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First-winter survival of rainbow trout and brook trout in the Henrys Fork of the Snake River, Idaho

Kevin A. Meyer and J.S. Griffith

Abstract: We used caged fish with a cobble–boulder substrate to test the effect of fish size on first-winter survival of rainbow trout, *Oncorhynchus mykiss*, to compare survival of rainbow trout and brook trout, *Salvelinus fontinalis*, and to test for a temperature effect in each experiment. At the warmer site, over 90% of the rainbow trout in the size experiment survived the winter, and there was no significant difference between >90 and <90 mm fish. At the colder site, survival was 60% and all mortality occurred in fish <90 mm. Survival of brook trout (60%) was significantly less than that of rainbow trout (87%) but did not differ between the warmer and colder sites. Brook trout that survived were significantly larger than those that did not. Results suggest that size-dependent mortality may be more likely to occur when environmental conditions are more severe (e.g., lower temperatures, less suitable habitat). Rainbow trout experienced less mortality than brook trout when using cobble–boulder substrate as cover during their first winter; this may be the result of different winter-habitat preferences between the two species.

Résumé : Nous avons utilisé des poissons en cage sur un substrat de petits et de gros cailloux pour déterminer l'effet de la taille des poissons sur la survie au cours du premier hiver chez des Truites arc-en-ciel, *Oncorhynchus mykiss*, pour comparer la survie des Truites arc-en-ciel à celle des Ombles de fontaine, *Salvelinus fontinalis*, et pour déterminer l'effet de la température dans chacune de ces expériences. Au site le plus chaud, plus de 90% des Truites arc-en-ciel de l'expérience sur la taille ont survécu à l'hiver, et il n'y avait pas de différence significative de survie entre les truites de >90 mm et celles de <90 mm. Au site le plus froid, la survie a été de 60% et la mortalité affectait seulement les poissons de <90 mm. La survie des Ombles de fontaine (60%) était significativement plus faible que celle des Truites arc-en-ciel (87%), mais ne variait pas du site le plus froid au site le plus chaud. Les ombles qui ont survécu étaient significativement plus gros que ceux qui n'ont pas survécu. Les résultats indiquent que la mortalité est influencée par la taille surtout quand les conditions du milieu sont plus rigoureuses (e.g., températures plus basses, habitat moins approprié). Les truites ont subi moins de mortalité que les ombles lorsqu'elles ont utilisé le substrat de petits et de gros cailloux au cours de leur premier hiver; ce phénomène peut dépendre des préférences d'habitat différentes au cours de l'hiver entre les deux espèces.

[Traduit par la Rédaction]

Introduction

The winter ecology of stream-resident salmonids has received increasing attention in recent years. However, knowledge gaps exist regarding their behavior and ecology during winter (Marcus et al. 1990), including factors affecting survival during the first winter. There are numerous factors which may affect that survival, and of these, we examined the role of fish size and species and water temperature, using caged fish.

Smaller members of a cohort have relatively high mass-specific basal metabolic rate and lack a correspondingly high capacity to store energy (Shuter and Post 1990). Hence, smaller age-0 fish would be expected to exhaust stored energy reserves earlier and would be more vulnerable to starvation in winter. Nevertheless, there is contradictory evidence in the literature regarding size-related winter mortality in juvenile salmonids. Hunt (1969), Holtby (1988), and Smith and Griffith (1994) found positive relationships between mean length of fish at the onset of winter and subsequent

winter survival in field studies of juvenile brook trout, *Salvelinus fontinalis*, coho salmon, *Oncorhynchus kisutch*, and rainbow trout *O. mykiss*, respectively. However, in a laboratory study, Toneys and Coble (1980) found no size-related mortality in juvenile brook trout kept at temperatures of 2–4°C. We speculated that environmental conditions such as temperature severity and habitat suitability could have an influence on whether size-dependent mortality occurs.

