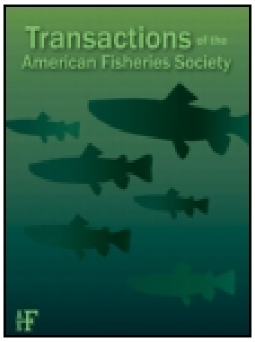

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Transactions of the American Fisheries Society

ISSN: 0002-8487 (Print) 1548-8659 (Online) Journal homepage: http://afs.tandfonline.com/loi/utaf20

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To cite this article: R. W. Smith & 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, 123:5, 747-756, DOI: 10.1577/1548-8659(1994)123<0747:SORTDT>2.3.CO;2

To link to this article: http://dx.doi.org/10.1577/1548-8659(1994)123<0747:SORTDT>2.3.CO;2

Transactions of the American Fisheries Society 123:747–756, 1994

Survival of Rainbow Trout during Their First Winter in the Henrys Fork of the Snake River, Idaho

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Abstract.—To evaluate their first-winter survival, wild rainbow trout *Oncorhynchus mykiss* (78–169 mm total length) were placed in small wire-mesh cages at four sites along a thermal gradient in the Henrys Fork of the Snake River in October 1989. Four cages at each site contained cobble rock cover and four had no cover. Our hypotheses were that test fish would have better survival if cover were available or if water temperatures were higher at the site, and that larger fish would have better survival than the smaller fish of the test group. Survival ranged from 100% at a spring-fed site to 63% at the coldest site. In the cages checked periodically, 95% of the mortality occurred during early winter and no mortality occurred during late winter. Survival was 11–24% higher in cages with cover than in those without cover; and was higher for larger fish than for smaller ones. Fish smaller than 100 mm in October did not survive the winter. Water temperature in spaces among cobble rock cover in the cages was 0.2–1.0°C higher throughout winter than in the overlying water. Survival rates of the test fish in the colder sites were probably higher than those of free-living wild fish in the study area because the cages protected test fish from predators and shifting ice.

The winter ecology of stream-dwelling salmonids is not well understood. Research to define the aspects of the habitat that are critical to winter survival is of great interest to fisheries biologists (Marcus et al. 1990). Such information, coupled with an understanding of "normal" mortality rates, might identify new management options for fish populations whose winter survival is suboptimal.

Recent observations by Campbell and Neuner (1985), Cunjak and Power (1986), Contor (1989), and Heggenes et al. (1993) suggest that juvenile trout have winter habitat requirements and mortality factors that differ substantially from those of adult trout. Here we limit our analysis to survival during the first winter. We summarized population studies of wild salmonids in streams that remained near 0°C for prolonged periods and were not affected by winter floods (Needham et al. 1945; McFadden 1961; Hunt 1969; Alexander 1979; Bustard 1986; Everest et al. 1986; Seelbach 1987). In combination, these studies incorporated a total of 24 population estimates, and the overall average survival of the salmonids during their first winter was 49.8% (SD = 18.0%).

Multiple-year studies for an individual population indicated that survival rates vary greatly among years. For brown trout *Salmo trutta* in Convict Creek, California, first-winter survival was 15–84% over four successive winters (Needham et al. 1945). Survival of brook trout *Salvelinus fontinalis* during their first winter in spring-fed Lawrence Creek, Wisconsin, was 35–73% over 11 successive winters (Hunt 1969). In Carnation Creek, a British Columbia stream subject to winter floods, first-winter survival of coho salmon *Oncorhynchus kisutch* ranged from 16 to 84% during 1970–1987 (Holtby 1988; Hartman and Scrivener 1990).

Such variability in survival among winters suggests that a number of factors are causing mortality. Previous studies (Hunt 1969; Seelbach 1987; Holtby 1988) noted that survival rates appeared to be independent of initial fish density. In this study we evaluated cover availability, water temperature, and fish size. Cover consisting of interstitial spaces in cobble or boulder substrate (Hartman 1965; Chapman and Bjornn 1969) and woody debris and undercut banks (Bustard and Narver 1975) is a key attribute of daytime winter habitat for juvenile salmonids in stream environments. When midday water temperatures drop below about 8°C, juvenile salmonids commonly begin moving deep into this cover (Chapman and Bjornn 1969), sometimes penetrating 15–30 cm beneath the substrate surface (Everest 1969). We have referred to this behavior as concealment (Griffith and Smith 1993). In winter, juvenile salmonids are most abundant in areas with unembedded substrate (Bjornn 1971; McMahon and Hartman 1989), especially where it occurs along stream margins (Contor 1989; Griffith and Smith 1993). The addition of cobble clusters to sections of an Idaho stream where cover was previously not available resulted in an eightfold increase in the number of juvenile chinook salmon *Oncorhynchus tshawytscha* in those sections in winter (Hillman et al. 1987). Although these and other studies indicate that cover quality affects the distribution and abundance of juvenile salmonids in winter, direct observations of survival or mortality in specific cover types have not been made.

