the experimental trials, each pair of trout was video recorded (Canon XA10; Canon Inc.; sourced from Umeå, Sweden) during four 10-min-long recording sessions throughout the day. Two of the recording sessions were conducted in darkness (< 0.05 lx), and occurred early in the morning and late in the afternoon. The remaining two recording sessions were conducted in daylight (300 lx) in the morning and afternoon, between the two recordings in darkness. We used infrared illuminators (IR illuminator No. 40748, Kjell & Co Elektronik AB) and the infrared function on the camera to enable observations of fish in darkness. Four infrared illuminators were used for each flume, attached to wood posts 50 cm directly above the water surface. During two of the four recording sessions, one in darkness and one in daylight and either in the morning or in the afternoon, fish were subjected to simulated ice cover by placing the plastic boards directly on the water's surface. We placed or removed artificial ice cover at least 5 h before any observations of fish behavior. We randomized whether trout were subjected to surface ice cover in the morning or in the afternoon.

We fed trout one red chironomid larvae (> 10 mm long) every 15 s during the first three minutes of each recording session. Prey items were flushed with water through a funnel and delivered through a plastic tube, which entered the flume through an opening in the net screen in the middle of the upstream cross-section of the trout arenas at a water depth of 5 cm. During the last 7 min of each recording session, trout were not fed but behavioral observations still continued. We decided to feed trout for three minutes to prevent fish from becoming satiated and thus be less willing to forage during the remaining recording sessions throughout the day. When four 10-min recording sessions (during darkness/daylight and with ice cover/no ice cover) had been carried out for all three predator treatments (burbot, pike, control), trout were removed from the flumes and replaced with new pairs of trout. In total, 12 pairs of trout were tested for each of the three predator treatments, resulting in 72 trout being used for this experiment. When all experimental trials had been carried out, all fish, including the pike and burbot, were returned to the sites where they were caught.

2.3. Data Collection and Statistical Analyses

We examined the effects of predator presence, ice cover and light by quantifying data for seven response variables. These data were obtained by the first author from watching and scoring the following behaviors from the films: (1) whether trout foraged or not; (2) the number of consumed prey; (3) whether trout exhibited aggressive behaviors or not; (4) proportion of time that trout were active; (5) proportion of time that trout sheltered; (6) distance between the trout's anterior end and the upstream predator arenas (hereafter referred to as *distance from predator arena*, regardless of predator presence/absence) and (7) the average longitudinal distance between the two trout in each pair.

Foraging behavior was quantified both as a binomial response, if trout within a pair foraged or not, and as the total number of prey that trout consumed (0 to 13 prey per trial). Aggression was measured as a binomial response, whether trout pairs exhibited aggressive behaviors or not. Activity was measured as the proportion of time that trout were actively moving during each 10-min observation period, and shelter use was quantified as the proportion of time that trout spent under the overhead shelter. To meet the assumptions for statistical testing, we analyzed all variables expressed as proportions as arcsine transformed proportions [50], based on the arithmetic mean for each pair of trout. The position of each trout in the upstream-downstream (longitudinal) direction was measured every 15 s, and from these values, we could estimate the average trout distance from the predator demarcation and the average distance between trout in the upstream-downstream direction (longitudinal) during every recording session. Trout distances were measured in body lengths, based on the average length of the two trout in each pair.

We analyzed all data using generalized linear mixed models. The models included predator treatment as a between-subject factor and ice cover and light treatments as within-subject factors. We also included the 3-min session when trout received food and the subsequent 7-min session when trout did not receive food as two different levels in a within-subject factor, hereafter referred to as the "feeding" term. Statistical models used to analyze foraging behavior did not include this within-subject feeding term as an explanatory variable, as trout were only exposed to drifting prey (i.e., foraging) during the first three minutes of the 10-min observation period. All treatments were tested in full-factorial models that included all interaction terms. In addition, we added the mean body mass of each trout pair as a covariate to the models. We also conducted three pairwise contrasts (burbot vs.

control, pike vs. control, burbot vs. pike), which were determined *a priori*. For all behaviors except foraging and aggression, a linear distribution was used, as these datasets met assumptions of normality and homoscedasticity. Whether trout fed or exhibited aggressive behaviors or not (i.e., binary outcomes), was analyzed using a binomial distribution. We analyzed the number of consumed prey by using a negative binomial distribution. For the model on aggression, we excluded observations in darkness, as no trout exhibited aggressive behaviors in the presence of pike in darkness or in the presence of burbot under ice cover in darkness. We used compound symmetry covariance structures, as all models included repeated measures [51]. All statistical analyses were conducted in IBM SPSS Statistics 26 (IBM).