Environmental factors might influence winter survival of species differently. Although studies have shown that habitat use by salmonids in winter may vary between species (Bustard and Narver 1975a, 1975b; Cunjak and Power 1986; Swales et al. 1987), direct comparisons of survival have not, to our knowledge, been made. In most streams, some habitat types may be limited or absent; in our study stream, concealment habitat that remains throughout the winter is essentially limited to cobble–boulder substrate (Griffith and Smith 1995). Since summer habitat preferences have been shown to differ between rainbow and brook trout (Cunjak and Green 1983, 1984), their winter preferences may also differ. We speculated that, if this was true, it could translate into differences in survival rates if cobble–boulder substrate was the only cover habitat present and it was more suitable cover habitat for one species than the other.

The objective of this study was to directly monitor first-

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winter survival of caged fish. The null hypotheses were that survival would not differ between small and large rainbow trout or between rainbow trout and equal-sized brook trout. These experiments are subsequently referred to as size and species experiments, respectively. The experiments were carried out at sites with two different water temperature regimes to additionally test for a temperature effect.

Methods

Experiments were conducted in cages in the Henrys Fork of the Snake River, a fourth-order stream at the study area (44°22'N, 111°23'W) located in Fremont County in southeastern Idaho. Discharge was mainly controlled by Island Park Dam, located 8 km upstream of the study area at a river elevation of 1876 m, and ranged from 13.4 to 21.7 m³ · s⁻¹ during the study period of November 1993 to March 1994 (U.S. Geological Survey 1994).

Two study sites were used for the experiments. At the Last Chance study site, the channel width averaged 90 m and the gradient was 0.31%. The substrate was gravel and midchannel areas contained aquatic macrophyte beds dominated by *Myriophyllum exalbescens* Kunth. and *Ranunculus aquatilis* L. Surface ice formation at Last Chance was infrequent, but a thin layer of ice occurred occasionally along the stream margin during the study period. The Harriman East study site was located 11.2 km downstream from Last Chance. The channel width averaged 105 m and the gradient was 0.12%. The substrate was gravel mixed with sand and silt, and *Elodea canadensis* Michx. was common in midchannel areas. Surface ice first formed on 26 November 1993, and covered the study site (up to 30 cm thick) for approximately one-third of the time from December to February.

Cages were constructed of 2.5-mm (size experiment) or 5-mm (species experiment) galvanized steel mesh attached to a triangular angle-iron frame with no top, and were placed within 5 m of the stream margin. Each side was 2 m wide and 1 m tall and the enclosed area was 1.5 m². The bottom of each cage, also covered with steel mesh, was filled with gravel and a layer of 15–40 cm diameter cobble–boulder substrate (cf. Platts et al. 1983), which we felt would provide more than enough interstitial spaces for concealment (Meyer and Griffith 1997).

Mean depth and velocity in the cages ranged from 19 to 30 cm and from 5 to 20 cm · s⁻¹, respectively. A staff gauge at Last Chance indicated that depth varied less than 8 cm all winter at this site. Because previous research using cages at the study sites showed that the mean relative stomach content wet masses for juvenile rainbow trout inside the cages did not differ from those for free-ranging juvenile rainbow trout outside the cages (Smith 1992), and velocities were adequate to cause small invertebrates, at least, to drift into the cages, supplemental feeding was not provided. Water temperature (hourly averages of 1-min recordings) was monitored at both sites using Campbell Scientific Model CR-10 dataloggers and thermocouples (accuracy ±0.05°C), but because of datalogger failure, complete temperature data for both sites were obtained only from late December to the end of the study.

For the size experiment, rainbow trout were electrofished from the river at Last Chance in areas adjacent to the cages. Rainbow and brook trout for the species experiment were electrofished along the stream margin from the Buffalo River, approximately 0.5 km upstream from its confluence with the Henrys Fork near Island Park Dam. They were measured to the nearest millimetre for total length and weighed to the nearest 0.25 g. Ten trout were added to each cage, for a density of 6.7 fish/m², within the range of 4–14 fish/m² that was previously observed in cobble–boulder habitat in this study area (Smith and Griffith 1994).