Low water temperature might influence winter survival of juvenile salmonids. In Lawrence Creek, Wisconsin, Hunt (1969) found a significant positive correlation over five winters between first-winter survival of brook trout and the number of hours in January during which water temperature exceeded 4.5°C. A similar but nonsignificant trend was noted between survival and the number of hours above 4.5°C throughout the entire winter. In the Little Manistee River, Michigan, second-winter (but not first-winter) mortality of steelhead *Oncorhynchus mykiss* was significantly correlated with the number of days during which minimum air temperature was less than or equal to −12°C (Seelbach 1987).

For many nonsalmonid fishes, larger members of a cohort survive their initial winter better than do smaller individuals (Toneys and Coble 1979). For salmonids, a size effect has been shown under hatchery conditions by Lindroth (1965) and Pickering and Pottinger (1988), but not by Toneys and Coble (1980). Data from 11 winters indicated that first-year survival of wild brook trout in Lawrence Creek tended to increase with an increase in mean fish length in late fall (Hunt 1969). Holtby (1988) and Hartman and Scrivener (1990) noted a similar pattern for juvenile coho salmon in Carnation Creek, British Columbia, in 1970–1987.

The objective of this study was to assess survival of wild rainbow trout (nonanadromous *O. mykiss*) during their first winter in cages along a thermal gradient in the Henrys Fork of the Snake River. We defined winter as the period during which rainbow trout in the study area adopted concealment behavior, which typically occurred at water temperatures below 8°C (Contor 1989). We tested the hypotheses that the test fish would survive better during winter if cover was available or if water temperatures were higher at the site, and that larger fish would survive better than the smaller members of the test group.

Study Area

A fourth-order reach of the Henrys Fork of the Snake River, Fremont County, southeastern Idaho, from immediately below the Island Park Dam (44°25'N, 111°24'W) at a river elevation of 1,896 m and to 19.2 km downstream, was used as the study reach. Discharge from the dam increased from 5.5 to 10.4 $m^3 \cdot s^{-1}$ during the study period, October 1989 through March 1990 (USGS 1990–1991), and was supplemented by a relatively constant discharge of 6.0 $m^3 \cdot s^{-1}$ from the Buffalo River, which enters immediately below the dam. Channel width was 60–105 m and gradient was 0.12–0.45%.

Study sites were located along the thermal gradient that was created as water released from the hypolimnion of Island Park Reservoir gradually cooled. The Box Canyon site was approximately 1 km below Island Park Dam; no ice formed at this site during the study period. At the Last Chance site, 8 km below the Island Park Dam, surface ice formed along the banks during a few days in January and during much of February 1990. The Cold Springs site was 18.9 km below the Island Park Dam in a spring-fed (approximately 0.3 $m^3 \cdot s^{-1}$) pool along the river's edge. No ice formed at the site. At the Harriman East site, 19.2 km below the Island Park Dam, surface ice as thick as 30 cm covered much of the site during late December and most of January and February.

Methods

Experimental Design

Eight cages holding wild rainbow trout were placed in each of the four study sites. Because of the potential for damage from drifting ice and debris, cages in the Box Canyon, Last Chance, and Harriman East study sites consisted of 5-mm-mesh galvanized screen attached to a triangular angle-iron frame; each side was 2 m long and 1 m deep, and thus the area enclosed was 1.5 m^2. Rectangular cages of similar material were used at the Cold Springs study site, which was not subject to ice formation. The tops of all cages were covered with a screen of 2.5-cm wire mesh to exclude predators. Because of the erodible nature of the fine sand and silt substrate at the Harriman East site, floors of galvanized wire mesh were added to those cages. At the other study sites, the lower edges of the cage sides were buried to a depth of 5–10 cm in the substrate. To provide additional protection from drifting ice and debris, deflectors (panels of 5 × 15-cm wire mesh held in place by steel fence posts driven into the substrate) were placed perpendicular to the flow, 10 m above the Last Chance and Harriman East cage sites.

