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Seasonal Survival, Movement, and Habitat Use of Age-0 Rainbow Trout in the Henrys Fork of the Snake River, Idaho

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Abstract.—We quantified seasonal abundances, apparent survival rates, movements, and habitat use of age-0 rainbow trout *Oncorhynchus mykiss* in a 25-km reach of the Henrys Fork of the Snake River, Idaho, to determine what factors limit recruitment to the population. Natural production of rainbow trout occurred in each year of the study (1995–1997) and ranged from 158,000 to 306,000 age-0 fish each summer. No significant loss of age-0 rainbow trout occurred between summer and autumn; suitable habitat was present throughout the channel in all reaches and supported large abundances of age-0 rainbow trout through this period. The greatest losses (77–100%) occurred during winter and primarily involved fish from center-channel macrophyte beds. Most river sections, which had only simple bank habitat, did not support any age-0 rainbow trout through the entire winter. Overwinter survival was greatest (18–23%) in Box Canyon, a river section characterized by complex bank habitat, high gradient, and large substrate. Fish that were marked in river sections with simple bank habitat in autumn had moved to sections with complex bank habitat by the following spring. Winter habitat limits rainbow trout recruitment in the Henrys Fork.

Recruitment, the cumulative outcome or survival through a series of life stages (Trippel and Chambers 1997), of rainbow trout *Oncorhynchus mykiss* to the adult stage declined in the Henrys Fork of the Snake River, Idaho, during the 1980s and 1990s as judged by estimates of adult abundance (Van Kirk and Gamblin 2000). However, those estimates did not reveal the causes of this particular recruitment pattern or, because sampling was directed at adults, at what life stage the recruitment was limited. The abundance of adults depends necessarily on survival through early life stages, beginning with spawning and fertilization and extending through the juvenile life stage. Therefore, understanding year-class formation and changes in fish populations requires elucidation of the dynamics of early life history stages (Elliott 1994; Trippel and Chambers 1997), and sampling must be directed specifically at juveniles if inferences concerning juvenile abundances are to be made.

Griffith (1988) hypothesized that habitat restrictions limited overwinter survival, and therefore recruitment, of age-0 rainbow trout in the Henrys Fork. That supposition led to a series of studies examining the winter ecology of juvenile trout in this system. Juvenile rainbow trout were found to use cobble–boulder concealment cover along banks in winter and moved to these banks from midstream macrophyte beds as winter progressed and the macrophytes senesced (Contor 1989; Griffith and Smith 1995). Winter survival of age-0 rainbow trout was greater in cages with cobble–boulder substrate than in cages without cover (Smith and Griffith 1994) and also was more in cages at warmer than at cooler water temperatures (3.1–4.3°C versus 1.5–4.3°C; Meyer and Griffith 1997). Most mortality in cages was observed in early winter (95%; Smith and Griffith 1994) and was size dependent (Smith and Griffith 1994; Meyer and Griffith 1997). Although these studies supported Griffith's (1988) original hypothesis and led to a better understanding of the mechanisms possibly involved in limiting recruitment in the Henrys Fork, the studies were limited temporally and spatially, and the applicability of the cage experiments to riverwide recruitment was uncertain.

Our goal was to develop a comprehensive understanding of recruitment dynamics of age-0 rainbow trout in a 25-km reach of the Henrys Fork of the Snake River, with emphasis on determining what factor or factors limited recruitment in this population. Comprehensive evaluation of recruitment dynamics can be accomplished only by estimating temporal and spatial abundances of a cohort through its early life stages with sampling and analytical techniques directed specifically at those life stages. Concurrent estimation of seasonal survival

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and movement rates allows interpretation of these changes in abundance. Seasonal survival rates may be related to environmental conditions, and spatial changes may be related to the movement of juvenile fish as habitat availability and habitat requirements change. Therefore, an inclusive assessment of recruitment limitations should include the estimation of juvenile abundance, survival, movement, and habitat use across time and space. We quantified these aspects of three juvenile rainbow trout cohorts (1995–1997) in the Henrys Fork.

