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ARTICLE

Use of Cover for Concealment Behavior by Rainbow Trout: Influences of Cover Structure and Area

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Abstract
Concealment behavior by stream salmonids can benefit individuals and populations, but the availability of concealment habitat may be limited in many streams. Quantification of concealment habitat is likely to be a valuable process in the management of stream salmonids; it is a necessary step in the application of spatially explicit, individual-based models that incorporate concealment behavior. We conducted a series of laboratory experiments with Rainbow Trout *Oncorhynchus mykiss* to aid in the identification and quantification of concealment habitat. Overall, individual Rainbow Trout about 12 cm FL readily used low-ceiling spaces with one, two, or four openings for concealment. Structures analogous to weakly undercut banks were used less. Mean use of different cover types was less variable in an experiment in which groups of three fish were tested. Individuals in groups rarely shared cover spaces, even though in another experiment individual fish readily occupied spaces less than 25% of the area of the spaces they rarely shared. One cover structure that was not preferred in a simple choice experiment was used as much as the preferred structure when the former was the only cover available, indicating that habitat preference experiments provide limited information when the issue is whether fish are willing to use specific habitats.

Researchers have long recognized that even in the absence of short-term stimuli, such as an approach or attack by a predator, salmonid fishes at times conceal themselves in the substratum, sometimes for lengthy periods (Hartman 1963; Bustard and Narver 1975). The use of hiding or concealment behavior commonly results in diel patterns in the use of the water column by salmonids (Gries and Juanes 1998; Meyer and Gregory 2000; Bradford and Higgins 2001; Reeves et al. 2010). A wide variety of factors influence this behavior, including, for example, shelter availability (Larranaga and Steingrímsson 2015), food availability (Metcalfe et al. 1999), temperature (Fraser et al. 1993), physiological state (Metcalfe et al. 1998), aggressive behavior (Gregory and Griffith 1996a), and the life stage of the fish (Imre and Boisclair 2004).

The opportunity to engage in concealment behavior can be important to individuals and probably also populations. Evidence from habitat selection in an experimental setting supports the hypothesis that concealment is at least, in part, a predator avoidance behavior (Valdimarsson and Metcalfe 1998), but reduced energy expenditure is another likely benefit. In one field experiment, the presence of cover enhanced the survival of salmonids, even when predators were excluded (Smith and Griffith 1994). Experiments in artificial streams have revealed positive relationships between the number of sites suitable for concealment and fish growth (Finstad et al. 2007; Koljonen et al. 2012). The amount or quality of concealment habitat has been positively related to local salmonid density (Hillman et al. 1987; Van Dyke et al. 2009). The last point suggests that the amount of concealment habitat can influence population dynamics and that increasing concealment habitat where it has been reduced is likely to benefit populations. However, tools to estimate the quantitative benefits for salmonid populations of a given increase in concealment habitat are limited, particularly in relation to the benefits of alternative actions.

Spatially explicit, individual-based models offer one approach to evaluating the influence of concealment behavior

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and the amount of concealment habitat on populations. Models for salmonids that include (Railsback et al. 2005) and exclude (Railsback et al. 2009) concealment behavior are available. A recent comparison of those models (Harvey et al. 2014) suggested that concealment behavior, and therefore the amount of concealment habitat, could be important in the responses of salmonid populations to environmental variation such as altered streamflow regimes. However, one significant challenge for spatially explicit models is the need to quantify concealment habitat in real streams. Investigators must be able to answer the key question, “What is concealment habitat?” For example, should a slightly undercut bank that provides overhead cover be included? Additional important issues for individual-based modeling are the amount of concealment cover individual fish require and the influence of interactions among individuals on the use of cover for concealment.

Progress has been made in identifying concealment habitat through a combination of observations of fish in natural settings and via experimental studies. Field studies have found a variety of salmonids in the interstitial spaces of unembedded cobbles and boulders (Rimmer et al. 1983; Cunjak 1988; Griffith and Smith 1993). Field manipulation of cobbles has shown that their arrangement influences the number of fish retained (Meyer and Griffith 1997). While some fish were apparently willing to use individual unembedded cobbles, more fish were retained when cobbles touched each other, and a double layer of cobble led to about twice the retention of fish as a single layer of cobble, per area of cover. A laboratory study that gave fish the option of selecting among spaces varying in size and shape indicated a preference for interstitial spaces wider than the width of fish with pectoral fins extended and with height less than that of the fish with dorsal fin extended (Gregory and Griffith 1996b). One consideration in applying existing information to the real-world challenge of quantifying concealment cover is the distinction between preferences among habitat types versus the willingness to use a particular habitat type.