Cages were placed along the stream margin at locations where water velocity through them was 12–20 $cm \cdot s^{-1}$, which is within the range used by juvenile rainbow trout at night in winter in the study area in 1986–1987 (3–20 cm·s^{-1}: Contor 1989). Water depth in all cages was 33–43 cm at the start of the study. One layer of 10–40-cm-diameter cobble (following the classification of Helm 1985) was placed in four randomly selected cages at each site to provide cover. In addition, 1–3-cm-diameter gravel was placed to a depth of 4 cm in cages located in areas without a gravel substrate. Debris was removed from the wire mesh and water velocity was checked two to three times per week, except at the Harriman East site while it was ice covered.

Age-0 rainbow trout were obtained from the Box Canyon and Last Chance study sites with backpack and boat-mounted electrofishing gear. Fish tested in the Box Canyon cages were obtained from that site, and those placed in cages at the other sites were caught at Last Chance. Fish were weighed to the nearest 0.1 g and measured to the nearest millimeter (all fish lengths are given as total lengths). Also, distinguishing coloration, parr marks, and other marks were noted to aid subsequent recognition of individual fish. We placed 15 fish in each cage on 21 October 1989, when midday water temperatures were approximately 6°C. The resulting density in each cage (10 fish·m^{-2}) was typical of the density we observed by snorkeling at night adjacent to high-quality cover in the study area during the winter of 1988–1989 (range, 4–14 fish·m^{-2}; mean, 10.2; Smith 1992), and was higher than the maximum of 8.6 fish·m^{-2} observed there in 1986–1987 by Contor (1989). Fish averaged 125 mm in length (range, 78–169 mm). Rainbow trout in this size range had been identified as age 0 in studies done in previous years at this reach (Angradi and Contor 1989). We confirmed the age estimate by examining scales from all fish larger than 150 mm. Fish were selected for each cage-group so that there was no significant difference in average length of fish among sites (analysis of variance, ANOVA; $P > 0.05$) or between sets of cover and noncover cages at each site (t-test; $P > 0.05$).

Fish survival was evaluated at the end of 7-week intervals in early winter (8 December 1989), midwinter (26 January 1990), and late winter (16 March 1990). At the end of early winter and midwinter, fish from four of the eight cages at each study site (from two cages containing concealment cover and from two cages without cover) were removed from the cages by a combination of dip netting and electrofishing and used to assess survival. Fish were removed from all cages at the end of late winter. We were able to identify each survivor and establish its initial (October) length and weight. Following Cone (1989), we used analysis of covariance (ANCOVA), Tukey's test, and the t-test to compare the slopes and elevations of length–weight regressions of test fish that died with those of fish that survived the winter. The same procedure was used for data on survivors: slopes and elevations of length–weight regressions based on October size data were compared with those of regressions based on March size data.

Two cages in Box Canyon containing cover were disturbed during early winter and some or all fish escaped from them. Data from those cages were not included in the analysis. Also, during the end of early winter, water level at the Cold Springs site fell enough to partly expose the rock in two of the cover cages. As a result, water temperatures in spaces in the rocks averaged 2–4°C lower than in the other Cold Springs cages and 14 of the 30 fish died during early winter. Fish from these two cages were not used in data analysis. Because of these missing data, we evaluated the effects of cover availability and water temperature (site) on survival (arcsine-transformed data from the 28 individual cages) with an analysis of variance (ANOVA) that nested cover within site.

We compared the length–weight relationships of caged fish at Box Canyon on 8 December and of caged fish at Last Chance on 16 March with those of free-ranging fish captured at those sites on those dates (group comparison t-test). Too few free-ranging rainbow trout were caught at the Harriman East and Cold Springs sites to permit a similar comparison there.

