Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and in turbid water conditions

Jim S. Gregory and J.S. Griffith

Abstract: The proportion of rainbow trout (*Oncorhynchus mykiss*) concealing themselves in simulated interstitial spaces was examined in the presence of surface ice, in turbid water, and in clear water. Tests were conducted in enclosures in a small Idaho stream with structures that provided five rectangular spaces varying in width and height, one circular space, and one triangular space. Space use was assessed each morning by trapping test fish inside the structures. Significantly more fish concealed themselves under clear water conditions than under either surface ice or turbid water conditions. Spaces narrower than the width of a test fish with extended pectoral fins and spaces taller than the height of a test fish with dorsal fin extended were used less than would be expected if space use was random. The frequency with which two or more fish occurred together in the same space was similar to that expected if fish occurred together at random. Fish rarely returned to the same space on consecutive nights.

Résumé : La proportion des Truites arc-en-ciel (*Oncorhynchus mykiss*) qui se sont cachées dans des interstices artificiels a été examinée en présence de glace de surface, en eau turbide et en eau claire. Les tests ont été effectués dans des enceintes, dans un petit ruisseau d'Idaho comportant des structures offrant divers types d'abris, cinq interstices rectangulaires de largeur et hauteur variables, un interstice circulaire et un interstice triangulaire. Chaque matin, le nombre de poissons expérimentaux dans les interstices était relevé. Les poissons ont utilisé les abris plus fréquemment en eau claire qu'en eau turbide ou que sous la glace. Les interstices plus étroits que la largeur d'un poisson expérimental avec les nageoires pectorales étendues et les interstices plus hauts que la hauteur des poissons expérimentaux avec la nageoire dorsale étendue étaient utilisés selon une fréquence moindre que la fréquence aléatoire théorique. La fréquence avec laquelle deux poissons ou plus se retrouvaient dans le même interstice était semblable à la fréquence théorique aléatoire. Les poissons occupaient rarement le même espace au cours de deux nuits consécutives.
[Traduit par la Rédaction]

Introduction

Interstitial spaces in the substratum provide important habitat for many species of trout and salmon during their first winter. When water temperatures drop below a threshold level, usually about $7-10°C$, subyearling salmonids use these spaces for concealment (Hartman 1965; Chapman and Bjornn 1969; Rimmer et al. 1983; Cunjak 1988). Campbell and Neuner (1985) found that, in winter, subyearling rainbow trout conceal themselves during the daytime and emerge at night. This pattern has been described as a response to temperature (Rimmer et al. 1983) and light (Kwain and MacCrimmon 1969; Contor and Griffith 1995). It has been hypothesized that daytime concealment reduces energy expenditure (Heggenes et al. 1993), helps fish avoid displacement by ice or floods (Hartman 1965), and reduces the risk of predation (Fraser et al. 1993).

These hypotheses have been developed primarily by observing fish in clear, ice-free streams. Although rock substratum, surface ice, and turbid water all offer cover habitat (as defined by Shirvell 1990), we use t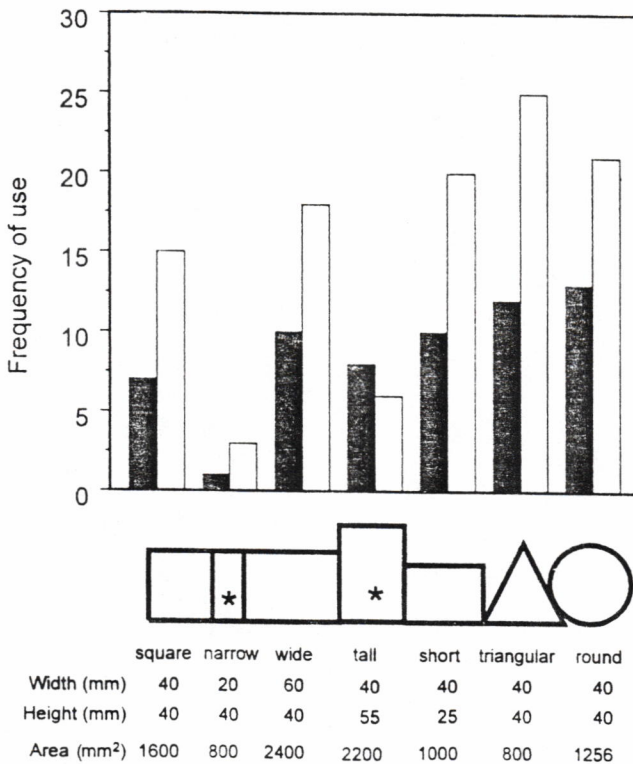he term concealment to refer to fish moving into interstitial spaces (Griffith and Smith 1993). If fish are concealing themselves to conserve energy or avoid displacement, we hypothesize that they also display such behaviour when the water is turbid or when surface ice is present. However, if fish are concealing themselves in rock substratum primarily to avoid aerial or aquatic predators, we hypothesize that most fish conceal themselves under clear, open water conditions, fewer under surface ice, and even fewer in turbid water conditions, as each situation progressively offers protection from a wider variety of predators. To test these hypotheses, one objective of this study was to assess the proportion of subyearling rainbow trout that concealed themselves during the day when surface ice was present and in turbid water and clear water conditions.