3. Results

3.1. Foraging Behavior

Only the presence of a predator ($F_{2,127} = 4.35$, $p = 0.02$) and light conditions ($F_{1,127} = 14.14$, $p < 0.001$) had significant effects on the number of trout pairs that foraged; none of the other factors were significant (Appendix A). Pairwise contrasts between predator treatments showed that the number of trout that foraged differed statistically between burbot and control treatments ($p = 0.017$), and pike and control treatments ($p = 0.001$), but not between burbot and pike treatments ($p = 0.25$). More trout foraged in daylight (86%) than in darkness (66%) (Figure 2A). In the darkness, fewer trout foraged in the presence of a pike (42%) and burbot (75%) than in the control treatments (83%) (Figure 2A). This difference was not as pronounced in daylight, where 75% of trout foraged in the presence of pike, 92% in the presence of burbot and 92% in the control treatments.

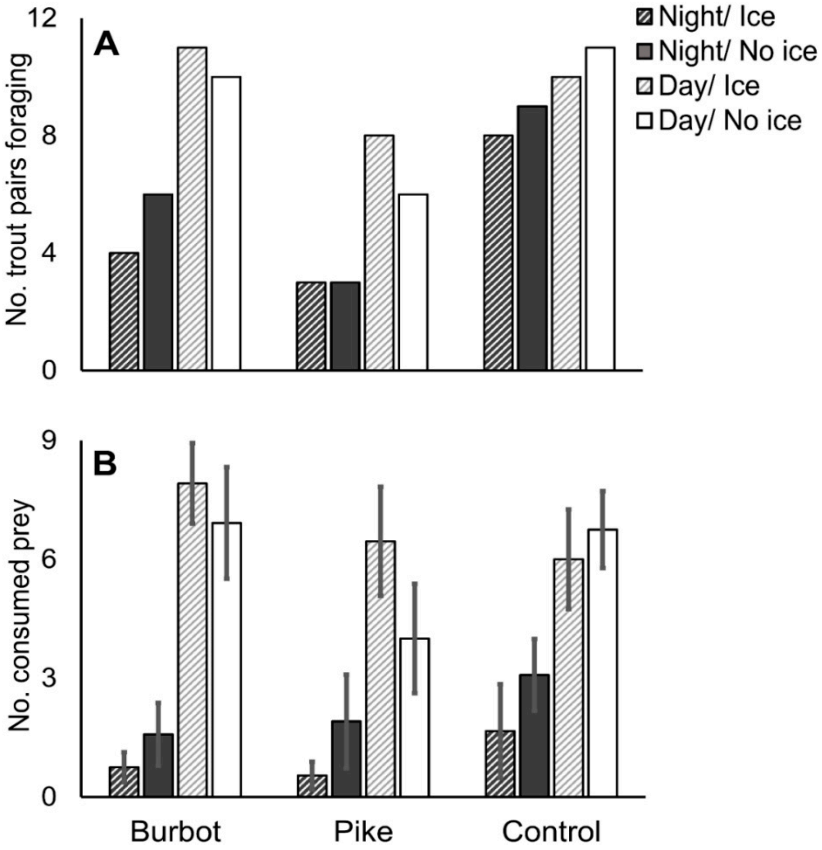

Figure 2. Effects of the presence of piscivorous fish, surface ice cover and light conditions on the (day/night) foraging behavior of juvenile brown trout. Foraging behavior is quantified as (**A**) the number of trout pairs (out of 12) that foraged and (**B**) the number of consumed prey (out of 13). Error bars in panel B indicate ± 1 SE.

Light conditions ($F_{1,127} = 53.55$, $p < 0.001$) and the light x ice cover interaction ($F_{1,127} = 6.25$, $p = 0.01$) affected the foraging rate of trout. Trout consumed almost four times as much prey in daylight compared to darkness. When ice cover was present, trout consumed more prey during the day but fewer prey in darkness (Figure 2B). The number of consumed prey also differed with trout size ($F_{1,127} = 4.49$, $p = 0.04$), as larger trout captured fewer prey. None of the other fixed terms or interactions had a significant effect on foraging behavior (Appendix A).