Study Area

The Henrys Fork of the Snake River is a medium-sized river in eastern Idaho, its mean annual discharge at Island Park Dam for 1995–1997 being 24.3 m^3/s (annual range, 6.9–78.4 m^3/s). The river elevation of the Henrys Fork at Island Park Dam is 1,897 m, and the river drains a 1,246-km^2 area. The Buffalo River joins the Henrys Fork about 0.6 km downstream of Island Park Dam (Figure 1). The Buffalo River is spring-fed and has a relatively constant discharge of about 6 m^3/s. Until the installation of a fish ladder in October 1996, the dam at the mouth of the Buffalo River prevented upstream migration of rainbow trout except during spring runoff.

For sampling juvenile rainbow trout we divided the Henrys Fork from the confluence with the Buffalo River to Riverside Campground into the following five sections: (1) Box Canyon (length = 4 km, mean width = 70 m), (2) Last Chance (4 km, 95 m), (3) Harriman State Park (8 km, 125 m), (4) Harriman East (3 km, 100 m), and (5) Pinehaven–Riverside (3 km, 85 m) (Figure 1). These study sections were based on similarity of habitat types, as described below. Box Canyon was further divided into upper Box Canyon (length = 1.5 km, mean width = 56 m) and lower Box Canyon (2.5 km, 79 m) for sampling purposes. Harriman State Park was divided at the Railroad Bridge into a 5-km upper reach and a 3-km lower reach. The 5-km upper reach of Harriman State Park and a 3-km reach between Harriman East and Pinehaven–Riverside were not sampled.

Box Canyon has a relatively high gradient (0.45%) with cobble–boulder substrate; it is characterized by an abundance of rocks and woody debris along the banks and sparse macrophytes across the channel. Upper Box Canyon has areas of rapids, deep holes ($>$1 m deep), and large, uneven substrate. The channel depth in lower Box Canyon is usually less than 1 m. Generally, no ice forms in Box Canyon because winter water temperature is moderated by hypolimnetic releases from Island Park Reservoir (2–4°C) and water from the spring-fed Buffalo River (1–6°C).

Last Chance has an intermediate gradient (0.3%) with cobble substrate; it is characterized by dense macrophyte beds across the channel and a lack of cover along the banks. Macrophyte beds decrease (but are not eliminated) through winter because of natural senescence and grazing by trumpeter swans *Cygnus buccinator* and other waterfowl (Van Kirk and Martin 2000). No ice formation occurs in Last Chance except along the margins of the river. The channel depth is usually less than 1 m throughout this section.

Harriman State Park has a low gradient (0.1%) with a highly embedded sand–gravel substrate. It is characterized by a patchy distribution of dense macrophyte beds, a general lack of cover in the channel, and little cover along the banks. Most of the dense macrophyte beds occur in a 1-km area downstream of the Railroad Bridge, where the average width is about 80 m and the channel depth is usually less than 1 m. Many macrophyte beds are thinned or eliminated by spring. The remaining 2 km are characterized by slower water velocities, fewer macrophytes, a greater area of sand substrate, greater width (up to 150 m), and a channel depth of 1–2 m. The 5-km upper reach of Harriman State Park is also characterized by the presence of fewer macrophytes and increased width (up to 200 m), but the channel depth is usually less than 1 m. Surface ice forms across the channel in many areas of Harriman State Park during winter.

Harriman East has a low gradient with a silt–sand substrate; it is characterized by a patchy distribution of sparse macrophytes and no cover along the banks. Most macrophytes are eliminated by spring. The channel depth is usually about 1–2 m throughout the river section. Surface ice forms across the channel in many areas of Harriman East during winter.

The gradient increases to an intermediate level about 1 km downstream of Harriman East and through about the first 2 km of Pinehaven–Riverside. The substrate consists of a mixture of cobble- and boulder-sized rocks and patches of sand near dense clumps of macrophytes. Some fallen trees and large rocks lie along the banks, but generally little complex bank habitat is present. The last 1 km of Pinehaven–Riverside flows through a canyon and has a high gradient, a deep channel (1–3 m), and large boulders scattered throughout the channel and along the banks. Bank areas are generally inundated with silt. Surface ice forms