Monitoring of Temperatures

Temperatures were monitored with data loggers (Campbell Scientific models CR-10 and 21X) and thermocouples accurate to ±0.05°C at Box Canyon, Last Chance, and Harriman East. Each thermocouple was calibrated against a National Bureau of Standards reference thermometer at 0, 4, and 8°C in a PolyScience series 730 recirculating-water bath; data-logger program corrections were made as required for each thermocouple. At the conclusion of the study, each thermocouple was rechecked against the reference; all had remained in calibration. At the Box Canyon, Last Chance, and Harriman East sites, temperatures in one randomly selected cage were measured in the water column a few meters outside the cage; in the water column in the cage; and in the interstitial space among the cobbles in the center of the cage, about

TABLE 1.—Water temperatures (mean, and instantaneous minima and maxima) and maximum accumulated thermal units (ATU) in cages at three sites on the Henrys Fork of the Snake River, winter 1989–1990.

Variable	Box Canyon	Last Chance	Harriman East
	Water column		
Temperature (°C)			
Mean	4.4	2.2	0.8
Minimum	3.1	0.0	−0.8
Maximum	5.4	7.5	8.8
ATU	730	591	432
	Interstitial space		
Temperature (°C)			
Mean	4.8	2.5	1.5
Minimum	3.1	0.6	−0.4
Maximum	5.5	7.5	8.8
ATU	757	788	467

3 cm above the natural substrate. Air temperature was monitored at each data logger. Temperature data were recorded every 60 s, and 60 consecutive values were combined into an hourly average that was stored by the data logger. Water column temperatures in the cages were used in the analysis of the effects of temperature on survival of the test fish. Maximum accumulated temperature units (ATUs) at Box Canyon, Last Chance, and Harriman East were calculated for the study period by summing daily degrees above 0°C, based upon daily maximum temperatures.

At Cold Springs, temperature was checked twice daily, 2–3 d/week, with a handheld thermometer (Miller and Weber, Inc., SURFACE-TEMP model, accurate to ±0.1°C) and occasionally with a maximum–minimum thermometer. The observed daily maxima ranged only from 6.6 to 7.1°C, and we estimated ATUs based upon those values.

Results

Water Temperature

Mean water column temperatures within the cages were the same as those outside the cages at the Cold Springs site, but were significantly lower (*t*-test, $P \leq 0.01$) in the cages than outside the cages at Box Canyon (0.1°C lower) and at Last Chance and Harriman East (0.2°C lower). When air temperature dropped to −28°C on 15–16 February 1990, supercooled temperatures were recorded for several hours in cages at the two colder sites (Table 1). Temperatures as low as −0.1°C were concurrently recorded outside the cages at Harriman East.

Mean water column temperatures in the cages (6.5°C at the Cold Springs site, 4.4°C at Box Canyon, 2.2°C at Last Chance, and 0.8°C at Harriman East) were significantly different from one another (ANOVA; $P \leq 0.01$). Instantaneous-minimum water column temperatures during the study were 3.1, 0, and −0.8°C at the latter three sites, and these minima were all recorded in February. Instantaneous maxima were reached in March and ranged from 5.4 to 8.8°C among the three sites (Table 1). Maxima for December–February were 5.1, 4.5, and 3.1°C at those sites. Maximum ATUs for the water column were highest in the Cold Springs (972), followed by Box Canyon (730), Last Chance (591), and Harriman East (432).

Temperatures in interstitial spaces among cobbles were significantly higher (*t*-test; $P \leq 0.01$) than water column temperatures both within and outside the cages for the overall study period, and this difference was greater at the colder sites (Table 1). In cages, mean interstitial space temperature was 0.2–0.6°C higher than water column temperature at any given time in January–March at Box Canyon, 0.2–0.7°C higher at Last Chance, and 0.8–1.0°C higher at Harriman East. Twenty spot measurements at Cold Springs showed no difference between interstitial space and water column temperatures. Maximum ATUs in spaces among cobbles were 4% higher than water column ATUs at Box Canyon, 33% higher at Last Chance, and 8% higher at Harriman East (Table 1).

Survival of Rainbow Trout

In the four cages at each site that were checked every 7 weeks, 95% of the 37 rainbow trout that died did so during early winter, and the remaining 5% of the deaths occurred during midwinter (Figure 1). No mortality occurred during late winter. At the end of the study, there was no significant difference in survival between fish that had been temporarily removed from cages at the end of early winter and midwinter by electrofishing and dipnetting and those that had not been disturbed (chi-square; $P > 0.05$).