3.2. Aggression

No trout exhibited aggression in the presence of pike in darkness, or in the presence of burbot in darkness when surface ice cover was present (Figure 3). Only 8% of trout exhibited aggression in darkness during foraging trials, compared to 42% in daylight. During the 7-min observation periods after the foraging trials, 19% of trout exhibited aggression in darkness and 56% in daylight. In the presence of ice cover, 47% of trout exhibited aggression, compared to 39% when no ice cover was present. In the presence of burbot, 75% of trout exhibited aggression, similar to the control, whereas in the presence of pike only 33% of the trout exhibited aggression (Figure 3). Predator, ice cover and light treatments did not have significant effects on aggression (Appendix A). The only significant difference in the number of trout pairs that exhibited aggression was between the initial three minutes of foraging and the following seven minutes ($F_{1,127} = 6.53$, $p = 0.01$). In total, 47% of trout exhibited aggression during the 3-min long period when drifting prey were delivered, whereas 58% did so during the subsequent 7-min period without drifting prey.

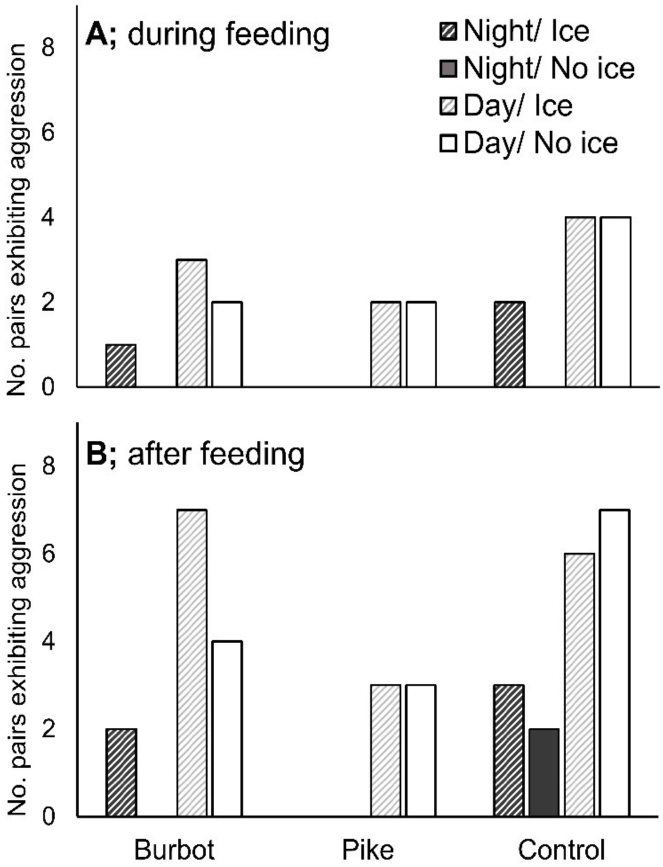

Figure 3. The number of trout pairs (out of 12) that exhibited aggression under different predator, ice cover and light treatments (day/night), both during the 3-min period when drifting prey were delivered (foraging trials) (**A**) and the 7-min period immediately after (**B**).

3.3. Activity and Shelter Use

Trout reduced their swimming activity both in the presence of a predator ($F_{2,271}$ = 7.29, $p < 0.001$) and in darkness ($F_{1,271}$ = 25.81, $p < 0.001$). Pairwise contrasts indicated statistical differences between burbot and control treatments (p = 0.026), and pike and control treatments ($p < 0.001$), but not between burbot and pike treatments (p = 0.10). There was a significant interaction effect between predator and light treatments ($F_{2,271}$ = 6.52, p = 0.002). On average, trout were 29% less active in darkness than in daylight (Figure 4A,B), and this difference was almost entirely attributed to the behavioral change of trout in the presence of predators. Trout in the control treatment spent on average the same amount of time active (67%) regardless of light treatment. In the presence of burbot and pike, trout were 33 and 51% less active in darkness than in daylight, respectively (Figure 4A,B).