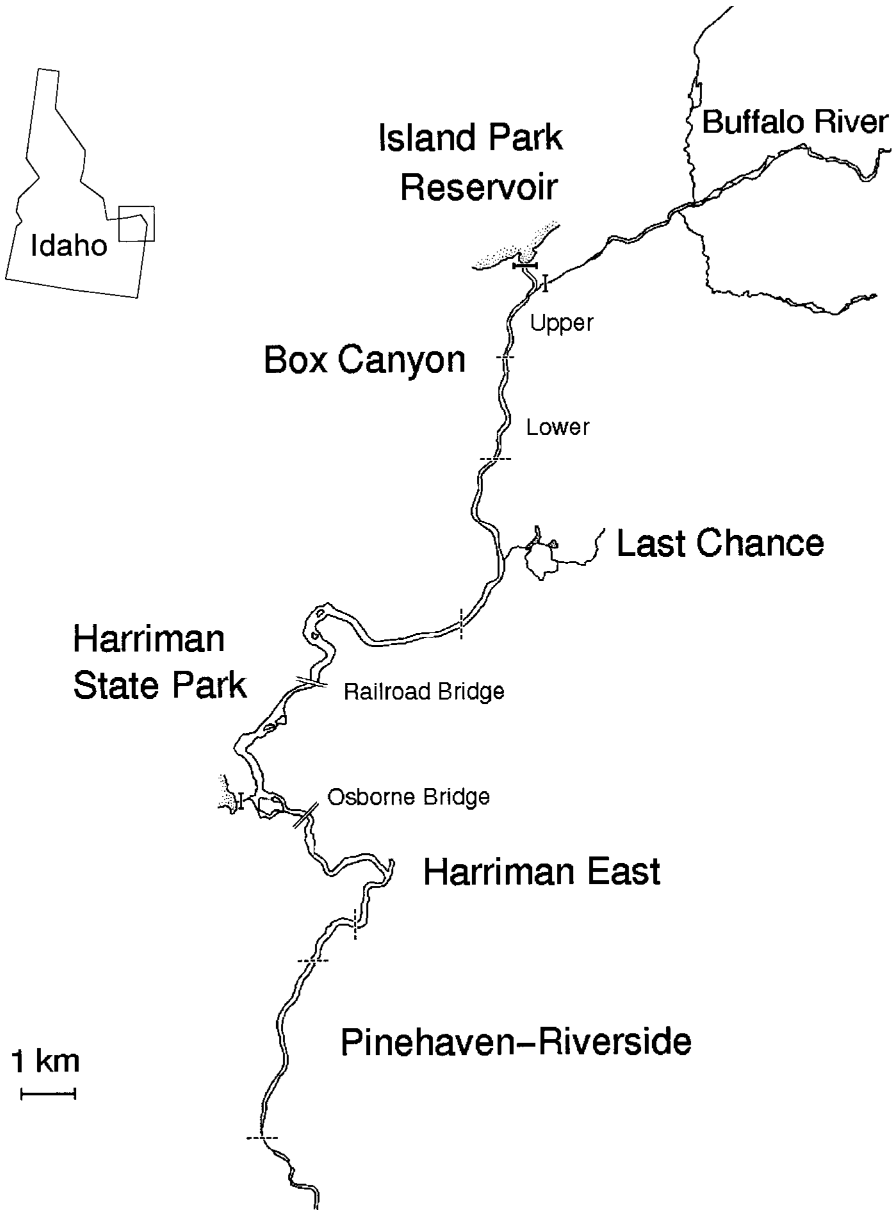

FIGURE 1.—River sections of the Henrys Fork downstream of Island Park Reservoir: Box Canyon (upper and lower), Last Chance, Harriman State Park, Harriman East, and Pinehaven–Riverside. Lines with end-caps = dams, dashed lines = river section boundaries, and parallel lines = bridges (Osborne Bridge separates Harriman State Park and Harriman East).

along bank areas in Pinehaven–Riverside during winter.

Downstream of Pinehaven–Riverside is a river section locally referred to as Cardiac Canyon, with a 35-m waterfall (Mesa Falls) at 18 km. We did not sample this river section. This high-gradient river section comprises a series of rapids and has a large, rocky substrate. There are some large rocks along the banks but few fallen trees, resulting in little complex bank habitat.

Methods

Juvenile rainbow trout sampling.—Sampling seasons were summer (August), autumn (October to mid-November), and spring (mid-May to mid-June). We sampled the five river sections in nine seasons from summer 1995 to spring 1998 and thereby examined recruitment dynamics of the three rainbow trout year-classes produced in 1995, 1996, and 1997. Sampled areas were considered closed for within-season sampling periods (i.e., days) and open between seasons. Closed population models, which allow for unequal capture probability, were used to estimate abundance within a season.