To our knowledge, limited information addresses the significance of cover area on its use for concealment by fish. Previous studies have established that salmonids will use spaces just slightly wider and longer than themselves (Gregory and Griffith 1996b), but aggressive behavior limits sharing of larger spaces (Gregory and Griffith 1996a; Armstrong and Griffiths 2001). For example, individual Rainbow Trout *Oncorhynchus mykiss* 10–13 cm TL readily occupied areas of about 80 cm^2 (Gregory and Griffith 1996b), but Atlantic Salmon *Salmo salar* about 7 cm TL shared an area of about 150 cm^2 for 27% of the time the area was occupied by at least one fish (Armstrong and Griffiths 2001). Overall, existing information leaves investigators seeking to quantify the area of concealment cover in field settings needing to apply considerable subjectivity.

We addressed the need for more information on the characteristics and use of concealment cover through a series of laboratory experiments using Rainbow Trout. The experiments were focused on cover types of particular interest based on our efforts to quantify concealment cover in natural streams for the purpose of spatially explicit individual-based modeling. We completed a series of four experiments to (1) contrast the use of four different cover types by individual fish, (2) contrast use of the same four cover types by groups of fish, (3) quantify habitat preferences of individual fish offered pairs of cover types, and (4) compare the extent of use of cover structures of different sizes by individual fish.

METHODS

We conducted experiments in two circular holding tanks with bottom areas of 0.66 m^2 and a recirculating stream with an area of 4.5 m^2, all linked to a central water chiller and filtration system. Water velocity was negligible in the experimental arenas. Because concealment behavior is usually more pronounced at cold temperatures (Reeves et al. 2010), we maintained water temperature in the range 5–7.5°C during these experiments. We maintained water depth at approximately 50 cm in the holding tanks and stream. The tanks and stream were housed in a glass-walled greenhouse with a nontranslucent roof, so we supplemented natural ambient light with 8 h/d of daylight-spectrum artificial light via 75-W overhead lamps. We completed experiments 1 and 2 between early February and early May 2014. Experiments 3 and 4 were completed between early April and early August 2015.

Rainbow Trout used in the experiments were captured with a backpack electrofisher in upper Jacoby Creek near Arcata, California. Fish used in experiments 1 and 2 were captured in 2014 and fish used in experiments 3 and 4 were captured in 2015. We used fish 82–140 mm FL because they compose the majority of post-age-0 fish in nearby populations (Harvey et al. 2014). Fish were acclimated for 5–7 d in one of the circular holding tanks. Following the initial acclimation, we anaesthetized the fish in water with sodium bicarbonate and then weighed and measured the length of each fish. We also inserted a 12.5-mm passive integrated transponder (PIT) tag into the body cavity of each fish. After tagging and measurement, we isolated fish to prevent agonistic interactions and allowed a minimum of another week of acclimation prior to use in experimental trials. While in holding, fish were fed frozen chironomid larvae, mysid shrimp, and calliphorid larvae ad libitum. In all four experiments, we refrained from feeding fish 24 h before use in a trial and introduced fish to an experimental arena 16–24 h prior to recording any observations. Fish spent a minimum of 24 h in holding between trials.

The cover structures used in these experiments were designed to approximate natural spaces in cobble substratum. Field observations (J. L. White and R. J. Nakamoto, U.S. Forest Service, personal observations) suggested that the number of access openings could affect the probability of use of concealment spaces by salmonids; the literature is equivocal on the significance of this characteristic (Rimmer et al. 1983). In addition, field attempts to quantify concealment cover raised the question of the usability of exposed edges of cobbles and boulders, which provide overhead cover, and weakly undercut banks that provide spaces with similar characteristics. Therefore, we included four types of structure in the experiments: three spaces with low horizontal ceilings with one, two, and four openings, and a more open, undercut structure. We constructed the structures using a slate tile (1 cm thick, 30 × 30 cm) and various arrangements of clay bricks (Figure 1). The horizontal ceilings in the first three structure types were about 4 cm high. To construct the undercut cover type, we buried approximately half of the slate tile in the gravel with the remainder protruding at an angle of about 25° from horizontal. A brick placed over the buried half kept the unit in place. The various cover types each provided about 450 cm^2 of covered area.