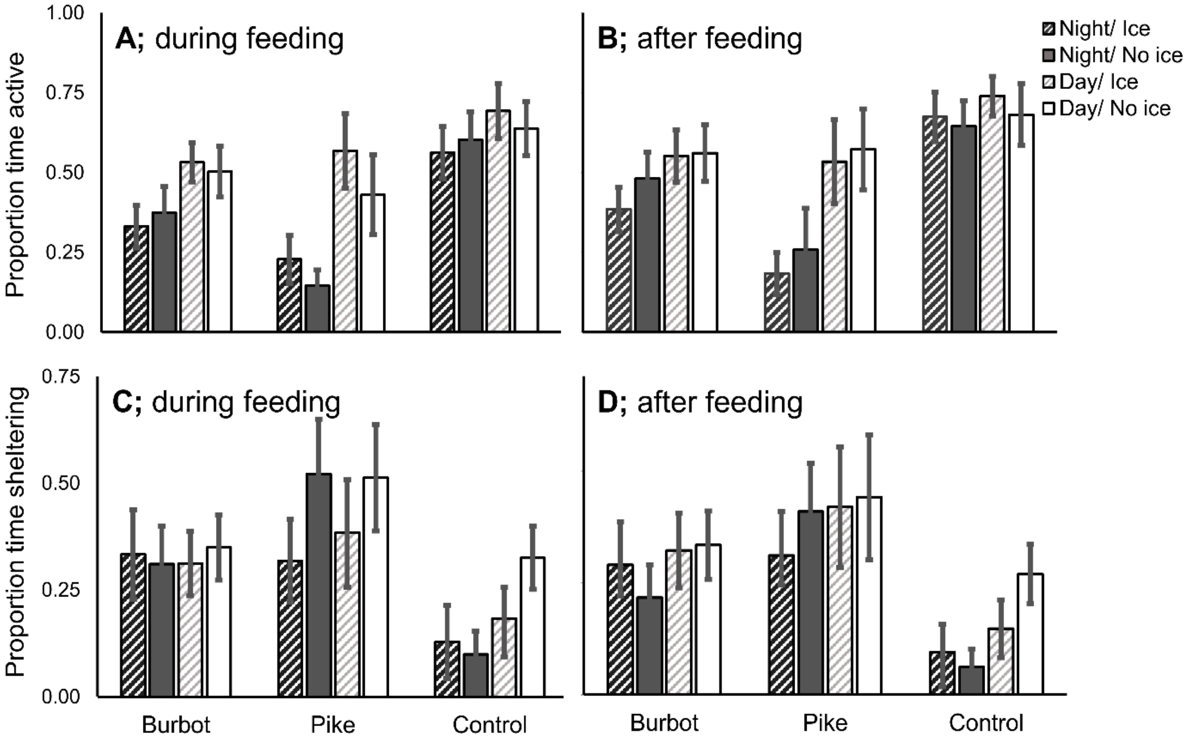

Figure 4. Effects of the presence of piscivorous fish, surface ice cover and light conditions on the (day/night) proportion of time that juvenile brown trout are (**A**,**B**) actively swimming and (**C**,**D**) seeking shelter under overhead cover, during and after the feeding period, i.e., during the 3-min period when drifting prey were delivered and the 7-min period immediately after. Error bars indicate ± 1 SE.

Both predator presence ($F_{2,271}$ = 3.70, p = 0.03) and light treatment ($F_{1,271}$ = 11.35, $p < 0.001$) had significant effects on the amount of time that trout spent sheltering. Pairwise contrasts between predator treatments indicated that only the difference between pike and control treatments was statistically significant (p = 0.007), not differences between burbot and control treatments (p = 0.11) or burbot and pike treatments (p = 0.25). Trout spent more time sheltering when pike was present and in daylight (Figure 4C,D). On average, trout spent 30% of their time sheltering in the presence of a burbot, 37% in the presence of a pike and 16% when no predators were present. The amount of time that trout spent sheltering was, on average, 35% higher in daylight than in darkness. None of the other fixed terms or interactions had significant effects on the proportion of time that trout spent actively swimming or sheltering (Appendix A). Trout mass had a significant effect on both the proportion of time that trout spent actively swimming ($F_{2,271}$ = 8.72, p = 0.003) and sheltering ($F_{2,271}$ = 8.94, p = 0.003) (Appendix A). Time that trout spent being active correlated negatively with body size, whereas the time they spent sheltering correlated positively with size.

