

## Effects of Cobble-Boulder Substrate Configuration on Winter Residency of Juvenile Rainbow Trout

KEVIN A. MEYER AND J. S. GRIFFITH<sup>1</sup>

Department of Biological Sciences, Idaho State University  
Pocatello, Idaho 83209, USA

**Abstract.**—We assessed first winter habitat use by placing wild rainbow trout *Oncorhynchus mykiss* (52–155 mm total length) in wire-mesh enclosures with different cover treatments and at varying fish densities. Cobble-boulder substrates (20–40 cm diameter) were arranged in four different configurations: (1) no cobble-boulders, (2) cobble-boulders present but not touching, (3) cobble-boulders touching in a single layer, and (4) cobble-boulders touching and stacked in two layers. As the configuration of rock substrate was changed to create more concealment cover, the number of fish remaining in the enclosures after 96 h increased significantly, even though the quantity of rock substrate did not change. The initial stocking density of fish had no overall significant effect on the number of fish remaining in enclosures after 96 h. However, analysis of each cover  $\times$  density treatment showed that when the substrate arrangement created little concealment cover, the number of fish remaining in the enclosures did not increase with an increase in initial fish density, but when the substrate arrangement created relatively more concealment cover, more fish remained in the enclosures when the initial fish density was increased. In trials with rock cover present, fish emigrating from the enclosures were larger than those remaining in the enclosures. Our results demonstrate the importance of the configuration of cobble-boulder substrate in determining its suitability as winter cover for rainbow trout.

The winter ecology of stream-dwelling salmonids has been the subject of substantial interest in recent years. Studies of overwinter survival (Hunt 1969; Seelbach 1987; Smith and Griffith 1994) and seasonal habitat shifts (Rimmer et al. 1983; Johnson and Kucera 1985; Hillman et al. 1987; Baltz et al. 1991; Nickelson et al. 1992; Riehle and Griffith 1993) have demonstrated the importance of winter habitat requirements in the management of salmonid populations.

When water temperature drops below about 8°C at the beginning of winter, juvenile salmonids typically adopt an activity pattern consisting of daytime concealment in cover and nighttime emergence (Chapman and Bjornn 1969; Heggenes et al. 1993; Contor and Griffith 1995). A primary type of winter concealment cover is interstitial spaces between and under rocks. Although numerous studies have demonstrated the importance of cobble-boulder substrate as winter habitat for juvenile salmonids in general (Hartman 1965; Chapman and Bjornn 1969; Griffith and Smith 1993) and for rainbow trout *Oncorhynchus mykiss* in particular (Campbell and Neuner 1985; Baltz et al. 1991; Griffith and Smith 1995), none have clearly defined the characteristics of the substrate that determine its suitability. Because a stream's winter carrying capacity of juvenile salmonids de-

pends primarily on the quality and quantity of concealment spaces (Chapman 1966), it is important for fisheries managers to understand the relationship between cobble-boulder substrate configuration and its use as cover by juvenile salmonids.

The objective of this study was to assess the relationship between the arrangement of rock substrate and the density of rainbow trout remaining in instream enclosures. We hypothesized that as we changed the configuration of cobble-boulder substrate to create more concealment cover, the density of fish remaining in the enclosures would increase. Initial fish stocking density was also tested in an attempt to evaluate the rainbow trout carrying capacity of the rock substrate at different configurations.

### Methods

The experiment was conducted in four enclosures placed in the Henrys Fork of the Snake River, a fourth order stream located in Fremont County in southeastern Idaho. Our study site (44°22'N, 111°23'W) was near Last Chance, 8 km below Island Park Dam at a river elevation of 1,876 m. Discharge from the dam ranged from 9.1 to 13.2 m<sup>3</sup>/s during the study period of 25 January through 17 March 1994 (USGS 1995) and was supplemented by a relatively constant water flow of 6.0 m<sup>3</sup>/s from the Buffalo River that entered immediately below the dam. Channel width was 90 m, and gradient was 0.31%.

<sup>1</sup> To whom correspondence should be addressed.