All fish at the Cold Springs site survived the study (Table 2). Survival to the end of late winter for all cages combined at the other sites was influenced by water temperature, cover availability, and fish size at the onset of winter. Survival differed significantly among sites (ANOVA; $P \leq 0.0001$) and was higher at warmer sites. For all cages combined, winter survival was 81% at Box Canyon, 82% at Last Chance, and 63% at Harriman East (Table 2). At the four sites, arcsine-transformed percent survival was positively correlated with the number of ATUs in the water

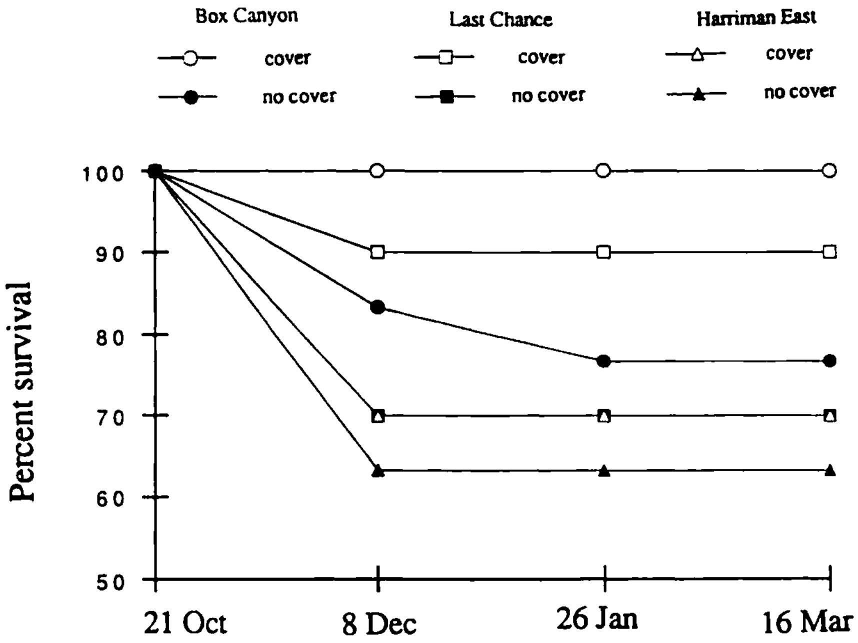

FIGURE 1.—Percent survival of rainbow trout in two cages containing cobble cover and two cages without cover at each of three sites on the Henrys Fork of the Snake River, 1989–1990. Fish were placed in cages on 21 October and checked for survival on the other dates given here.

column (r^2 = 0.94) and in space among cobbles (r^2 = 0.86).

Overall (data from all four sites combined), rainbow trout survival within a site was significantly greater in cages with cover than in cages without cover (ANOVA; $P \leq 0.001$). Survival of test fish at Box Canyon, Last Chance, and Harriman East was 11–24% greater in cages with cover (Table 2). Survival averaged 86% for fish in cages with cover and 76% in cages without cover (Table 2).

Combined data from cages with and without cover at the three colder sites indicated that survival varied according to length of the fish at the beginning of the study (Figure 2). None of the 20 rainbow trout survived that were smaller than 100 mm in October. Survival of 130–160-mm fish exceeded 90%. Of the four fish larger than 160 mm, three (all in cages without cover at the coldest site) died. Fish that were longer than the average of 125 mm for all test fish in October had significantly higher survival through late winter than did fish that were smaller than the average (combined data from cover and no-cover cages; t-test; $P \leq 0.05$). Survival of the smaller fish (mean length, 104 mm) was 76% at Box Canyon, 76% at Last Chance, and 48% at Harriman East. For the longer fish (mean length, 133 mm), survival was 81, 82, and 94% at these sites.

Among the three sites where mortality oc-

TABLE 2.—Survival from late fall to the end of late winter, 1989–1990, for 420 rainbow trout in cages containing or not containing cobble cover at sites on the Henrys Fork of the Snake River.

Study site	Initial number in cages: With cover	Initial number in cages: Without cover	Number (%) surviving at end in cages: With cover	Number (%) surviving at end in cages: Without cover	Number (%) surviving at end in cages: Overall
Cold springs	30[a]	60	30 (100)	60 (100)	90 (100)
Box Canyon	30[a]	60	29 (97)	44 (73)	73 (81)
Last Chance	60	60	54 (90)	44 (73)	98 (82)
Harriman East	60	60	41 (68)	34 (57)	75 (63)
All	180	240	154 (86)	182 (76)	336 (80)

[a] Excludes two cages that were disturbed or partly exposed.