The diversity of habitat types and seasonal conditions in the Henrys Fork necessitated use of different sampling gears, strategies, and analytical treatments in different sections and seasons to provide the most credible area- and time-specific abundance estimates. These included electrofishing removal along banks (Mitro and Zale 2000a) and mark–recapture methodologies in either 100-m sample areas (Mitro and Zale 2002) or throughout a section by using a driftboat to estimate abundance. Apparent survival (i.e., mortality and emigration were not distinguished) was estimated by comparing abundances from one season to the next.

In several cases, we were unable to calculate abundance estimates because too few fish were captured or none was recaptured. Such sampling results were always an indication that abundances were negligible in comparison with abundances estimated in those sections in other seasons. In such cases, we estimated apparent survival in a section by comparing seasonal electrofishing catch rates. To verify the validity of this approach, we compared catch per unit effort (CPUE) with the abundances that we could estimate to determine whether or not CPUE was linearly related to abundance, in which case CPUE could be used as an indicator of change in abundance or apparent survival. However, no correlation existed between CPUE and estimated abundance in summer samples (r^2 = 0.006; Figure 2). Thus a comparison of CPUE between seasons was not a reliable estimator of summer-to-autumn apparent survival. However, a positive linear relation existed between CPUE and estimated abundance in autumn (r^2 = 0.54; Figure 2), which suggested that a comparison of CPUE between autumn and spring (rather than comparisons of estimated abundance) could be used to estimate apparent survival. We did not expect to detect small changes in abundance (and hence small changes in apparent survival) through catch rates. Rather, we used comparisons of CPUE when catches suggested present abundances were negligible and we suspected that large changes in abundances had occurred.

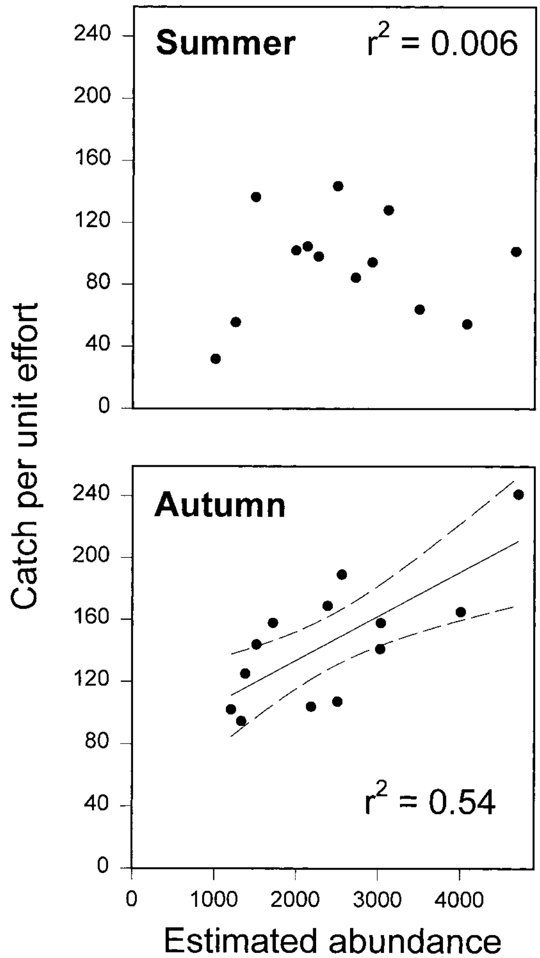

FIGURE 2.—Relation between catch per unit effort and estimated abundance for sample areas in Box Canyon, Last Chance, and Harriman State Park in summer (N = 13) and autumn (N = 13). Solid line = fitted linear regression; dashed lines = 95% confidence interval for regression.

Separation of age-0 and age-1 rainbow trout.—We separated age-0 rainbow trout for analysis by using length–frequency histograms to identify age-0 fish according to length and by determining the age of a subset of sampled rainbow trout (Mitro and Zale 2002). Scales were collected from as many as10 juvenile rainbow trout in each 10-mm size-class, ranging from 60 to 310 mm total length (TL), in each river section and season from summer 1995 to autumn 1997. No scales were collected in spring samples in Last Chance, Harriman State Park, and Harriman East. Mitro and Zale