Enclosures consisted of 2.5-mm-mesh galvanized screen held in place by steel fence posts; they were constructed within 5 m of the stream margin and about 10 m apart. Each of the enclosures, which we buried in the gravel substrate, measured 1 m wide  $\times$  3.33 m long and extended approximately 0.30 m above the water surface. A funnel trap with a 14-cm  $\times$  20-cm opening was located at the downstream end of each enclosure and extended into a 1.5-m<sup>2</sup> cage outside the enclosure, in which emigrating fish were captured and held. For protection from drifting ice and debris, deflectors made of 5-cm  $\times$  15-cm wire mesh were held in place by fence posts at a 45° angle to the flow 10 m above the enclosures.

Water temperatures were monitored with a data logger (Campbell Scientific, model CR-10) and thermocouple that was accurate to  $\pm 0.05^\circ\text{C}$ . Temperatures were recorded as hourly averages of 1-min subsamples. Depths and mean water column velocities (measured at 0.6 times the depth; Platts et al. 1983) in the enclosures were measured with a meter stick and a Marsh-McBirney model 201 velocity meter (accuracy,  $\pm 2\%$ ) in the center of each enclosure on 29 January and 6 March. Depths ranged from 29 to 31 cm and water column velocities ranged from 9 to 24 cm/s; measurements were identical for both dates, and we assumed no changes occurred during the experiment. Because each test run was of short duration, supplemental feeding was not provided. Adult aquatic Chironomidae were present on the water surface inside the enclosures during all visits to the study site, and velocities appeared adequate to drift at least small invertebrates through the hardware cloth into the enclosures. In previous research in the study area that used instream cages with 5-mm-mesh screen, the mean relative stomach content wet weights for caged juvenile rainbow trout that were feeding mostly on emerging Chironomidae were not significantly different from those of free-ranging juvenile rainbow trout outside the enclosures (Smith and Griffith 1994).

Juvenile rainbow trout were captured by electrofishing in the river 4 km upstream. Fish were measured to the nearest millimeter for total length and given an individual clip on the adipose fin or on a lobe of the caudal fin. Captured fish were held 2–4 h after electrofishing before being added to the enclosures. Fish averaged 96 mm (range, 52–155 mm) in length; scale analysis of fish at least 150 mm long indicated the fish were age 0. They were distributed among enclosures so that the mean fish length was not significantly different in

any experimental trial (analysis of variance,  $P = 0.88$ ). Individual fish were reused a maximum of two times in the experiment.

Three initial fish densities were tested: 4.5, 6.0, and 9.0 fish/m<sup>2</sup> (15, 20, and 30 fish, respectively, per enclosure). These densities were within the range of 4–14 rainbow trout/m<sup>2</sup> that had been previously observed in high quality cobble–boulder habitat in the study area (Smith and Griffith 1994).

Cover treatments included (1) no rock cover (control); (2) 20 rocks scattered across the bottom of an enclosure, with no rock touching any other; (3) 20 rocks, all touching in a single layer and covering roughly 50% of the bottom of an enclosure; and (4) 20 rocks, all touching in a double layer and covering roughly 25% of the bottom of an enclosure. For each treatment, we used 10 angular river-rounded basalt rocks that were cobbles (20–30 cm diameter) and 10 rocks that were boulders (30–40 cm diameter; see Platts et al. 1983). By using 20 rocks for each cover treatment, we kept the volume of rock structures constant and could presumably change the amount of concealment cover in the rock structures by changing the arrangement of rocks. The number of rocks used was based on juvenile rainbow trout densities present in 18 sections (2 m wide by 8 m long) along the stream margin in the study area. In late October 1993, we electrofished each section, enumerated all rainbow trout present, and counted the number of unembedded rocks (>20 cm diameter) present. Rocks were considered unembedded if approximately 5% or less of their surface was covered with sediment (Platts et al. 1983). There was a positive relationship between the density of unembedded rocks and the density of age-0 rainbow trout in those sections ( $r = 0.76$ ,  $df = 16$ ,  $P = 0.0003$ ; Meyer 1995). From this regression, we estimated that 20 rocks would provide adequate cover for our highest stocking level of 30 fish.