3.4. Position of Trout in the Flumes

Ice cover ($F_{1,267} = 13.48$, $p < 0.001$) and light treatments ($F_{1,267} = 8.16$, $p = 0.01$) had significant effects on the distance the trout were from the predator arena. On average, trout positioned themselves further upstream when ice cover was present and in daylight (Figure 5A,B). Both the predator x ice cover interaction ($F_{1,265} = 6.60$, $p < 0.001$) and ice cover x light interaction ($F_{1,265} = 4.72$, $p = 0.03$) had significant effects on the longitudinal distance between trout within pairs. Trout positioned themselves closer to one another when surface ice cover was absent, but only in the presence of a pike. When both surface ice cover and pike were present, trout on average kept a longitudinal distance of 4.3 body lengths from each other. In pike treatments without surface ice cover, trout kept an average distance of 2.7 body lengths from each other (Figure 5C,D). In general, trout kept a greater distance from each other when ice cover was present in darkness, whereas in daylight this pattern was reversed. No other fixed factors or interactions had a significant effect on the position of trout in the flumes (Appendix A).

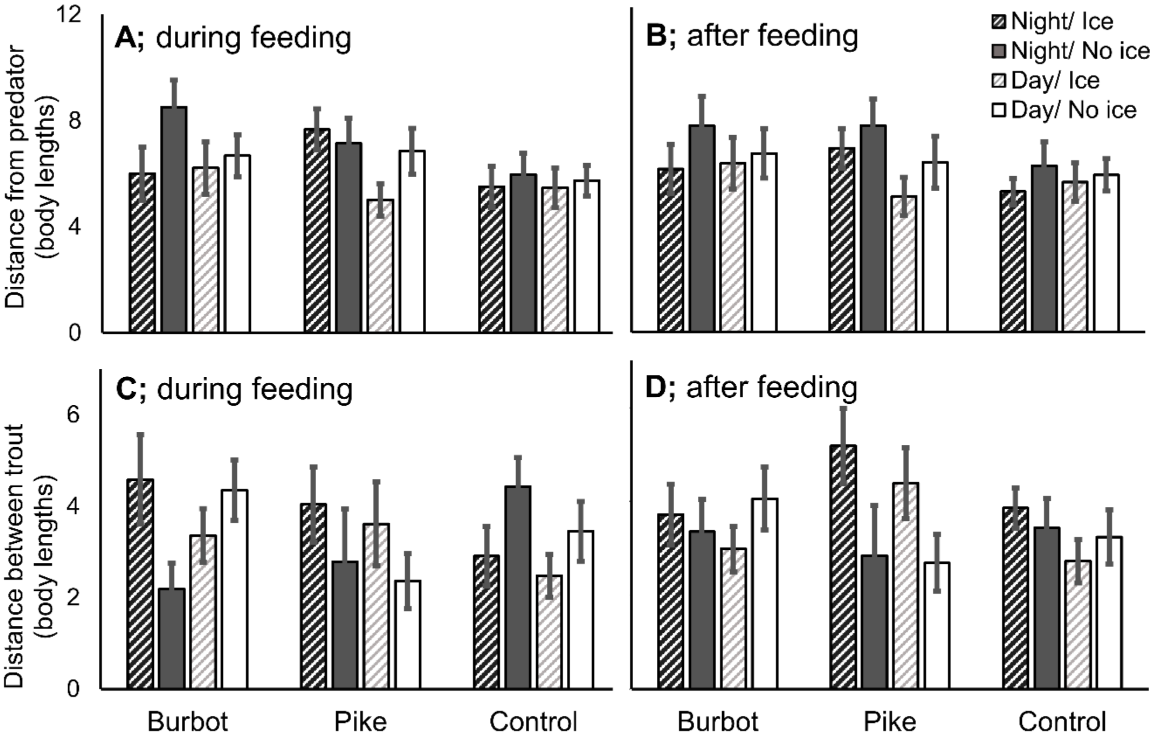

Figure 5. Effects of the presence of piscivorous fish, surface ice cover and light conditions (day/night) on the longitudinal distance between the trout pairs and between the trout and the predator arena (trout positions along the upstream-downstream axis) in the experimental flumes, during and after the feeding period, i.e., during the 3-min period when drifting prey were delivered and the 7-min period immediately after. The panels show (**A**,**B**) how far the trout positioned themselves downstream of the demarcation lines of the predator arenas (no predators present in control treatments), and (**C**,**D**) the average distance between the two trout in each pair. Error bars indicate ± 1 SE.