Experiment 1.—In this experiment we tested for variable use of different cover types by individual fish. We measured use of the four cover types by individual fish over separate 24-h trials. Twenty-two fish were each tested with each cover type (88 total trials; fish size ranged from 82 to 139 mm FL). We subdivided one circular holding tank to form two experimental arenas and constructed two additional experimental arenas by subdividing a pen (60 × 120 cm) in the artificial stream. The cover units were placed on clear acrylic trays (45 × 30 cm, 10 cm deep) filled with aquarium gravel that were placed on the fiberglass bottoms of the experimental arenas. We positioned digital cameras above each pair of arenas and programmed them to take hourly photographs. Photographs were taken over 24 h, beginning at 0800 hours, following the acclimation period. Individual fish were exposed to the four cover types in random order in separate trials. At the completion of a trial, we examined the hourly photos and recorded whether a fish was exposed or concealed under cover. The response was the proportion of photos in which fish were concealed. For all experiments, fish with ≥75% of their length concealed were categorized as concealed.

Experiment 2.—This experiment tested for variable use of cover types by groups of fish. We measured the use of single concealment cover structures by 15 groups of three fish each. Each group was separately tested with each of the four cover types (60 total trials; fish size ranged from 84 to 147 mm FL). Seventeen of the 45 fish in this experiment also participated in experiment 1. (We determined a posteriori that prior experience did not detectably influence the response of the groups to the treatments.) With the exception of testing groups of fish instead of individuals, we used the same basic set-up and approach as in experiment 1. We determined the number of exposed fish in each photo and used the mean number of concealed fish as the response variable. We also evaluated the sharing of cover units by quantifying the number of observations in which more than one fish occupied a cover