(2002) described the procedures for reading scales and partitioning fish into age-classes based on length by using logistic regression analysis. No overlap in length ranges of age-0 and age-1 rainbow trout was seen in 20 combinations of river sections and seasons as identified by length–frequency histograms and by reading scales to determine age. No age-1 rainbow trout was identified in 10 of these combinations. A classification length to delineate age-0 and age-1 rainbow trout for which length ranges did overlap was estimated for 14 combinations of river sections and seasons. The probability of correctly classifying a trout as age 0 ranged from 0.76 to 1.0 (median = 0.97) and the probability of correctly classifying a trout as age 1 ranged from 0.60 to 1.0 (median = 0.92). (See Mitro [1999] and Mitro and Zale [2002] for length–frequency histograms, length ranges, and classification lengths.)

Marking.—Juvenile rainbow trout were marked with visible implants of fluorescent elastomer (Northwest Marine Technology, Inc.) to identify capture seasons and capture sections. A mark was placed in the right postocular area of the fish in all river sections to indicate year of first capture for the year beginning in the summer sampling season, a different color being used for each year. An additional mark was used to denote the river section (using different colors) and season (using different marking locations) of capture. These were injected in the left postocular area, the pectoral fins, and the pelvic fins. Within-season capture histories were indicated by a unique fin clip for each capture occasion (Mitro and Zale 2002). Fin clips were small to allow mark recognition within a season and regeneration thereafter (Gowan and Fausch 1996).

Mark–recapture.—We conducted two different kinds of mark–recapture sampling to obtain abundance estimates: wading in sample areas and drifting through entire river sections. Abundance estimates were obtained for sample areas in lower Box Canyon, Last Chance, and Harriman State Park in summer and autumn; high discharge necessitated the use other sampling techniques in spring (Mitro and Zale 2002). Estimates for sample areas were extrapolated to estimate total abundance in a river section. Sample areas were defined as bank-to-bank areas about 100 m long. Juvenile rainbow trout were collected in a sample area by wading with boat-mounted electrofishing gear (continuous DC, 250 V) along eight transects extending from bank to bank perpendicular to the current. We sampled two sample areas in Box Canyon, two in Last Chance, and one in Harriman State Park. A stratified-random procedure was used to select the sample areas; sample areas were separated by at least 1 km to reduce the likelihood that fish marked in one area would move to another within a season. The same sample areas were used in each season and year.

Sample areas were sampled each season on three to five occasions. The mark–recapture data were analyzed by using the Chao M_t estimator in program CAPTURE (Chao 1989; Rexstad and Burnham 1991; Mitro and Zale 2002). Sampling effort equaled the summed length of all transects on all capture occasions.

Mark–recapture data were collected in Harriman East and Pinehaven–Riverside in all seasons by drifting with electrofishing gear (continuous DC, 175–250 V). We also used this method to sample Last Chance and Harriman State Park in spring. Two electrode rings were suspended by booms off the bow of the drift boat in a downstream direction. One person netted fish from the bow and another person rowed. Two drifts through an entire section (except Last Chance, in which only 2 km were sampled), one in each half of the river (left versus right), constituted a sample. River sections were sampled each season on one to five occasions. The boat was rowed in a zigzag pattern to ensure a representative sample of river habitat. Sampling effort equaled the length of the sampled river section. The mark–recapture data were analyzed by using the Lincoln–Petersen estimator for two capture occasions and the Chao M_t estimator for three or more capture occasions (Ricker 1975; Chao 1989; Rexstad and Burnham 1991; Mitro and Zale 2002).

Removal.—A removal methodology was used to sample and estimate the abundance of age-0 rainbow trout along banks, particularly in river sections with complex bank habitat and in river sections and seasons in which the channel could not be waded. Fish were collected in bank sampling units with a hand-held probe operated from boat-mounted electrofishing gear (continuous DC, 250 V) and wading upstream from the anchored boat. Bank units were known-length sections of bank (about 15 m) extending out into the channel at least 2 m, or further, if necessary, to encompass any structure associated with the bank, such as a fallen tree. A subset of the total population of bank units in a river section was selected by a systematic random procedure and sampled by three-pass or single-pass removal. Three-pass removal data were analyzed with the Zippin maximum likelihood removal estimator (Zippin 1956; Otis et al. 1978; Rexstad and Burnham 1991); single-pass removal data were analyzed with a mean capture probability model based on three-pass capture probabilities for the Henrys Fork (Mitro and Zale 2000a). The mean number of age-0 trout per bank unit was extrapolated to provide an estimate of total abundance along the banks in a river section (Mitro and Zale 2000a); confidence intervals included within-bank unit, among-bank unit, and extrapolation error. Sampling effort equaled the sum length of all sampled bank units.