Each test run lasted 96 h. At 1200 hours Mountain Standard Time on the first day, fish were added to the enclosures and allowed to acclimate over the next 48 h with the trap entrances blocked. At 1200 hours on the third day, traps were opened, and fish were allowed to emigrate from the enclosures. At 1200 hours on the fifth day, the test run was terminated. Fish were emptied from the traps with a dip net, enumerated, and measured. The rocks were then removed from the enclosures, traps were reopened, and the remaining fish were maneuvered by hand into the traps and netted.

Three observations were made for each cover  $\times$  density treatment during 9 test runs for a total

of 36 trials, with treatment combinations assigned randomly during each test run. Because the data were normally distributed with equal variances, we used a two-way analysis of variance to test cover type and fish stocking density as the main factors in determining fish residency in the enclosures and to test for significant interaction. Duncan's multiple-range tests were used to test for differences between overall means and between cell means at specific levels of each factor. Mean water temperature during each test run was included in the model as a continuous variable to test for its effect on fish residency. In order to control for the difference in velocity between enclosures, enclosures were given a specific number which was recorded for each trial and included in the original model; we assumed that water velocity was the only difference between the enclosures. Wilcoxon paired-sample tests were used to test for differences between the length of fish remaining and those leaving each enclosure during each trial. We used SPSS (SPSS 1986) to perform Bartlett's homoscedasticity test and SAS (SAS Institute 1987) for all other analyses.

### Results

During the experiment 97% of the fish were recaptured either in an enclosure or in a trap. The other 3% evidently escaped from the experiment, escaped capture during the experiment, or died via aerial predation or within the enclosures or traps and went unnoticed.

Significantly more rainbow trout remained in enclosures in the rock configurations that were intended to create more concealment cover ( $P = 0.0001$ ; Figure 1). Compared with the control, the number of rainbow trout remaining in enclosures increased an average of 365% (range, 231–440%) with the addition of any cobble–boulder treatment to the enclosures. Additionally, an average of 53% more fish remained for the two treatments where rocks were touching than where they were not touching, but no significant difference was detected between single-layered and double-layered cobble–boulder treatments.

Initial fish stocking density had no overall significant effect on the number of fish remaining in enclosures ( $P = 0.10$ ), but because of the low  $P$ -value, we analyzed stocking density for each cover treatment separately. With no rock cover present, the number of rainbow trout remaining in the enclosures did not differ significantly among initial stocking densities ( $P = 0.49$ ; Figure 1). Final fish density was less than 0.9 fish/m<sup>2</sup> (3 fish/enclosure)

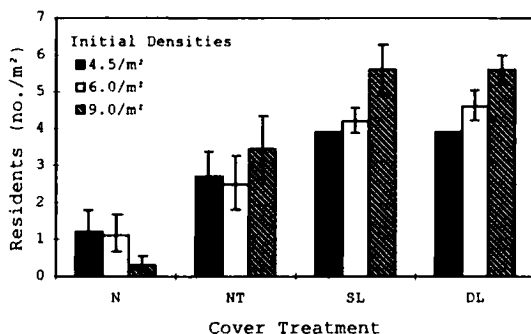


FIGURE 1.—The number of resident juvenile rainbow trout (mean  $\pm$  SE) remaining after 96 h in each cover  $\times$  fish density treatment in enclosures in the Henrys Fork of the Snake River, Idaho. Cover treatments are as follows: N = no cobble–boulders, NT = 20 nontouching cobble–boulders, SL = 20 touching cobble–boulders in a single layer, and DL = 20 touching cobble–boulders in a double layer.