While conducting population estimates of free-ranging fish at Last Chance in October 1993, we estimated the mean size of age-0

rainbow trout to be approximately 86 mm (range 53–152 mm, SD = 19.2 mm, $n = 69$). During the winter of 1989–1990, no caged rainbow trout that were <100 mm in October survived the winter in the study area (Smith and Griffith 1994). However, mean fish length in October 1989 (125 mm) was nearly 40 mm greater than in October 1993 (Smith and Griffith 1994), in part because of below-normal temperatures during the summer of 1993. We speculated that the smaller size of the 1993 cohort would greatly reduce over-winter survival. Subsequently, for the size experiment, a total length of 90 mm was chosen as the separation between ‘‘large’’ and ‘‘small’’ fish, and cages were divided into three groups. One group held 10 small fish that averaged 72.7 mm (range 59–89 mm) in length, the second group contained 10 large fish that averaged 114.9 mm (range 90–152 mm), and the third group contained 5 fish in each size category that averaged 95.8 mm (range 60–145 mm). This design allowed some small fish to be separated from large fish to reduce a confounding effect that might have resulted from agonistic interactions, but also allowed other small and large fish to occur together as they would under natural conditions. Mean fish size was 94.9 mm and fish size in any one cage within each group did not differ from any other (ANOVA, $P = 0.99$). Four cages of each group were located at the Last Chance study site. The Harriman East study site contained four cages of the mixed-size group only.

In the species experiment, a fish of one species was matched within 1–2 mm with a fish of the other species, and five matched pairs were added to each cage. Both the Last Chance and the Harriman East study sites contained four cages. Mean fish length was 115.8 mm for both rainbow trout (range 87–146 mm) and brook trout (range 89–148 mm), and there was no significant size difference between cages (ANOVA, $P = 0.81$).

The experiments began on 14 November 1993, and survival was evaluated during three consecutive 7-week intervals ending on 29 December 1993 (early winter), 12 February 1994 (midwinter), and 27 March 1994 (late winter). During each evaluation the cobble–boulder substrate was removed from each cage and fish were captured with a dip net. Fish were weighed and measured and, after the cobble–boulder substrate was replaced, were returned to the cages. During early winter, floating ice and ice buildup caused damage to some cages at Harriman East, resulting in the removal of one species-experiment cage and all but one size-experiment cage from further analysis. This precluded statistical analysis to test for differences in survival between sites for the size experiment. Additionally, erosion at Last Chance under one species-experiment cage and two size-experiment cages resulted in gaps in the bottom through which fish might have escaped. These cages were removed from further analysis. For the size experiment, differences in survival between size categories at Last Chance were investigated using a Kruskal–Wallis one-way test. A Kruskal–Wallis two-way test was used for the species experiment, with species and site as the main factors. Both tests were performed on ranked percent survival data. A multiple regression model with indicator variables (Neter et al. 1989) was used to assess if length–mass regressions were different in slope or elevation at the onset of winter, at the onset versus the end of winter, and at the end of winter. Following Cone (1989), no log-transformations were made on the data, though a few regressions did appear to be slightly curvilinear. A Student's t test was used to assess differences in water-column temperatures inside the cages between sites. We used SAS (SAS Institute Inc. 1987) to perform all analyses.

Results

During periods when temperature was recorded at both sites, the water was significantly colder ($P < 0.0001$) at Harriman East than at Last Chance. Mean water column temperatures

Table 1. Percent survival of first year rainbow (RBT) and brook (BKT) trout in cages in the Henrys Fork of the Snake River, Idaho, in the winter of 1993–1994.

Cage variable				Percent survival in cages on:			
Study site	Species	Initial size (mm)	No. of cages	14 Nov.	29 Dec.	12 Feb.	27 Mar.
Size experiment							
LC	RBT	59–89	3	100	100	100	100
LC	RBT	90–152	4	100	98	98	95
LC	RBT	60–142	3	100	100	93	93
HE	RBT	65–132	1	100	60	60	60
Species experiment							
LC	RBT	87–146	3	100	93	87	87
HE	RBT	94–141	3	100	87	87	87
LC	BKT	89–148	3	100	60	53	53
HE	BKT	96–143	3	100	80	67	67

Note: LC, Last Chance; HE, Harriman East.

inside the cages for January, February, and March were 1.5, 1.8, and 4.3°C at Harriman East and 3.1, 3.1, and 4.3°C at Last Chance, respectively. The air temperature dropped to as low as –25°C in January and minimum water-column temperatures inside the cages were –0.5°C at Harriman East and 0.3°C at Last Chance.