The removal method was used in upper Box Canyon each summer and autumn and throughout Box Canyon each spring. About 85% of the samples were collected by three-pass removal and 15% by single-pass removal. The number of bank units sampled on each side of the river was equal but on one occasion differed by one. We sampled 4 to 10 bank units each summer and autumn and 20 to 50 bank units each spring (the number of bank units sampled increased as the study progressed). Bank units in all river sections ranged from 8 to 33 m long but were generally about 15 m long.

We also sampled along the banks in Last Chance and Pinehaven–Riverside in some years and seasons. We sampled 20 bank units by three-pass removal in Last Chance in spring 1997. In Pinehaven–Riverside, we sampled 4 to 10 bank units in summer 1995 and 1996, autumn 1995, and spring 1996 and 1997. About half of the samples in Pinehaven–Riverside were by single-pass removal rather than three-pass removal.

Apparent survival.—We estimated seasonal apparent survival of age-0 rainbow trout by comparing total estimates of abundance from season to season for each river section. Apparent survival was estimated by dividing the estimated abundance at time $t + 1$ by the estimated abundance at time t. Apparent survival estimates greater than one indicated recruitment had occurred (via birth or immigration). If abundance estimates were unavailable, we estimated apparent survival by comparing CPUE when appropriate, as described earlier.

We obtained a more detailed description of apparent survival during winter in Last Chance by sampling once per month and using a CPUE methodology. Ten random bank-to-bank transects were sampled by electrofishing from November through April during winters 1996–1997 and 1997–1998. Comparing monthly catch identified changes in apparent survival.

Movement.—Seasonal movement (or lack thereof) was detected by recapturing juvenile rainbow trout marked with visible implants of elastomer. The same sample areas were resampled from season to season such that a large number of juvenile rainbow trout in these areas were marked. Recapturing fish originally marked in these areas indicated the marked trout had not moved to another section. Long-range movement was detected by sampling many areas throughout the five study sections and by recapturing marked individuals in sections other than those in which they were marked.

Immigration of hatchery rainbow trout.—About 25% of 750,000 hatchery juvenile rainbow trout stocked in Island Park Reservoir in each year from 1995 to 1997 (about 187,500) received an adipose clip to allow us to recognize reservoir fish that moved past the dam into the Henrys Fork. All rainbow trout captured in the Henrys Fork below Island Park Dam were inspected for an adipose clip.

Habitat use.—We identified the relative use of bank habitat versus channel habitat from catch data collected along transects in sample areas in lower Box Canyon, Last Chance, and Harriman State Park during summer and autumn 1996 and 1997. The channel location of each juvenile rainbow trout collected along a bank-to-bank transect (perpendicular to flow) was recorded. Fish captured within 2 m of either bank or near any structure associated with the bank, such as a fallen tree, were classified as using bank habitat. All other rainbow trout were classified as using center channel habitat. Winter habitat use was similarly identified in Last Chance during winters 1996–1997 and 1997–1998 from samples of random transects. Statistical differences or similarities between bank and center channel habitat use were identified at the $\alpha = 0.05$ level by comparing confidence intervals.

Results

Abundance

Summer and autumn.—Most age-0 rainbow trout in summer and autumn were found in Box Canyon and Last Chance (Figure 3). About 2.5 times as many age-0 rainbow trout were present in Last Chance as in Box Canyon in summer and autumn each year. Few age-0 fish were observed in most of Harriman State Park. However, a limited abundance of age-0 rainbow trout were in a 1-km reach in Harriman State Park below the Railroad Bridge in summer and autumn. Few age-0 rainbow fish were captured and none was recaptured in Harriman East in summer. However, more age-0 fish