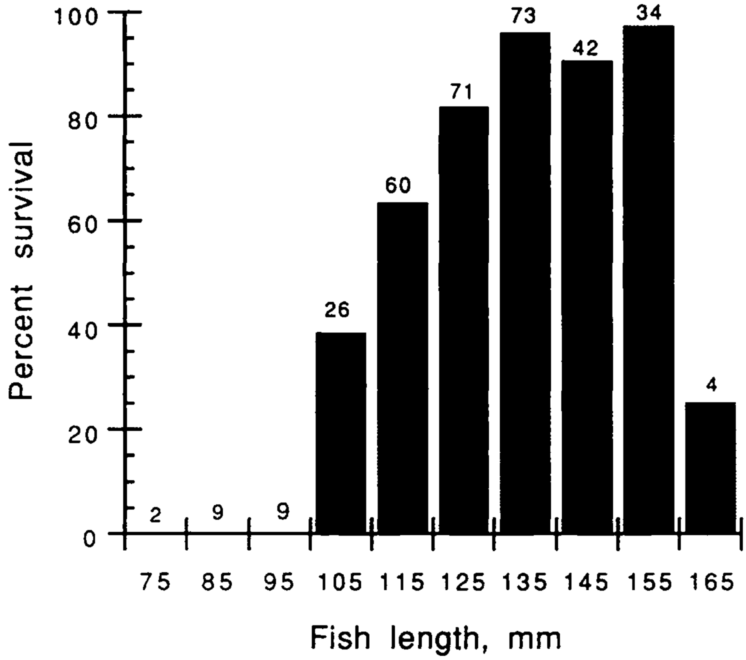

FIGURE 2.—Percent survival from late fall to the end of late winter, 1989–1990, for rainbow trout, by 10-cm total-length intervals, in cages at the Henrys Fork of the Snake River (all sites combined). Size-groups are indicated by their midpoints. Sample sizes are given at the top of each bar.

curred, the October length–weight relationships of fish that survived the winter were significantly different (ANCOVA; $P \leq 0.001$) in both slope and elevation from those of fish that died. Within a site, survivors were typically heavier per unit of length than were those that died (Figure 3). Fish that died at the colder sites were heavier per unit length than those that died at the warmer sites.

The length–weight relationship of 39 free-ranging rainbow trout collected in the river adjacent to the Last Chance site on 8 December 1989 was not significantly different (t-test; $P > 0.05$ for both slope and elevation) from that of caged fish at the same site on that date. There was also no significant difference in the length–weight relationships of 27 free-ranging fish collected at Box Canyon on 16 March 1990 and the caged fish at Box Canyon.

Discussion

Our results indicate that the early part of winter was critical to the first-winter survival of caged Henrys Fork rainbow trout. Nearly all mortality occurred during the initial 7 weeks of this study, and virtually all survivors of early winter survived the remainder of winter, even though temperatures then were coldest. These findings are consistent with observations by Gardiner and Geddes (1980), who noted that Atlantic salmon *Salmo salar* lost weight particularly during the first half of their first winter in a stream in England. A metabolic deficit hypothesis was developed by Cunjak et al. (1987) and Cunjak and Power (1987), who showed that during early winter, trout underwent physiological changes that resulted in declining body condition and depletion of lipid reserves. Cunjak et al. (1987) hypothesized that brook trout exposed to decreasing water temperatures experience a metabolic deficit that cannot be offset by net energy intake and forces them to use lipid reserves to maintain metabolic functions. Depletion of lipid reserves would lower body condition and cause some mortality in early winter.

Mortality of Henrys Fork fish was greater at the colder sites, as was expected from previous studies that correlated survival over several years with winter severity. Hunt (1969) found a significant positive correlation over five winters between first-winter survival of brook trout in Lawrence Creek, Wisconsin, and the number of hours in January during which water temperature exceeded 4.5°C. Based on 3 years of data, second-winter mortality of steelhead in the Little Manistee River, Michi-