In some streams in North America the availability of winter habitat appears to limit the abundance of subyearling salmonid fishes (Bustard and Narver 1975; Mason 1976; Nickelson et al. 1992). Smith and Griffith (1994) found, in an Idaho river, that subyearling rainbow trout survival was $11-24\%$ higher in enclosures containing rock which provided interstitial spaces versus enclosures without rock, even though enclosures excluded predators. Higher survival in enclosures containing rock was attributed to protection from physical damage by ice, reduction in daytime energy expenditure, and a thermal benefit offered by interstices in rock. Field studies have described the minimum rock size necessary to produce interstitial spaces that fish will utilize

Fig. 1. Frequency of use and dimensions of spaces of different shapes. Observations from test 1 (solid bars) and test 2 (open bars) were combined for analysis, based on the results of the heterogeneity χ^2 test. An asterisk indicates a space shape that was used less than would be expected if space use was random.

	square	narrow	wide	tall	short	triangular	round
Width (mm)	40	20	60	40	40	40	40
Height (mm)	40	40	40	55	25	40	40
Area (mm²)	1600	800	2400	2200	1000	800	1256

(Bustard and Narver 1975; Griffith and Smith 1993), but little is known about the interstitial spaces themselves. We hypothesized that selected space width and height are a function of fish body dimensions, and we therefore offered artificial structures containing spaces of various sizes (relative to the width and height of the fish) and shapes to caged subyearling rainbow trout.

Our third objective was to assess whether subyearling rainbow trout share concealment spaces. Aggregations of subyearling salmonids in the water column can occur as water temperatures decline in autumn (Hillman et al. 1987; Riehle and Griffith 1993) and during winter in thermal refuges such as point-source groundwater discharges (Cunjak and Power 1986), but whether fish aggregate in the substratum is unknown. Fish have been observed most often in interstitial spaces singly (Rimmer et al. 1983; Cunjak 1988), and some aggressive behaviour of subyearling salmonids within concealment habitat during winter has been noted by McMahon and Hartman (1989) and Glova (1986). We provided a surplus of spaces and monitored whether they were shared by test fish.

Materials and methods

In January and February 1994 we electrofished 60 rainbow trout from rock concealment habitat in Warm Springs Creek, a tributary to the Big Lost River in central Idaho. The fish were 100–126 mm in total length and, based on scale analysis, were in their first winter. Fish were held in 6 mm mesh hardware cloth enclosures

($1.5 \times 0.5 \times 0.6$ m tall) that were placed midstream in Pocatello Creek, a first-order stream near Idaho State University. The enclosures were placed in 20 cm deep water over silt substratum, were open only on top, and contained hollow ceramic blocks that provided cover for fish. Fish were allowed to acclimate for at least 2 d before experiments began.