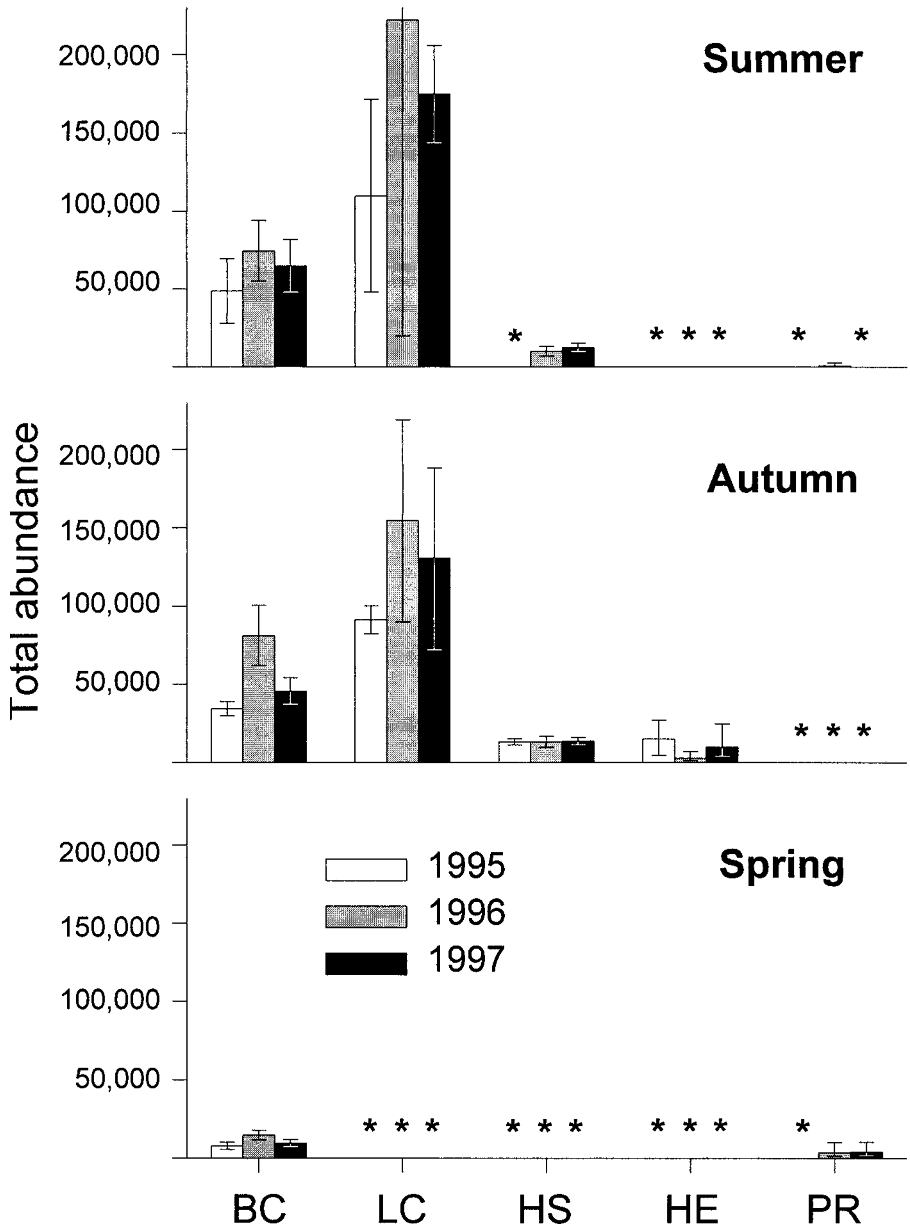

FIGURE 3.—Total abundance and 95% confidence intervals of age-0 rainbow trout in Box Canyon (BC; 4 km), Last Chance (LC; 4 km), Harriman State Park (HS; 1 km, downstream of Railroad Bridge), Harriman East (HE; 3 km), and Pinehaven–Riverside (PR; 3 km) in summer and autumn 1995–1997 and spring 1996–1998; * = no estimate available.

were present in Harriman East in autumn. In Pinehaven–Riverside in summer and autumn, few age-0 rainbow trout were captured and none was recaptured. Most rainbow trout captured in this river section were age 1 rather than age 0.

The density of age-0 rainbow trout was about one and a half times greater in Last Chance than in lower Box Canyon (Table 1). Density decreased downstream in the 1-km reach below the Railroad Bridge in Harriman State Park and in Harriman East. The density of age-0 fish along the banks in upper Box Canyon was about nine times greater than the density along the banks in the upper 2 km of Pinehaven-Riverside (Table 2).

TABLE 1.—Number of age-0 rainbow trout per 100 m^2 (95% confidence intervals) in lower Box Canyon, Last Chance, Harriman State Park, and Harriman East in summer and autumn 1995–1997.