4. Discussion

In this study, we found that juvenile brown trout exhibited anti-predator behaviors in the presence of piscivorous fish, e.g., reduced propensity to forage, lower activity and increased time spent sheltering. Piscivorous fish have been previously shown to affect the ecology and behavior of overwintering stream salmonids [11,12,20,21]. Diel variation in behavior during winter has however often been attributed to the diurnal activity of semi-aquatic mammals and birds [13,34,36]. Predation from these endothermic animals is likely one of the main contributors to fish mortality in winter, and a major driver of behavioral adaptation to avoid predators. However, piscivorous fish may also constitute an essential part of the predatory landscape of stream salmonids in winter [21,52], and light and ice cover conditions can affect how juvenile salmonids respond in the presence of piscivorous fish.

Trout in our study had similar activity levels in daylight, regardless of whether a predator was present or not, but were less active in darkness when predators were nearby. Considering the fact that piscivorous fish are targeted as prey by mammals and birds, these fishes are also likely to reduce their activity during the day in winter. This could explain the higher vigilance of juvenile salmonids in the presence of piscivorous fish at night. Likewise, as juvenile salmonids are more vigilant towards predatory birds and mammals in daylight they may not pay as much attention to piscivorous fish. In addition, some piscivorous fish species that occur in boreal streams are generally nocturnal, such as the winter-active burbot that we used in this experiment [53–56]. Stream salmonids are mainly nocturnal in winter and tend to forage in darkness as long as their energetic needs can be fulfilled [22], but have higher foraging efficiency in daylight than in darkness [30,57]. A high energetic demand may explain why trout in this study mainly were active and foraged in daylight. Trout positioned themselves further upstream in daylight than in darkness, which also may indicate active foraging behavior during the day. Prior to each behavioral trial, we did not feed trout for 48 h, which may have resulted in the trout having a high propensity to forage during the trials. In addition, the water temperature during this experiment was relatively high (4 °C).

We used both burbot and northern pike as predators in our study. Burbot are mainly nocturnal, active at low temperatures, can locate their prey by olfactory cues, and are known to excavate the streambed in search of prey [48,53,55,56]. Pike is a diurnal visual predator that has reduced foraging success at low temperatures [49]. In our study, trout exhibited similar changes in foraging behavior and activity to both predators. Both burbot and pike may constitute a threat under low light conditions when semi-aquatic endothermic predators are not as active. Burbot and pike are common in the stream where we captured trout for this study (Karl Filipsson, personal observations during electrofishing), and it therefore seems plausible that trout from this stream would have anti-predator responses to both burbot and pike. In addition, fishes (including juvenile salmonids) elicit more pronounced anti-predator responses if the predator has been feeding on conspecifics [58,59]. Studies of European perch (*Perca fluviatilis* Linnaeus, 1758) show that fish can respond stronger to predators when they can both see and smell them [60], and if predators have consumed the prey prior to experimental testing, the prey may respond even stronger to the predators. Both burbot and pike were fed brown trout prior to the experimental trials, which may have increased the vigilance and resulted in more pronounced anti-predator responses by the trout in our study.

Trout consumed more prey when surface ice cover was present in daylight than at night. Earlier work shows that when ice cover is present juvenile brown trout may forage more during the day [37], although other studies show no effect of surface ice cover on foraging behavior [36]. In the study by Watz et al. [37] trout were tested in pairs, similar to in this study, whereas in the study by Watz et al. [36] trout were tested in groups of four. It is thus possible that the behavior of juvenile trout is affected by group dynamics and social interactions that depend on the number of fish present. Similarly, trout in the study by Watz et al. [36] exhibited higher swimming activity and more aggressive behaviors when surface ice cover was present, which we did not observe in our study. We used plastic boards to simulate ice cover, and it is possible that real surface ice has properties other than reducing light and functioning as a physical barrier and insulation, which may affect fish behavior. For example, surface ice cover in contact with stream surface water affects hydrology [61], and light conditions differ depending on the thickness of both the ice cover itself and the snow layer on top of the ice. Real ice cover has been used in some experimental studies on salmonid behavior [36,37], but plastic sheets [34] and reduced light [30] have been used to simulate ice cover as well. All of these studies have generated the predicted biological responses of salmonids under surface ice. We also found that trout positioned themselves further upstream (nearer to the predator arena) when ice cover was present, possibly at locations more beneficial for foraging. In treatments with pike, trout also positioned themselves further away from each other (longitudinal direction) when ice cover was present. This could be a response to the lunging foraging style of pike, assuming pike would forage more when ice cover is present, and thus trout attempt to reduce their risk of being preyed upon by keeping a greater distance from conspecifics. Current knowledge only provides limited insights into the behavioral effects of surface ice cover. Research on this topic thus seems especially timely considering the current loss of winter ice cover at northern latitudes.