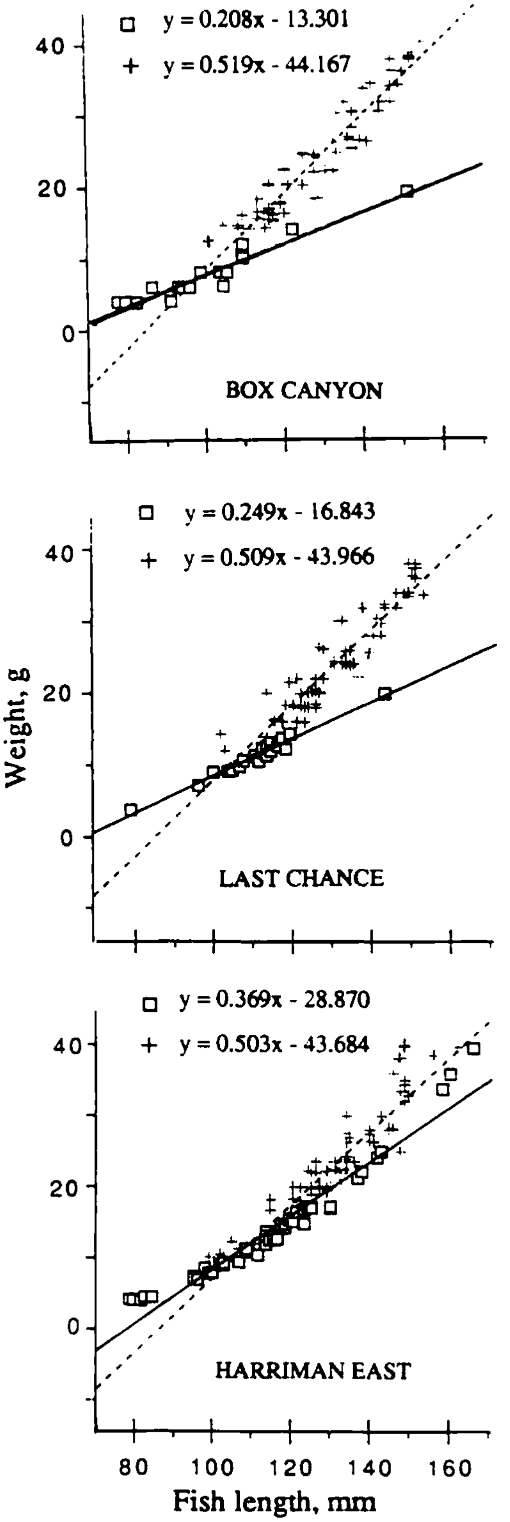

FIGURE 3.—Total lengths and weights, in October, of rainbow trout that died (boxes and solid lines) and those that survived the winter (crosses and dashed lines) in cages at three sites on the Henrys Fork of the Snake River ($r^2 > 0.88$ for each regression).

gan, was significantly correlated with the number of days during which minimum air temperature was less than or equal to −12°C (Seelbach 1987). No such correlation was noted by Seelbach for first-winter mortality, however, and this inconsistency emphasizes the complexities of the relationships and the need for additional study. For example, if early winter mortality is a widespread occurrence, an index of the severity of early winter should be a more effective predictor of survival than indices like those of Hunt (1969) and Seelbach (1987), which are based on mid and late winter temperatures.

The availability of cobble cover had a significant effect on survival in our cages, and cages may not have fully tested that effect. At Last Chance and Harriman East, cages that contained no rock accumulated loose, fine sediment in their corners. Test fish were never visible in these cages during the study, and we believe that some buried themselves in the sediment, perhaps increasing their survival.

Streams such as the Henrys Fork that have the type of cover that enables fish to conceal themselves during the day appear to provide several winter survival benefits. Fish might avoid physical damage from the collapse of shelf ice and stranding as anchor ice melts and water level drops (Needham and Jones 1959), as well as predation and the daytime expenditure of energy. This study suggests that interstitial spaces also provide a thermal benefit for fish. At the Henrys Fork sites, with the exception of the Cold Springs site, which is spring fed, temperatures in the interstices of cobble introduced into cages followed the same pattern as those in the water column, but were higher than the water column temperatures. Similar differences between stream and intragravel temperatures have been noted outside the cages in the study area (R. W. Smith, unpublished data), in streams in British Columbia and Alaska (Shepherd et al. 1986), and in streams in Michigan (White et al. 1987).

Winter cover for juvenile salmonids has been shown (e.g., Everest et al. 1986) to be limited in quantity in some streams. Nickelson et al. (1992) concluded that the production of wild coho salmon smolts in Oregon streams where spawning escapement was adequate was probably limited by the availability of adequate winter habitat. Furthermore, such habitat is vulnerable to sedimentation and, in streams that are regulated or partially dewatered, this habitat is also vulnerable to low winter flows.