Tests were conducted in Pocatello Creek in two enclosures that were identical with the holding enclosures. In each of the test enclosures we placed three cover structures. Structures were made of 6 mm thick plywood and PVC pipe and were painted black inside and out. Each structure contained seven spaces of various cross-sectional areas and shapes that were randomly arranged in each structure (Fig. 1). Space dimensions were based on the hypothesis that fish select the space with the smallest cross section that allows fin movement. For all test fish, the distance between the tips of the extended pectoral fins was <40 mm, the body width was <20 mm, the distance from the ventral surface of the fish to the tip of the extended dorsal fin was <40 mm, and the height of the body was <25 mm. In each structure an array of spaces was constructed in such a way that some were too small for the fish to enter with fins extended, some were just large enough for the fish to enter with fins extended, and some were much larger than the width of the fish with fins extended (Fig. 1). Throughout this paper these spaces will be referred to as square, narrow, wide, tall, short, triangular, and round as they appear in Fig. 1. This design provided an array of spaces with cross-sectional areas ranging from 800 to 2400 mm². Fish in the triangular space, which contained the smallest cross-sectional area, had free fin movement. Fish in the round space had to remain off the bottom in order to have free fin movement.

All structures were 195 mm deep, which was 95 mm longer than the shortest fish. This ensured that if two fish used the same space their bodies would overlap or at least one would extend beyond the end of the structure. On both ends of each structure, 6 mm mesh hardware-cloth doors were built that opened downwards and could be closed by pulling a single string above the structure. Three fish were placed in the same enclosure with the three structures, each of which contained all 7 spaces so that 21 spaces were available to each group of three fish. Therefore, it was possible for each fish to choose the same space height and width and still occupy that space solitarily.

The two test enclosures were placed serially (30 cm apart) with their long axes parallel to the flow direction. Three structures were placed serially in each enclosure with their long axes parallel to the flow direction, and were submerged by placing a masonry brick on top of them. The water velocity where the structures were placed was 2–9 cm/s. The structure doors were opened and the strings were arranged so that the doors on all structures could be closed simultaneously by an observer ca. 5 m away.

Every morning (ca. 09:00) of the test periods three fish were placed in each test enclosure and held overnight. The next day at 08:00, unless ice conditions prevented it, the doors were closed on all structures. Space use was assessed by removing fish from the spaces individually and recording the size and shape of the space each fish was using, the position of that space from the closest end of that structure, and the structure's position relative to the other structures in that enclosure. Surface ice was recorded as either present (ice completely covering the water surface in the enclosure) or absent (some open water in the enclosure) and water as either turbid or clear, depending on whether we could see the stream bottom in 20 cm deep water. Since turbid water never occurred with surface ice we considered three treatments: clear water with surface ice (ice), clear water without ice (clear), and turbid water (turbid). Only clear water and ice conditions occurred during the first experiment, but during the second experiment ice and clear water conditions were interspersed with turbid water conditions (Table 1).

Multiple observations were recorded for individual fish from two test groups. The first group, which was collected on January 17 and tested from January 19 to February 10, consisted of 29 fish that

Table 1. Number of fish-nights on which clear water, surface ice, and turbid water conditions occurred and the numbers of fish that concealed themselves under these conditions.

	Clear water		Surface ice		Turbid water	
	No. of fish-nights	No. of fish	No. of fish-nights	No. of fish	No. of fish-nights	No. of fish
Exp. 1	24	21 (88)	60	40 (67)	0	—
Exp. 2	42	40 (95)	30	23 (76)	60	45 (75)

Note: Numbers in parentheses are percentages.

were used two or three times each but not on consecutive days. After each day of testing, fish were dye-marked on a specific fin with a Panjet needleless inoculator to indicate which space they had occupied. The fish were then placed back in the holding enclosure to be used later. The second group, which was collected on February 3 and tested from February 11 to March 7, consisted of 31 fish that were used three to five times on consecutive days. Before the testing began, all fish in this group were marked with an adipose clip and (or) a dye mark on two fins for individual identification. For both groups we recorded each fish's individual marks each time it was removed from a structure, so the history of space use could be traced. Tests were conducted for 36 nights to yield 216 fish-nights.

The water temperature throughout the experiment, continuously recorded using a Ryan thermograph, ranged from 0 to 8°C but was always <4°C at the time space use was assessed. On 9 February a light-intensity meter (Onset Instruments HOBO-LI) was placed in a waterproof container and anchored to the stream bottom between the test enclosures. Under turbid water conditions, light intensity at the time concealment was assessed exceeded 18 lx · m^{-2} only once, when it reached 30 lx · m^{-2} and the minimum and mean light intensities recorded under turbid water conditions were 3 and 11 lx · m^{-2}, respectively. The maximum, minimum, and mean light intensities recorded under surface ice conditions were 68, 3, and 26 lx · m^{-2} and under clear water conditions were 51, 22, and 35 lx · m^{-2}, respectively. Anchor ice formed repeatedly downstream from the test enclosures in January and February and the resulting ice dam caused the water depth in the enclosures to vary from 20 to 30 cm. Anchor ice was never observed on the concealment structures. Shelf ice formed on 15 nights, but we were able to pull the structures through it except on 13 February. On that day, we waited until the ice melted a few hours later and assumed that space use was the same as it would have been in the morning. On January 30, shelf ice became so thick (>15 mm) that the experiment was postponed until February 9.