5. Conclusions

Changes in snow and ice cover are some of the most evident effects of climate warming in temperate and boreal regions [2,9,62,63]. These changes have resulted in less ice cover spatially and temporally and in more erratic ice cover formation and breakup throughout winter [7,10], which can have a major impact on the ecology of overwintering fishes [30,33,34]. This study presents results on the diel winter behavior of a juvenile salmonid and shows that behavioral responses are affected by the presence of piscivorous fish and by surface ice cover. Ice cover and light conditions play an important role in behavioral trade-offs of overwintering stream fishes [12,34]. These trade-offs revolve around whether or not fish should allocate time to foraging or be vigilant to predators [21]. Behavioral decisions can affect overwinter survival, and thus population dynamics, but also how anti-predator responses are shaped through evolutionary adaptation [41,42]. Evident changes to the northern winter environment, i.e., loss of ice and snow, are already noticeable [2,7] and will likely have major effects on the dynamics of predator-prey interactions. Results from experimental studies like the one we present here thus provide knowledge on how overwintering stream fishes are adapted to encounters with predators, and the possible effects that global change has on these interactions.

Author Contributions: Conceptualization, methodology, K.F., V.Å., E.B., L.G., M.Ö. and J.W.; formal analysis, K.F.; investigation, K.F. and V.Å.; resources, Karlstad University; writing—original draft preparation, K.F.; writing—review and editing K.F., V.Å., E.B., L.G., M.Ö. and J.W.; supervision, E.B., L.G., M.Ö. and J.W.; project administration, E.B.; funding acquisition, Karlstad University. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding. Instead, it was funded by Karlstad University, through its special program for the university's strong research environments.

Institutional Review Board Statement: The Swedish Ethical Committee on Animal Welfare approved this study, both fish collection in the field (5.8.18-03819/2018; ID no. 001530) and the laboratory experiments (5.8.18-03818/2018; ID no. 001500).

Data Availability Statement: https://doi.org/10.6084/m9.figshare.24125931 (accessed on 15 October 2023).

Acknowledgments: The authors owe immense gratitude to Niclas Carlsson, who generously provided the pike for this study. Jeffery Marker, Roman Motyka and Sebastian Rock also provided valuable assistance during fish collection in the field. We are grateful to members of the Övre Gla fishing district and to the County Board in Värmland, who allowed us to capture trout in Barlingshultälven.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Appendix A

Table A1. Fixed effects from generalized linear mixed models, exploring the behavioral responses of juvenile brown trout under experimental winter conditions. The effects of predator presence (between-subject treatment), surface ice cover, light conditions and differences during and after the feeding period (i.e., during the 3-min period when drifting prey were delivered and the 7-min period immediately after, i.e., the within-subject factor "feeding"), as well as all interactions between these treatments, are included. Trout body mass is included as a covariate. *p*-values in bold denote statistically significant effects.

Variable	Source of Variation	*F*	*df*	*p*
Foraging (Y/N)	Predator	4.35	2, 127	**0.02**
binomial distribution	Ice cover	0.01	1, 127	0.91
	Light	14.14	1, 127	**<0.001**
	Predator x Ice cover	0.44	2, 127	0.65
	Predator x Light	0.61	2, 127	0.55
	Ice cover x Light	0.51	1, 127	0.48
	Predator x Ice cover x Light	0.34	2, 127	0.72
	Mass	0.79	1, 127	0.38
Foraging rate (continuous)	Predator	1.96	2, 127	0.15
linear distribution	Ice cover	3.12	1, 127	0.08
	Light	53.55	1, 127	**<0.001**
	Predator x Ice cover	0.07	2, 127	0.94
	Predator x Light	1.94	2, 127	0.15
	Ice cover x Light	6.25	1, 127	**0.01**
	Predator x Ice cover x Light	0.43	2, 127	0.65
	Mass	4.49	1, 127	**0.04**
Aggression (Y/N)	Predator	1.00	2, 131	0.37
binomial distribution	Ice cover	0.34	1, 131	0.56
	Feeding	6.53	1, 131	**0.01**
	Predator x Ice cover	0.79	2, 131	0.46
	Predator x Feeding	0.26	2, 131	0.77
	Ice cover x Feeding	0.01	1, 131	0.93
	Predator x Ice cover x Feeding	0.16	2, 131	0.85
	Mass	3.62	1, 131	0.06
Swimming activity (proportion)	Predator	7.29	2, 271	**<0.001**
linear distribution	Ice cover	0.01	1, 271	0.91
	Light	25.81	1, 271	**<0.001**
	Feeding	3.02	1, 271	0.08
	Predator x Ice cover	0.31	2, 271	0.73
	Predator x Light	6.52	2, 271	**0.002**
	Predator x Feeding	0.01	2, 271	0.96
	Ice cover x Light	0.86	1, 271	0.36
	Ice cover x Feeding	0.33	1, 271	0.57
	Light x Feeding	0.02	1, 271	0.88