during most trials with no cover. On average, about 3.0 fish/m<sup>2</sup> (10 fish/enclosure) remained when 20 rocks were present but not touching, and no significant difference was detected regardless of the initial stocking density ( $P = 0.68$ ). For both the single-layered and double-layered cobble–boulder treatments, the fraction of fish remaining declined as stocking density increased but the total number remaining rose, with an average of 5.7 fish/m<sup>2</sup> (19 fish/enclosure) remaining in both cobble–boulder treatments when 9.0 fish/m<sup>2</sup> initially were added. The number of rainbow trout remaining in the enclosures increased with increasing stocking density for both single-layered ( $P = 0.08$ ) and double-layered ( $P = 0.06$ ) cobble–boulder treatments. Final fish densities for single-layered and double-layered treatments were 56% and 47% higher, respectively, in enclosures receiving 9.0 fish/m<sup>2</sup> than in those receiving 4.5 fish/m<sup>2</sup>.

Water temperature had no significant effect on the number of rainbow trout remaining in enclosures ( $P = 0.41$ ). A regression of mean temperature for each test run against the mean density of fish remaining in enclosures (all enclosures combined) for each test run explained only 0.4% of the variation (Figure 2). Mean temperature for all test runs ranged from 2.1°C to 5.1°C, and the range within each test run averaged 3.8°C. Velocity (i.e., enclosure number) had no significant effect on fish residency ( $P = 0.88$ ), and there was no significant interaction between any of the factors included in the original model ( $P > 0.12$ ).

On 3 February, one of the coldest days during the experiment, surface ice formed over more than

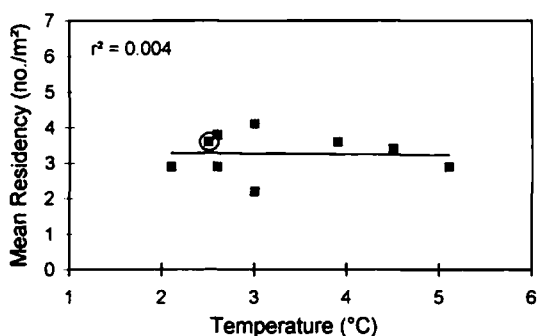


FIGURE 2.—Relationship between the mean temperature during a test run and the mean density of rainbow trout after 96 h (all enclosures combined) in enclosures in the Henrys Fork of the Snake River, Idaho. Circled data point excludes outlier from surface ice incident.

half of one enclosure (stocking density = 9.0 fish/m<sup>2</sup>, 20 rocks present but not touching). This enclosure had the lowest velocity (9 cm/s) of any enclosure. The density of fish remaining (7.0 fish/m<sup>2</sup>) was twice the mean from other trials with this cover × density treatment. The standardized residual value for this data point was 2.5 SDs from zero; it was judged to be an outlier (Montgomery 1991) and was not used in any of the analysis. No other enclosure on this or any other date had surface ice covering more than 10% of the surface area.

When rock was present, rainbow trout leaving the enclosures were larger (average, 103 mm) than those remaining (average, 92 mm;  $P = 0.005$ ; Table 1). This relationship was stronger when initial stocking densities were higher. When results were analyzed separately for each fish density treatment, the size of residents and emigrants did not significantly differ during trials with the lowest fish density ( $P = 0.50$ ), but emigrants were larger than residents for both the intermediate ( $P = 0.015$ ) and high ( $P = 0.010$ ) fish densities (Table 1). For the high-density trial, the mean size of emigrants was always larger than that of residents. Trials without rock were not used in this analysis because frequently no fish or only one remained in the enclosure.

### Discussion

This study demonstrates the importance of the arrangement of cobble–boulder substrate in determining its effectiveness as winter cover. Habitat use by juvenile salmonids during winter typically is higher where more concealment cover is present. Tschaplinski and Hartman (1983) found a strong

TABLE 1.—Mean length and differences (Wilcoxon paired-sample tests) between resident and emigrant juvenile rainbow trout. For cover treatments N = no cobble–boulders; NT = 20 cobble–boulders, none touching; SL = 20 cobble–boulders touching and in a single layer; and DL = 20 cobble–boulders touching and in a double layer. Signed rank scores are for overall test and tests for each fish density;  $P > 0.50$  for density of 4.5 fish/m<sup>2</sup>;  $P = 0.015$  for 6 fish/m<sup>2</sup>;  $P = 0.10$  for 9 fish/m<sup>2</sup>;  $P = 0.005$  for all density treatments combined.