Rainbow trout entering their first winter in the study area are typically larger than their counterparts in many streams and larger than members of other salmonid species. Nevertheless, we found that the smaller members of the cohort (fish < 125 mm long in October) had higher mortality than did larger fish and those smaller than 100 mm did not survive. Hunt (1969) noted, on the basis of data from 11 winters, that first-winter survival of brook trout in Lawrence Creek reflected their mean length ($r^2 = 0.69$). Holtby (1988) observed a similar trend for Carnation Creek coho salmon (data from 17 winters total; $r^2 = 0.83$). Hunt (1969) saw no indication that size-specific survival was a result of smaller fish being more vulnerable to predation.

The susceptibility of smaller members of a cohort to winter mortality may be due to their relatively high weight-specific basal metabolism (Shuter and Post 1990) and their apparent lack of a correspondingly high capacity to store energy. Mason (1976) found that the smaller members of a coho salmon cohort in a Vancouver Island stream lost 60–65% of their lipid reserves in the early and middle portions of their first winter, whereas larger fish lost only 20–25% of theirs.

Henrys Fork test fish that survived the winter typically weighed more per unit of length in October than those that did not survive. We did not analyze Fulton's condition factors (K) for the test fish because of potential biases identified by Cone (1989). However, for comparison with previous studies, our test fish died if their late-fall K values ($10^5 \times$ [mean weight, g]/[total length, mm]^3) were below 0.82 in the Harriman East site, below 0.79 at Last Chance, and below 0.77 at Box Canyon (Smith 1992).

We believe that our study underestimated the first-winter mortality of free-living rainbow trout in the study portion of the Henrys Fork. The caged test fish were protected from predators such as common mergansers *Mergus merganser* and river otters *Lutra canadensis*, which were observed throughout the winter in the study area and may be an important cause of winter mortality for small trout (Alexander 1979; Bustard 1986). The cages also protected fish from shifting ice, which may be another major cause of winter mortality (Needham and Jones 1959). On the other hand, fish were prevented from moving to more favorable habitat. From other observations (Contor 1989; J. S. Griffith, unpublished data), we believe that the cages containing cover represented quality habitat that would have been occupied in the study area throughout a typical winter. Free-living fish would not have been expected to occupy habitat similar to that in the cages without rock cover.

The cages might have increased mortality if they excluded critical food resources that were available to unrestrained rainbow trout. Riehle and Griffith (1993) found that rainbow trout fed on invertebrates at night during their first winter at water temperatures of 1–4°C in Silver Creek, Idaho. Stomach flushing of other caged rainbow trout at Box Canyon and Last Chance in October 1989 and February 1990 indicated that these fish were feeding at night, primarily on emerging midges (Chironomidae) (Smith 1992). Mean wet weights of stomach contents averaged 1.3% of fish body weight in October and 2.4% in February. Although these values were not significantly different from those of fish collected outside the cages (Smith 1992) and were similar to the values of 0.8% found in October and 2.1% in January at Silver Creek by Riehle and Griffith (1993), we cannot eliminate limited food availability as a possible source of bias.

Our use of electrofishing to collect and periodically monitor test fish did not increase mortality. All fish at the Cold Springs site survived repeated electrofishing, and there was no significant difference in survival between groups of fish that had been removed from and placed back into cages at the end of early winter and midwinter and those that had not been disturbed.

Our study was conducted during a winter that was normal for the study area in terms of severity. Results showed the importance of cover, water temperature, and fish size as determinants of survival. Tests conducted over a wider variety of conditions with larger enclosures, or in isolated stream sections where fish are exposed to predators and shifting ice, would more fully assess the effects of cover and early-winter conditions.

Acknowledgments

The Idaho State Board of Education funded this study through its Higher Education Research Council. We thank Jim Gregory for valuable field assistance. Charles Peterson, Bruce Eshelman, Kevin Meyer, and Rick Wilkison assisted in data analysis. The Harriman State Park of Idaho provided facilities and equipment, and the Henrys Fork Foundation provided a stimulating research environment. Reviews by Tom McMahon, Sam Loar, and Richard Cunjak greatly improved the manuscript.

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Received March 1, 1993
Accepted February 15, 1994