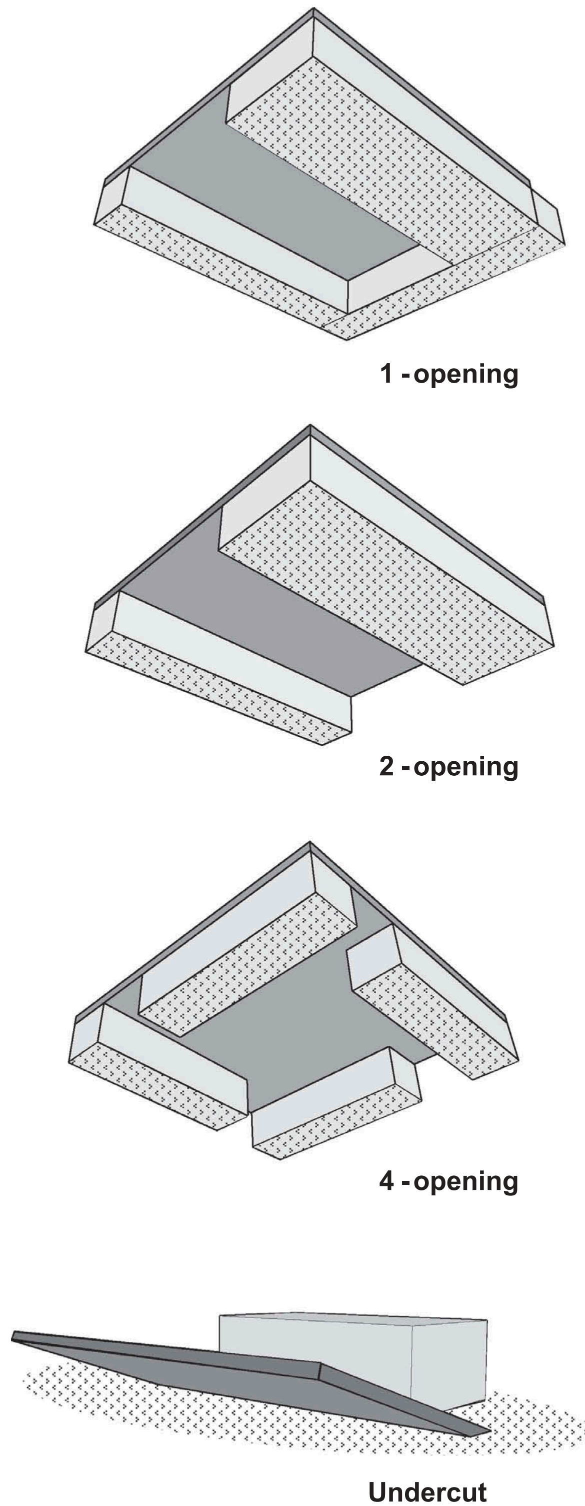

FIGURE 1. Schematic of the alternative structures used in experiments on the use of cover for concealment by Rainbow Trout. The three structures with horizontal ceilings (one-opening, two-opening, and four-opening) are viewed from below to illustrate differences. Stippling indicates surfaces that contacted the substratum. The undercut structure is viewed from the side; the brick associated with the undercut structure rested on the substratum.

structure as a proportion of the number of observations in which the structure was used by at least one fish.

Experiment 3.—We tested for cover preferences in experiment 3 by simultaneously offering individual fish two different cover types, using an entire circular tank as the experimental unit. The 12 fish included in this experiment had not been used in preceding experiments. We evaluated three separate contrasts of particular interest: one-opening versus four-opening, one-opening versus undercut, and two alternative sizes of one-opening structure. All of the fish in this experiment were used in all three contrasts (12 trials in each of the three contrasts; fish size ranged from 94 to 122 mm FL). The pairwise contrasts were completed in sequence: all 12 fish were tested in one contrast before the next contrast began. Some specific features of the experiment differed from experiments 1 and 2. The bottom of the circular tank was covered with 10 cm of gravel and structures were placed on that gravel. To facilitate the manipulation of cover types in the contrast of one-opening and four-opening structures, we modified the brick supports such that each structure had a covered area of 700 cm^2. The one-opening versus undercut contrast used structures with about 450 cm^2 of covered area. The third contrast offered one-opening structures of either 450 or 100 cm^2. To more closely mimic the mass of a natural cobble, we placed three standard bricks (18 × 9 × 6 cm) on top of the slate tile of each cover unit. We also increased the frequency of photographs to every 30 min. For observations in which photographs indicated fish were using cover, we determined the structure being used by fish with a flat-plate PIT tag antenna buried in the gravel underneath one of the cover units. We buried a nonfunctional antenna beneath the other cover unit (Figure 2); pre-experiment testing showed that the functional antenna detected PIT tags within the cover unit above it with 100% efficiency and also did not detect tags within the other cover unit. We programmed the PIT reader to continuously scan over a 4-min period bracketing the time of each photograph. A data logger recorded any tag detections along with a time stamp. In each trial, cover types were randomly assigned to two alternative positions: with or without the functional PIT antenna. For each trial, we measured the proportion of photographs in which each cover type was occupied. Exploration of the normality of alternative possible response variables motivated us to use the difference in the proportion of observations in which fish used the two available cover types.

Experiment 4.—Result of the experiment 3 preference test between one-opening cover structures of different sizes motivated a final experiment that contrasted the use of these structures when they were offered separately. Experiment 4 used one of the circular tanks divided into two semicircular units. The 12 fish from experiment 3 also participated in experiment 4 (24 total trials). Once again we used the proportion of observations in which fish used cover as the response variable.

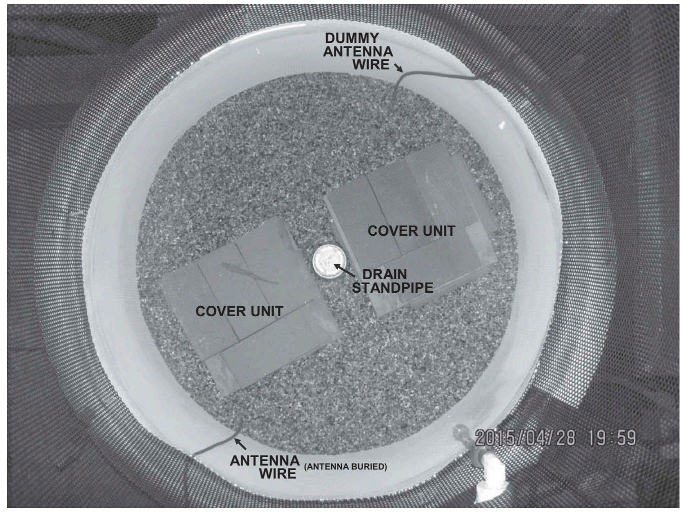

FIGURE 2. A photograph of the experimental unit used in experiment 3, in which alternative types of cover structures were simultaneously offered to individual Rainbow Trout. When a photograph indicated fish were concealed (≥75% of their length under cover), the cover type selected was determined from a passive integrated transponder tag antenna placed under one of the two cover units. In this example, the fish is unconcealed over the left-hand cover unit.