Cover	Fish mean total length (mm)			Signed rank scores	
	Initial	Residents	Emigrants	Within density treatment	Overall
<b>Initial density of 4.5 fish/m<sup>2</sup></b>					
N	96.2	99.0	79.5		
	94.7	96.7	93.3		
	102.4	99.7	103.3		
NT	98.6	94.2	114.7	5	17
	86.4	88.6	84.5	-2	-4
	96.6	100.8	69.0	-7	-22
SL	95.2	101.3	75.5	-6	-21
	94.8	89.5	129.5	9	26
	102.1	99.0	109.8	3	10
DL	95.2	88.5	124.3	8	23
	88.8	90.9	75.5	-4	-16
	106.4	106.5	105.0	-1	-1
<b>Initial density of 6.0 fish/m<sup>2</sup></b>					
N	87.0	88.0	86.9		
	103.8	102.5	103.9		
	93.4	117.9	92.5		
NT	98.0	91.8	100.6	3	6
	97.3	94.3	107.8	5	12
	100.1	80.7	118.2	9	24
SL	90.1	79.8	102.6	8	19
	100.5	101.3	98.0	-1	-1
	95.3	92.4	106.0	6	13
DL	94.9	92.3	101.2	4	7
	102.0	99.9	122.0	7	18
	94.6	95.5	91.8	-2	-3
<b>Initial density of 9.0 fish/m<sup>2</sup></b>					
N	102.2	146.0	99.0		
	101.6		101.6		
	98.9	89.0	99.6		
NT	a	a	a		
	99.1	91.5	106.7	6	15
	95.7	78.8	101.8	7	20
SL	90.8	87.9	94.0	1	5
	97.5	95.2	108.2	4	11
	91.9	88.0	98.3	3	9
DL	92.4	89.4	99.0	2	8
	96.9	90.2	105.2	5	14
	90.4	78.3	117.3	8	25

<sup>a</sup> Excludes outlier from surface ice incident.

positive relationship between the volume of woody debris and the number of juvenile coho salmon *Oncorhynchus kisutch* overwintering in sections of Carnation Creek, British Columbia. Using outdoor stream channels under winter conditions, McMahon and Hartman (1989) found that the number of juvenile coho salmon remaining increased significantly as additional cover types were added to the channels. In both of these studies, the numbers of fish increased with a concurrent increase in the quantity of cover structure. In our enclosures, the number of resident fish changed despite holding the quantity of cover structure constant, by manipulating the arrangement of the cover structure. This supports the findings of Fontaine (1987), who found that rock structures with the greatest number of crevices held the highest winter densities of steelhead; single boulders or boulder pairs that provided fewer interstitial spaces held fewer fish.

The density of fish in the no cobble-boulder and nontouching cobble-boulder treatments appeared to be at a carrying capacity for all density treatments, with about 3 and 10 fish remaining for these cover treatments, respectively, regardless of how many fish were initially added to the enclosures. Thus, only half the rocks, at the most, would have had fish concealed beneath them when the rocks present were not touching one another. Placing the rocks so that all were touching increased fish residency 63% at the high stocking density, but stacking rocks into two layers did not change the density of fish remaining in enclosures compared with a single layer of rocks. Although it is difficult to hypothesize whether any difference in carrying capacity would have materialized at higher stocking densities between these two cover treatments or whether a carrying capacity had already been reached at our highest stocking density, our results suggest that as long as the rocks are contiguous, fish densities under conditions similar to those we studied will be similar between stream sections with a single layer of rocks and sections with multiple layers, as long as the quantity of rocks is comparable.