A heterogeneity χ^2 test was conducted to assess whether data from the two groups could be pooled. A one-way ANOVA and Duncan's multiple comparison test were used to assess whether there was a difference in the numbers of fish concealed under clear water, turbid water, or surface ice conditions. Least squares regression was used to assess whether there was a relationship between light level and number of fish concealed. Logit analysis was then done to find which factors affected a fish's choice of a space. Space selection was tested with a χ^2 test using the null hypothesis that fish used spaces at random. The log-likelihood ratio was used to assess whether fish aggregated.

Results

Throughout the two experiments, which were combined for analysis on the basis of the results of the heterogeneity χ^2 test ($\chi^2_7 = 6.37$, $P > 0.25$), subyearling rainbow trout were concealed for 168 of 216 fish-nights. The proportion of fish concealing themselves under clear water conditions was

significantly greater ($F_{[2,33]} = 4.54$, $P = 0.018$) than the proportion concealed under either surface ice or turbid water conditions, and there was no significant difference ($P > 0.05$, $n = 36$) in the proportions of fish concealed under surface ice and turbid water conditions (Table 1). There was no significant linear relationship ($r = 0.366$, $P = 0.07$, $n = 36$) between light level and proportion of fish concealed, but the power of the test was low (40).

Space selection was influenced by the distance of the space from the closest end ($\chi^2_6 = 16.34$, $P < 0.02$), the end spaces being used proportionally less than the middle space. Cage and structure did not influence which concealment space fish chose ($\chi^2_1 = 0.00$, $\chi^2_2 = 0.83$, $P > 0.66$).

Fish occupied the narrow space for 2% of the time, the tall space 8%, and each of the remaining five spaces between 13 and 21% (Fig. 1). Fish used the narrow space significantly less ($\chi^2_6 = 33.58$, $P < 0.001$) and the tallest space significantly less ($\chi^2_5 = 12.42$, $P < 0.05$) than would be expected if they were selecting spaces at random; the remaining spaces were used randomly ($\chi^2_4 = 4.20$, $P > 0.25$) (Fig. 1). Fish randomly selected spaces that were shorter or wider than their extended fins (both 40 mm), but avoided spaces that were narrower or taller than their extended fins.

Individual fish did not consistently return to the same space each day throughout the tests. When only the 17 fish that were tested five times on consecutive days were considered, "space fidelity" (fish returning to a space of the same size and shape) was greatest for 4 fish, each of which used the same space three of five times. "Site fidelity" (fish returning to the same space in the same structure) was greatest for four fish that used the same space in the same structure on 2 consecutive days. One of the 17 fish that were tested five times on consecutive days selected a different space each night.

We observed two fish sharing the same space on two occasions during the 216 fish-nights of the experiment, with no individual fish occupying a space with another fish on more than one occasion. The three test fish in an enclosure were never found sharing a single space. This is not significantly different ($P > 0.05$) from what would be expected if two or more fish occurred together in the same space at random.

Discussion

The effect of ice and turbidity on the behaviour of stream fishes has rarely been examined closely, owing to the observational problems associated with these conditions. The extent to which our data, collected under experimental conditions, represent normal winter conditions and behaviour of

subyearling rainbow trout needs further evaluation. The spaces within our structures simulated, but were less complex than, the interstices in rock substratum to which the test fish were accustomed. Mason (1976), who unsuccessfully built structures to simulate winter habitat for coho salmon (*Oncorhynchus kisutch*), stated that winter habitat could not be created by "crude simulations."