Table A1. *Cont.*

Variable	Source of Variation	*F*	*df*	*p*
	Predator x Ice cover x Light	0.20	2, 271	0.99
	Predator x Light x Feeding	0.13	2, 271	0.88
	Ice cover x Light x Feeding	0.18	1, 271	0.67
	Predator x Ice cover x Feeding	0.78	2, 271	0.46
	Predator x Ice cover x Light x Feeding	0.08	2, 271	0.92
	Mass	8.72	1, 271	**0.003**
Shelter use (proportion)	Predator	3.70	2, 271	**0.03**
linear distribution	Ice cover	2.52	1, 271	0.11
	Light	11.35	1, 271	**<0.001**
	Feeding	0.72	1, 271	0.40
	Predator x Ice cover	1.88	2, 271	0.16
	Predator x Light	1.05	2, 271	0.35
	Predator x Feeding	0.13	2, 271	0.88
	Ice cover x Light	0.77	1, 271	0.38
	Ice cover x Feeding	0.23	1, 271	0.63
	Light x Feeding	0.33	1, 271	0.57
	Predator x Ice cover x Light	1.10	2, 271	0.34
	Predator x Light x Feeding	0.12	2, 271	0.88
	Ice cover x Light x Feeding	0.00	1, 271	0.97
	Predator x Ice cover x Feeding	0.27	2, 271	0.76
	Predator x Ice cover x Light x Feeding	0.03	2, 271	0.98
	Mass	8.94	1, 271	**0.003**
Distance from predator arena (continuous)	Predator	1.54	2, 267	0.22
linear distribution	Ice cover	13.48	1, 267	**<0.001**
	Light	8.16	1, 267	**0.01**
	Feeding	0.59	1, 267	0.44
	Predator x Ice cover	1.25	2, 267	0.29
	Predator x Light	2.55	2, 267	0.08
	Predator x Feeding	0.15	2, 267	0.86
	Ice cover x Light	0.01	1, 267	0.82
	Ice cover x Feeding	0.00	1, 267	0.98
	Light x Feeding	0.06	1, 267	0.81
	Predator x Ice cover x Light	2.84	2, 267	0.06
	Predator x Light x Feeding	0.09	2, 267	0.92
	Ice cover x Light x Feeding	0.36	1, 267	0.55
	Predator x Ice cover x Feeding	0.35	2, 267	0.70
	Predator x Ice cover x Light x Feeding	0.64	2, 267	0.53
	Mass	13.34	1, 267	**<0.001**
Distance between trout (continuous)	Predator	0.18	2, 265	0.83

Table A1. *Cont.*

Variable	Source of Variation	*F*	*df*	*p*
linear distribution	Ice cover	2.46	1, 265	0.12
	Light	2.76	1, 265	0.10
	Feeding	0.18	1, 265	0.67
	Predator x Ice cover	6.60	2, 265	**<0.001**
	Predator x Light	0.58	2, 265	0.57
	Predator x Feeding	0.29	2, 265	0.75
	Ice cover x Light	4.72	1, 265	**0.03**
	Ice cover x Feeding	0.16	1, 265	0.69
	Light x Feeding	0.01	1, 265	0.92
	Predator x Ice cover x Light	2.04	2, 265	0.13
	Predator x Light x Feeding	0.21	2, 265	0.81
	Ice cover x Light x Feeding	0.00	1, 265	0.98
	Predator x Ice cover x Feeding	1.78	2, 265	0.17
	Predator x Ice cover x Light x Feeding	0.75	2, 265	0.47
	Mass	1.21	1, 265	0.27

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