We do not know what types of interactions occurred, if any, between fish in the enclosures. Aggressive interactions between juvenile salmonids are generally less frequent during winter than in other seasons (Hartman 1963, 1965; Glova 1986), but such interactions have been documented (Glova 1986; McMahon and Hartman 1989; Gregory and Griffith, 1996b). Glova (1986), using experimental channels, found coastal cutthroat trout *O. clarki clarki* to be highly territorial within the de-

pressions under rocks, and typically only one fish was concealed under any one rock. Gregory and Griffith (1996b) suggested that aggressive behavior in winter may cause some underyearling salmonids to be excluded from concealment.

The evidence that rainbow trout leaving the enclosures were larger than those remaining concurs with McMahon and Hartman (1989), who found presmolt coho salmon emigrants were consistently larger than residents in stream channels. Although the differences in fish length were typically only a few millimeters and were rarely significant due to a much narrower range in the length of their test fish, the trend was the same as in our study. Alternatively, winter field studies have reported immigrating juvenile salmonids being smaller than residents. In three streams on Canada's Atlantic Coast, Cunjak and Randall (1993) reported that resident juvenile Atlantic salmon *Salmo salar* were consistently larger (by a few millimeters) than fish immigrating into the area during winter, and they suggested that the smaller fish were being displaced. Mason (1976) found smaller juvenile coho salmon moving downstream relative to resident salmon during winter in a stream with an apparent shortage of adequate concealment habitat. That the evidence of larger fish emigrating from our enclosures was strongest when there was less habitat per fish (i.e., the higher stocking densities) suggests a correlative link with density, but we cannot explain the mechanism behind the relationship. It is unlikely that smaller fish were displacing larger fish; most behavioral studies on juvenile salmonids have demonstrated that larger fish dominate smaller ones (Hartman 1963; Noakes 1980; Glova 1986) even during winter (Gregory and Griffith, 1996b). If any of the test conditions in our study were inadequate, larger fish might have been more willing to venture in search of more suitable positions for day time concealment or night time feeding. Had we offered substrate chambers too small for larger juvenile rainbow trout, the smaller fish would have been better suited for using the spaces available for concealment. Under winter conditions, Gregory and Griffith (1996a) observed rainbow trout avoiding concealment spaces where lateral fin constriction was necessary to enter the space. Existing literature on the characteristics and conditions of winter concealment spaces in the substrate selected by juvenile salmonids is sparse. Future research is needed to effectively appreciate the selection criteria that juvenile salmonids have for such concealment spaces during winter.

Results of this study suggest that juvenile rain-

bow trout will vacate areas lacking adequate winter concealment habitat, and support recent studies that have demonstrated habitat-related winter movements by juvenile salmonids. Cunjak and Randall (1993) found low site fidelity (2–30%) and significant movement of young Atlantic salmon during the winter, but site fidelity was greatest in streams with habitat that appeared to be most suitable for winter. They suggested that instream movements during winter may be triggered by near-freezing water temperatures and dynamic ice conditions that may alter the suitability of winter habitat. In the Henrys Fork of the Snake River, juvenile rainbow trout moved from midchannel areas in macrophyte beds early in the winter to concealment in the substrate along the stream margin as the winter progressed and the macrophytes sloughed off (Griffith and Smith 1995).

We believe the number of fish remaining in enclosures with no cover, although significantly lower than all other cover treatments, was higher than would occur under natural conditions with similar habitat present. Because the numbers of resident fish were typically low for this treatment, any resident fish were located inside the enclosures by mask and snorkel, cornered, and netted with a dip net, thereby allowing visual observation of fish concealment in these enclosures. Most were observed to be wedged against the gravel substrate and the bowing hardware cloth wall at the front of the enclosure, where they were barely visible. Occasionally fish would burrow into loose gravel substrate and only a portion of their dorsal or caudal fin would be visible. Similar burrowing by juvenile salmonids into loose, small particle-sized substrate for winter concealment has been previously observed for rainbow trout (Smith and Griffith 1994) and chinook salmon *O. tshawytscha* (Emmett et al., in press). This same concealment may also have occurred in enclosures with cobble-boulder substrate, which would have resulted in higher densities in these cover treatments than would be expected under natural conditions with similar habitat available.