There was no difference in the proportions of fish concealed under turbid water and surface ice conditions. This suggests that these conditions offered similar benefits and that at the water temperatures encountered in this study (at or near 0°C under surface ice and 1−4°C under turbid water conditions), concealment was not simply a function of water temperature. However, a significantly greater number of fish concealed themselves when the water was clear than when it was turbid or when surface ice was present. Although additional research is needed to assess cause and effect, these observations suggest that aerial predators might pose a greater threat to subyearling rainbow trout in winter than aquatic predators: ice would presumably offer physical protection from aerial predators but minimal protection (by reducing light intensity) from predators such as larger fish, mink (*Mustela vison*), and diving birds that hunt in the water column and can be major causes of salmonid mortality in small streams in winter (Gerell 1967; Alexander 1979; Heggenes and Borgstrom 1988). Gregory (1993) found that at 6−10°C the response of subyearling chinook salmon (*Oncorhynchus tshawytscha*) to simulated predators was less marked and of shorter duration under turbid than clear water conditions. Gregory (1993) also found that the fright response of subyearling chinook salmon to a simulated fish predator was less than the response to a simulated avian predator. Another possible explanation for our observation of reduced concealment under surface ice and turbid water conditions is that the main advantage offered by our structures might have been protection from predators. Therefore, fish may have been less likely to conceal themselves when they were otherwise protected.

Changes in weather during exp. 2 that caused an increase in turbidity also increased water temperature and discharge, and might have confounded the results. An increase in temperature would be expected to decrease the number of fish that conceal themselves only when the increase exceeded some threshold in the 7−10°C range. The water temperature in exp. 2 reached 8°C on 3 nonconsecutive days, but was always 4°C or less when space use was assessed. Increased discharge would, in a general sense, be expected to increase use of cover by fish (McMahon and Hartman 1989), as they respond to increased water velocity, and might have led to increased concealment during exp. 2. Although water velocities were not measured throughout the study, they were low enough throughout both experiments to cause fine sediment to be deposited in the cages, and we doubt that water velocity changes were sufficient to cause a shift in fish behaviour.

Although we reused fish, we do not believe that this biased the results, for the following reasons. In preliminary observations on subyearling rainbow trout in laboratory tanks at dawn (J.S. Gregory, unpublished data), fish explored a series of spaces before remaining in one. Therefore, when we recorded the space a fish occupied at 08:00, we assumed that it was already experienced and had already investigated some or all of the other spaces. Each time we recorded a fish's location, the fish was removed from the structure and again had to select a space. Griffith and Smith (1993) found that on the South Fork of the Snake River, Idaho, a mean of 61−66% of the cutthroat and brown trout estimated to be present during the day emerged from cover on a given night. If our fish behaved similarly, they would have selected a space when we put them in the enclosure in the morning, emerged at night, and selected a space again the next morning before we recorded their space use. Furthermore, the test fish were not simply returning to their original locations after they were removed from the structures, as shown by the low degree of space and site fidelity.

Fish avoided the spaces that were narrower than their extended pectoral fins and randomly used the spaces that were shorter than their extended dorsal fin. Since spaces were oriented parallel to the flow, selection against the narrow space might have been an artifact of water velocity through the spaces. Possibly, fish need to maneuver their pectoral fins when there is water flow through the spaces but do not necessarily require dorsal fin movement. Differential use of the narrow and short spaces suggests that the orientation and dimensions of the spaces are more important to fish than is cross-sectional area, as these two spaces were of nearly the same cross-sectional area.

Overall, the microsite characteristics most chosen in our experiment were a space wide enough for pectoral fin extension and short enough that the dorsal fin contacted the top of the space. Our results agree with those of Hartman (1965) and Rimmer et al. (1983), who observed that subyearling steelhead (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*) selected spaces under rocks more often than between rocks. Spaces between rocks probably more closely resembled the spaces in our structures that were taller than they were wide, whereas locations under rocks would more often resemble spaces in our structures that were wider than they were tall. Space use by our test fish was influenced by the position of the space relative to the end of the structure. This may have been a function of the brick, which did not extend across the entire length of the structure. However, any such effect would have been minimized because space shapes were randomly arranged within each structure.

Our test fish occasionally shared a space. Cunjak (1988) found a few groups of two or more subyearling Atlantic salmon under the same stone in a Nova Scotian river, while all the subyearling Atlantic salmon found beneath stones in a stream in New Brunswick by Rimmer et al. (1983) were solitary. Further study is needed to evaluate if agonistic behaviour plays a role in establishing the carrying capacity of winter habitat for subyearling salmonids.

Acknowledgements

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