Analysis.—We analyzed three of the experiments using SAS Procedure Mixed (SAS Institute, Cary, North Carolina), treating cover type as a fixed factor and individual fish (experiments 1 and 4) or groups of fish (experiment 2) as random factors. We tested for differential use of alternative cover types in experiment 3 using paired *t*-tests. Because we were mainly interested in contrasting the general use of different cover types, we focused on analyses of the overall results (including both day and night observations), but we also separately analyzed day and night observations. We made pairwise a posteriori contrasts using Tukey–Kramer analysis. We evaluated the normality of the data and the need for transformations using the information on residuals in SAS Procedure Mixed.

RESULTS

In the first experiment, use of cover by individual fish varied among cover types (Figure 3; $F_{3, 63} = 7.65$, $P < 0.001$), ranging from a mean of 0.48 for the one-opening structure to 0.17 for the undercut. Pairwise contrasts indicated significantly ($P < 0.05$) greater use overall of the one-opening structure than the two-opening ($t_{63} = 2.70$) and undercut ($t_{63} = 4.78$) structures. Individual Rainbow Trout were highly variable in their use of concealment cover; mean use of cover ranged from 0.07 to 0.75. In general, daytime use of concealment cover exceeded nighttime use. Nighttime use of the one-opening treatment (0.36) far exceeded nighttime use of the other cover types (all <0.12).

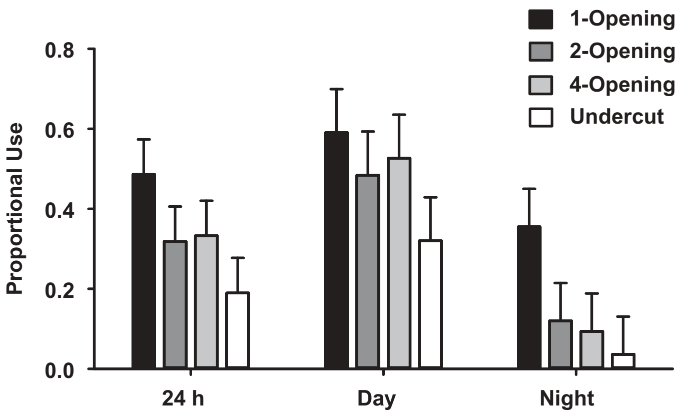

FIGURE 3. Mean (+1 SE) concealment use (experiment 1) of cover by Rainbow Trout in which 22 fish were separately offered cover structures of four types in separate trials (88 total trials). Use was defined as fish that were ≥75% under cover.

In contrast to the results of experiment 1, cover type did not influence the overall use of cover in experiment 2, which measured concealment behavior by groups of three fish. The mean number of fish occupying cover ranged from 0.57 to 0.74 among treatments (Figure 4; $F_{3,\ 42}$ = 2.07, P = 0.119). Use of cover varied among groups of fish, ranging from 0.26 to 0.91 fish on average. As suggested by the mean number of fish using cover, fish did not often share cover elements; multiple fish used the one available cover structure only 6% of the time that at least one fish occupied it. While groups varied in their willingness to share cover (0–27%), sharing did not vary detectably by cover type (range, 4–8% across treatments; $F_{3,\ 41}$ = 0.55, P = 0.651); one observation in which no fish used cover was excluded from the analysis of sharing).

In two out of three cases in experiment 3, fish expressed a significant preference for one cover type over another. Fish did not express a detectable preference when given the alternatives of one-opening and four-opening structures (Figure 5; t_{11} = 0.58, P = 0.572) but did prefer the one-opening treatment to the undercut treatment (Figure 5; t_{11} = 4.22, P = 0.001). Finally, fish preferred the one-opening structure with 450 cm^2 of covered area to a one-opening structure with 100 cm^2 of covered area (Figure 5; t_{11} = 2.88, P = 0.015). Even though fish had expressed a preference for the larger versus the smaller one-opening structure in experiment 3, in experiment 4 usage rates were not detectably different (overall: $F_{1,\ 11}$ = 1.93, P = 0.192) when the two structures were offered separately (Figure 6).