Although water temperature did vary throughout the study, the lack of any significant effect on the habitat use of rainbow trout suggests that the range in mean temperature (2–5°C) may not have been wide enough to cause a change in fish concealment behavior. Additionally, hourly recordings of 7°C were exceeded only 3% of the time, and no recordings exceeded 8.5°C. Campbell and Neuner (1985) and Riehle and Griffith (1993) both found that for rainbow trout, concealment in the substrate

occurred at water temperatures below about 8.5°C. Although velocities were not equal among enclosures, they were all within the range of 0–25 cm/s found by Baltz et al. (1991) to have high suitability (>0.7 suitability) for juvenile rainbow trout under winter conditions.

It appears that the dramatic increase in fish residency during the trial when a large portion of an enclosure was covered by ice was due to a behavioral response to the presence of surface ice. Recent studies have demonstrated that adult brown trout *Salmo trutta* moved off the stream margin and away from bank cover (Young 1995) and that juvenile rainbow trout concealed in artificial structures less frequently (Gregory and Griffith 1996a) when surface ice formed over the stream. Chinook salmon commonly used shelf ice that was connected to the shore as overhead cover during the day and at night (Emmett et al., in press). These recent observations lend further support to the hypothesis that salmonids use surface ice as cover during winter. Concealment may be less critical when surface ice provides adequate protection from overhead detection.

Our study demonstrates that juvenile rainbow trout will leave areas that lack concealment cover during winter and that the configuration of rock substrate may influence fish use as much as or more than its quantity. In habitat restoration or maintenance efforts that employ rock structures and in stream inventory methods that include cobble-boulder substrate as habitat, it is important for managers to understand the characteristics that determine the suitability of that habitat for juvenile salmonids during winter.

### Acknowledgments

This study was funded by the Henrys Fork Foundation, the Targhee National Forest of the U.S. Forest Service, and the Idaho Water Resources Research Institute. Thanks are due Jed Gregory and Lynn Sessions for providing invaluable field assistance. Michael K. Young, Ken Rodnick, Dudley Reiser, and an anonymous reviewer provided many helpful comments on an earlier version of the manuscript.

### References

- Baltz, D. M., B. Vondracek, L. R. Brown, and P. B. Moyle. 1991. Seasonal changes in microhabitat selection by rainbow trout in a small stream. *Transactions of the American Fisheries Society* 120:166–176.
- Campbell, R. F., and J. H. Neuner. 1985. Seasonal and