Size experiment

At Last Chance, there was no significant difference ($P = 0.44$) in survival between large and small age-0 rainbow trout that were held separately (Table 1). Survival averaged 95% for cages with large rainbow trout, 100% for cages with small rainbow trout, and 93% for cages containing both large (87% survival) and small (100% survival) rainbow trout. In all cages, at least 8 of the 10 fish survived the winter. Twenty-five percent of the mortality occurred in early winter, 50% in midwinter, and 25% in late winter.

At Harriman East, 60% of the rainbow trout survived in the cage with both size categories (Table 1). All large rainbow trout survived, whereas only 1 of the 5 small rainbow trout survived. All mortality at Harriman East occurred during early winter.

The length–mass relationship for rainbow trout in the size experiment did not change significantly over the winter at Last Chance. The length–mass regressions did not differ significantly in slope ($P = 0.77$) or elevation ($P = 0.69$) at Last Chance between rainbow trout at the beginning versus the end of winter ($n = 194$). The small sample size (16), due to lost cages, hindered similar analysis at Harriman East, though the regressions were nearly significantly different for both slope ($P = 0.07$) and elevation ($P = 0.07$).

Species experiment

Brook trout survival averaged 60% and was significantly lower ($P = 0.002$) than for equal-sized rainbow trout, which averaged 87% in the species experiment (Table 1). There was no significant difference in survival for either species between Harriman East and Last Chance ($P = 0.35$). For brook trout, 80% of the mortality occurred during early

winter and 20% occurred in midwinter, while for rainbow trout 60% of the mortality occurred in early winter and 40% in midwinter. No fish of either species died during late winter. Brook trout that died (mean length 101 mm, range 89–114 mm) were smaller (t test, $P < 0.001$) than those that lived (mean length 124 mm, range 110–148 mm), and there was minimal overlap in their ranges. The limited mortality observed in rainbow trout precluded similar analysis for that species.

The length–mass regressions were not significantly different between brook trout and rainbow trout at the onset (slope, $P = 0.12$; elevation, $P = 0.20$; $n = 60$) or end (slope, $P = 0.11$; elevation, $P = 0.22$; $n = 44$) of winter. Brook trout that lived through the winter had a significantly different length–mass slope ($P = 0.0009$) and elevation ($P = 0.0006$) than fish that died during the winter ($n = 30$).

Discussion

In this study, we found evidence both supporting and opposing the occurrence of size-dependent mortality in both experiments, but we do not believe that the results conflict. In the size experiment, survival of rainbow trout at the warmer Last Chance site was high regardless of their size, but at Harriman East survival of small juvenile rainbow trout was lower than that of large fish. This difference between sites did not occur in the species experiment, but there were no small fish in that experiment (the smallest fish was 87 mm long). Under conditions where habitat is suitable and temperatures are higher, such as the test conditions for rainbow trout at the Last Chance study site, energy reserves in even the smallest members of a cohort might be adequate to allow them to successfully survive their first winter, whereas the lower temperatures experienced at Harriman East may have reduced the survival of the small rainbow trout located there. [Hunt \(1969\)](#) found a strong positive relationship over 5 years between the winter survival of juvenile brook trout and the number of hours that the water temperature was above 4.5°C during January. [Smith and Griffith \(1994\)](#) found that survival

of caged juvenile rainbow trout during winter was higher at study sites where the water temperature was relatively higher.

In the species experiment, survival was lower for brook trout than for rainbow trout, and brook trout that survived were larger than brook trout that died. It is unlikely that the higher mortality rate of brook trout was caused by temperatures exceeding their thermal tolerance. Survival of brook trout did not differ between sites, though water temperatures were markedly different. The temperature preference of brook trout may differ from that of rainbow trout (Coutant 1977; Peterson et al. 1979), but existing data are inconsistent between studies and vary between life stages of the same species.

Alternatively, it is possible that the reduced survival and size-dependent mortality experienced by brook trout resulted from their being restricted to cobble–boulder substrate for concealment. Although cobble–boulder substrate appears to be suitable concealment habitat for rainbow trout during winter (Campbell and Neuner 1985; Smith and Griffith 1994; Griffith and Smith 1995; Meyer and Griffith 1997), this might not be true for brook trout. Gibson (1978) observed that brook trout concealed themselves under rocks at winter temperatures in laboratory stream channels. However, Cunjak and Power (1986) found that although cobble–boulder substrate was available at some sites, brook trout were never observed concealing themselves there; instead, they were located in pools or concealed under banks or in woody material and aquatic plants or some other form of cover (Cunjak 1996).