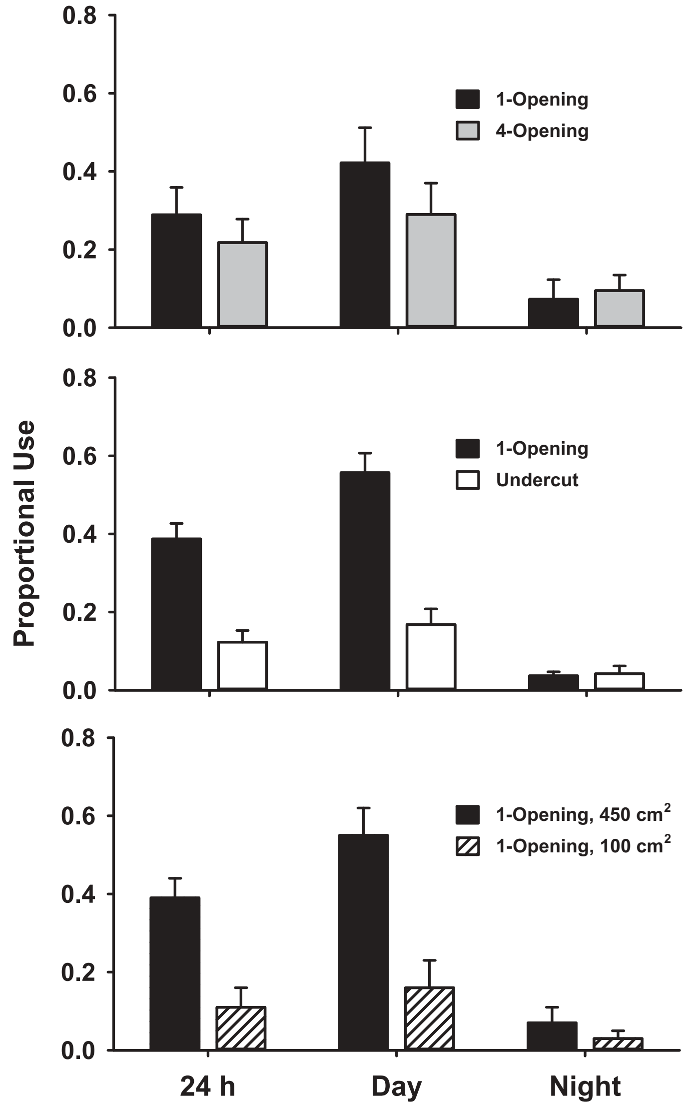

FIGURE 5. Mean (+SE) proportional use of alternative types of cover structures when simultaneously offered to individual Rainbow Trout (experiment 3). Use was defined as fish that were ≥75% under cover.

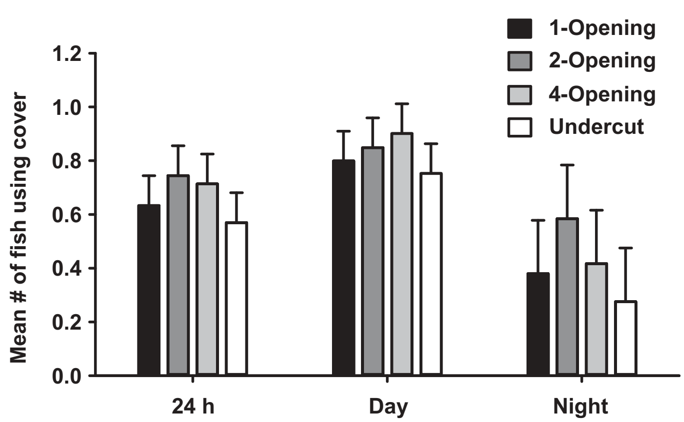

FIGURE 4. Mean (+SE) use of concealment cover by 15 groups of three Rainbow Trout offered individual cover structures of various types in separate trials (experiment 2; 60 total trials).