- diurnal shifts in habitat utilized by resident rainbow trout in western Washington Cascade mountain streams. Pages 39–48 in F. W. Olson, R. G. White, and R. H. Hamre, editors. Symposium on small hydropower and fisheries. American Fisheries Society, Western Division and Bioengineering Section, Bethesda, Maryland.
- Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. *American Naturalist* 100:345–357.
- Chapman, D. W., and T. C. Bjornn. 1969. Distribution of salmonids in streams, with special reference to food and feeding. Pages 153–176 in T. G. Northcote, editor. *Salmon and trout in streams*. H. R. MacMillan Lectures in Fisheries, University of British Columbia, Vancouver.
- Contor, C. R., and J. S. Griffith. 1995. Nocturnal emergence of juvenile rainbow trout from winter concealment relative to light intensity. *Hydrobiologia* 299:178–183.
- Cunjak, R. A., and R. G. Randall. 1993. In-stream movement of young Atlantic salmon (*Salmo salar*) during winter and early spring. Canadian Special Publication of Fisheries and Aquatic Sciences 118:43–51.
- Emmett, B., G. M. Kruzynski, and I. K. Birtwell. In press. The use of a pulp mill effluent mixing zone during winter by juvenile chinook salmon in the Fraser River at Prince George, British Columbia. Canadian Manuscript Report of Fisheries and Aquatic Sciences.
- Fontaine, B. L. 1987. An evaluation of the effectiveness of instream structures for steelhead trout rearing habitat in the Steamboat Creek basin. Master's thesis. Oregon State University, Corvallis.
- Glova, G. J. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and coastal cutthroat trout (*Salmo clarki*) in a laboratory stream. *Hydrobiologia* 132:155–168.
- Gregory, J. S., and J. S. Griffith. 1996a. Winter concealment by subyearling rainbow trout: space size selection and reduced concealment under surface ice and turbid water conditions. *Canadian Journal of Zoology* 74:451–455.
- Gregory, J. S., and J. S. Griffith. 1996b. Aggressive behaviour of underyearling rainbow trout in simulated winter concealment habitat. *Journal of Fish Biology* 49:237–245.
- Griffith, J. S., and R. W. Smith. 1993. Use of winter concealment cover by juvenile cutthroat trout and brown trout in the South Fork of the Snake River, Idaho. *North American Journal of Fisheries Management* 13:823–830.
- Griffith, J. S., and R. W. Smith. 1995. Failure of submersed macrophytes to provide cover for rainbow trout throughout their first winter in the Henrys Fork of the Snake River, Idaho. *North American Journal of Fisheries Management* 15:42–48.
- Hartman, G. F. 1963. Observations on behavior of juvenile brown trout in a stream aquarium during winter and spring. *Journal of the Fisheries Research Board of Canada* 20:769–787.
- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). *Journal of the Fishery Research Board of Canada* 22:1035–1081.
- Heggenes, J., O. M. W. Krog, O. R. Lindas, J. G. Dokk, and T. Bremnes. 1993. Homeostatic behavioural responses in a changing environment: brown trout (*Salmo trutta*) become nocturnal during winter. *Journal of Animal Ecology* 62:295–308.
- Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. *Transactions of the American Fisheries Society* 116:185–195.
- Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence, Wisconsin. *Journal of the Fisheries Research Board of Canada* 26:1473–1483.
- Johnson, J. H., and P. A. Kucera. 1985. Summer–autumn habitat utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. *Canadian Journal of Zoology* 63:2283–2290.
- Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *Journal of Wildlife Management* 40:775–788.
- McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:1551–1557.
- Meyer, K. A. 1995. Experimental evaluation of habitat use and survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. Master's thesis. Idaho State University, Pocatello.
- Montgomery, D. C. 1991. Design and analysis of experiments, 3rd edition. Wiley, New York.
- Nickelson, T. E., J. D. Rodgers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile coho salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:783–789.
- Noakes, D. L. G. 1980. Social behaviour in young charrs. Pages 683–701 in E. K. Balon, editor. *Charrs: salmonid fishes of the genus Salvelinus*. Dr W. Junk, The Hague, The Netherlands.
- Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian, and biotic conditions. U.S. Forest Service General Technical Report INT-138.
- Riehle, M. D., and J. S. Griffith. 1993. Changes in habitat use and feeding chronology of juvenile rainbow trout at the onset of winter in Silver Creek, Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 50:2119–2128.
- Rimmer, D. M., U. Paim, and R. L. Saunders. 1983. Autumnal habitat shift of juvenile Atlantic salmon (*Salmo salar*) in a small river. *Canadian Journal of Fisheries and Aquatic Sciences* 40:671–680.
- SAS Institute. 1987. SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, North Carolina.
- Seelbach, P. W. 1987. Effect of winter severity on steelhead smolt yield in Michigan: an example of the

- importance of environmental factors in determining smolt yield. Pages 441–450 in M. J. Dadswell and five coeditors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Smith, R. W., and J. S. Griffith. 1994. Survival of rainbow trout during their first winter in the Henrys Fork of the Snake River, Idaho. Transactions of the American Fisheries Society 123:747–756.
- SPSS. 1985. SPSS user's guide, edition 2. McGraw-Hill, New York.
- Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452–461.
- USGS (U.S. Geological Survey). 1995. Water resources data for Idaho, water year 1994. USGS Water-Data Report ID-94, Boise, Idaho.
- Young, M. K. 1995. Telemetry-determined diurnal positions of brown trout (*Salmo trutta*) in two south-central Wyoming streams. American Midland Naturalist 133:264–273.