During the summer juvenile brook trout tend to select areas with slower velocities than do juvenile rainbow trout (Cunjak and Green 1983), and to behaviorally dominate rainbow trout in such areas (Cunjak and Green 1984). Brook trout evolved in eastern North America in allopatry with Atlantic salmon, *Salmo salar*, whose microhabitat selection during winter parallels that of rainbow trout and consists mainly of cobble–boulder substrate in riffle-run areas (Rimmer et al. 1984; Cunjak 1988). The segregation of brook trout in low-velocity positions in pools and Atlantic salmon in high-velocity positions in riffles in sympatric conditions during the summer (Gibson 1966, 1978) is similar to the segregation seen between rainbow trout and brook trout during the summer (Cunjak and Green 1983). Pickering and Pottinger (1988) found that much of the winter mortality they observed in Atlantic salmon parr was due to chronic stress from nutritional deficiency, and suggested that meeting habitat requirements during winter may reduce the mortality rate. If cobble–boulder substrate is not suitable winter habitat for brook trout, their survival rate may be reduced when other forms of cover are lacking.

It is difficult to make a direct comparison between first-winter rainbow trout survival in 1989–1990 (Smith and Griffith 1994) and in our study because of the differences between years in experimental design, initial fish density, and initial fish size, and because of our incomplete water temperature data. Air temperatures, which can be used as an index of the severity of winter temperatures (e.g., Seelbach 1987), were similar between years; monthly means of maximum daily air temperatures were within 1.1°C between years during November–March. Nevertheless, while we appreciate the difficulty of directly comparing the two

studies, the smaller size of rainbow trout during our study did not result in reduced survival. Survival of rainbow trout in cages with cobble–boulder substrate was 90% at Last Chance and 68% at Harriman East in 1989–1990, compared with 96 and 60% (size experiment), respectively, at the same study sites in 1993–1994, when mean fish length was 40 mm less. Lindroth (1965) argued that a “smaller fish within a year-class is inferior to the ‘average fish’ in this same year class but, compared between year-classes, a smaller size does not necessarily reflect inferiority in general viability” because of differences in the environmental conditions being experienced each year. This reasoning contradicts the argument that winter mortality is a direct function of size-related metabolic rates (Shuter and Post 1990).

Our results lend further support to the importance of early winter as a critical period in first-winter survival of juvenile salmonids. For the two experiments combined, 68% of the mortality observed occurred in early winter and only 4% occurred during late winter. Furthermore, because cages were not in place until November, we may have missed additional mortality that could have occurred in early winter. Nevertheless, our data concur with those of Smith and Griffith (1994), who found that nearly all mortality of juvenile rainbow trout occurred during early winter, and with the early-winter metabolic deficit hypothesis developed by Cunjak et al. (1987) and Cunjak and Power (1987).

Our experiments used caged fish, which eliminated some of the factors that may influence the survival of free-ranging trout in the study area. In particular, the cages provided protection from in-stream predators (e.g., river otters, *Lutra canadensis*, mink, *Mustela vison*) and, we believe, from aerial predators (e.g., Common Mergansers, *Mergus merganser*, Belted Kingfishers, *Ceryle torquata*), owing to cage construction that restricted aerial maneuverability from above. The cages also protected fish from shifting ice, which may cause a large amount of mortality in the winter (Needham and Jones 1959). If our cages reduced the amount of food available to the fish in them, we could have increased the mortality. Since length–mass regressions did not change significantly over the course of the experiment, it is unlikely that fish were starving in the cages.

With the removal of the confounding influence of these factors, we believe that our results demonstrate the effects which fish size and species and temperature can have on the survival of juvenile trout during their first winter. Future research, conducted under both natural and experimental conditions, is needed to more fully assess how variables such as habitat suitability and availability, temperature, fish size, and ice independently affect winter survival, and interact to confound their influence. A better understanding of these relationships will help managers to recognize and protect important overwintering habitats of specific species.

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