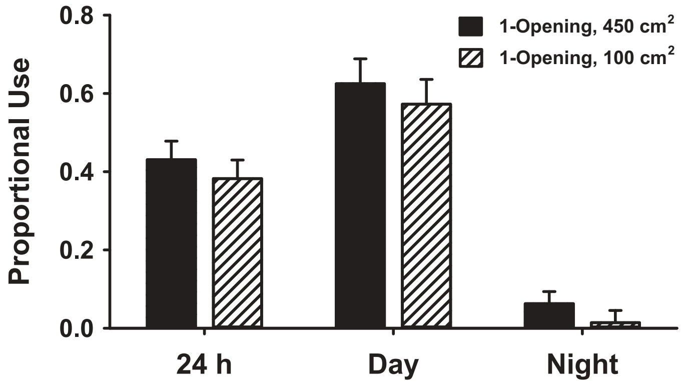

FIGURE 6. Mean (+SE) proportional use of cover by individual Rainbow Trout offered one-opening cover structures of two different sizes in separate trials (experiment 4). Use was defined as fish that were ≥75% under cover.

DISCUSSION

These experiments indicated that variable cover spaces likely to be encountered among unembedded cobble and boulder substratum in natural streams are generally suitable for use as concealment cover by salmonids. However, the relatively modest use of the undercut structure suggests that open structures providing little more than overhead cover (e.g., weakly undercut banks or partially embedded cobbles and boulders) are unlikely to provide concealment cover. While this conclusion might seem to be at odds with the results of experiment 2, in which groups of three fish used the undercut and other structures to similar extents, we hypothesize that some individuals in that experiment were using any available structure to avoid agonistic behavior from others.

The low level of sharing of cover structures in experiment 2, which parallels several previous studies (Gregory and Griffith 1996b; Armstrong and Griffiths 2001), is also relevant to efforts to model the use of concealment cover by salmonids. In experiment 2, fish rarely shared spaces that seemed large relative to the size of the fish: the areas of the spaces were more than 2 × (fish length)^2. Sharing of cover by salmonids is apparently a complex phenomenon influenced by differences in body size (Orpwood et al. 2003) and even the relatedness of individuals (Griffiths et al. 2003), but this study and previous research indicate that model formulations should avoid the assumption that juvenile salmonids routinely share even relatively large concealment spaces that do not provide visual isolation of individuals.

Comparison of experiments 3 and 4 highlights the contrast between the preference for certain habitats versus the willingness to use them. For the purposes of quantifying concealment habitat in simulation models, the latter is more important. In experiment 3, fish expressed a clear preference for the larger one-opening structure over the smaller one-opening structure, but in experiment 4, fish used the two structures to similar extents when they were offered separately. Combined with the rarity of sharing of cover spaces, these results would lead those quantifying concealment cover to consider the large and small one-opening structures equivalent. Use of even smaller structures by similar-sized salmonids (Gregory and Griffith 1996b) indicates that the assumption of equivalence could be extended to smaller spaces.

The artificial setting and structures used in the experiments presented here raise questions about interpretation of the results. The absolute frequencies of use of various cover structures in these experiments cannot reasonably be compared with field observations because of unnatural food availability, prevention of emigration, the artificiality of the structures, and perhaps other factors. However, our focus was on the willingness of fish to use structures and the relative comparisons of structure types. We found encouraging the fact that the diel patterns in concealment that we observed paralleled field observations (Bradford and Higgins 2001).

Existing information, including this study, leaves unanswered a variety of important questions about concealment cover. Answers to several fine-scale questions would be helpful. For example, Gregory and Griffith (1996b) observed in a preference experiment with Rainbow Trout that spaces taller than the fish with dorsal fin extended were used less than expected if space use was random, but the willingness to use such spaces in the absence of alternatives has not been investigated. People attempting to delineate concealment cover in the field would benefit from more information on the use of spaces of different heights. Fine-scale studies of concealment cover are particularly applicable to quantifying cover in small streams, where identification of individual interstitial spaces may be feasible, but for larger systems it would be useful to develop relationships between the quantity of various types of concealment cover and the number of fish that could be supported. This is not an easy task. For example, Meyer and Griffith (1997) showed that whether a patch of unembedded cobble is single-layered or multi-layered strongly influences the number of fish it can house. Establishing such relationships for more complex materials, such as woody debris, will be challenging but also important for models that incorporate concealment behavior.

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