River section	Number per 100 m^2					
	Summer			Autumn		
	1995	1996	1997	1995	1996	1997
Lower Box Canyon	24 (14–34)	36 (27–45)	31 (23–39)	15 (14–16)	36 (29–42)	21 (18–23)
Last Chance	29 (13–45)	58 (5–112)	46 (38–54)	24 (22–26)	41 (24–58)	34 (19–50)
Harriman State Park		13 (9–17)	16 (13–19)	17 (15–20)	17 (12–22)	18 (15–21)
Harriman East				5 (2–9)	1 (0–2)	3 (1–8)

Spring.—Most age-0 rainbow trout were found along the banks in Box Canyon after their first winter and to a lesser extent in Pinehaven–Riverside (Figure 3). The density of age-0 rainbow trout along the banks in Box Canyon was about 20-fold the density along the banks in the upper 2 km of Pinehaven–Riverside (Table 2). Few age-0 fish were captured, and none was recaptured in Last Chance, Harriman State Park, and Harriman East in spring.

We observed 25–35-mm age-0 rainbow trout (new cohort) in Box Canyon bank samples collected in May each year. We did not attempt to quantify new-cohort age-0 rainbow trout in Box Canyon. Many 21–54-mm-long new (1997)-cohort age-0 fish were collected in Last Chance bank samples in June 1997. (Only three 1996-cohort age-0 trout were captured in the same samples.) We estimated 69,058 (51,763–86,353) recently emerged age-0 rainbow trout along the banks in Last Chance in spring 1997. We sampled along the banks in Box Canyon a second time in 1997 (mid-June versus mid-May) when spring runoff had subsided. We did not capture any age-0 rainbow trout from the previous year's cohort but did capture many 25–45-mm fish from the new cohort that recently emerged.

Apparent Survival

Summer to autumn.—Comparisons of summer and autumn abundance estimates for age-0 rainbow trout for Box Canyon, Last Chance, and Harriman State Park indicated high apparent survival rates that were not significantly different from 1.0 (Table 3). We could not obtain summer-to-autumn apparent survival estimates for Harriman State Park in 1995 or for Harriman East and Pinehaven–Riverside in any year. Abundance estimates were not obtained for one or both seasons in these river sections, and comparisons of CPUE were considered unreliable.

Autumn to spring.—Autumn-to-spring apparent survival rates for age-0 rainbow trout were greatest in Box Canyon and Pinehaven–Riverside and near zero in the other river sections (Table 4). Apparent survival rates were significantly lower between autumn and spring than between summer and autumn (Tables 3, 4). We compared abundance estimates to estimate apparent survival for the Box Canyon section only. Too few rainbow trout were captured in the other study sections (where we therefore used a comparison of CPUE instead of abundance estimates), and none was recaptured in Pinehaven–Riverside in autumn or in Last Chance, Harriman State Park, and Harriman East in spring.

TABLE 2.—Number of age-0 rainbow trout per 100 m (95% confidence intervals) along the banks of upper Box Canyon (summer and autumn), Box Canyon (spring), and the upper 2 km of Pinehaven–Riverside.

River section	Number per 100 m								
	Summer			Autumn			Spring		
	1995	1996	1997	1995	1996	1997	1996	1997	1998
Box Canyon	58 (14–101)	144 (68–219)	146 (94–198)	141 (57–225)	378 (135–621)	178 (81–275)	99 (70–127)	185 (148–222)	122 (92–151)
Pinehaven–Riverside	6 (1–12)	13 (5–21)		20 (7–47)			3 (0–6)	11 (4–18)	

TABLE 3.—Summer-to-autumn apparent survival estimates (95% confidence intervals) of age-0 rainbow trout by river section and year.

River section	Summer-to-autumn apparent survival		
	1995	1996	1997
Box Canyon	0.70 (0.43–1.39)	1.09 (0.66–1.85)	0.70 (0.46–1.13)
Last Chance	0.83 (0.48–2.08)	0.70 (0.21–11.03)	0.75 (0.50–1.31)
Harriman State Park		1.30 (0.73–2.37)	1.10 (0.77–1.67)

Movement

We recaptured 245 of 11,881 age-0 rainbow trout marked with visible implants of elastomer; 210 were age 0 when recaptured and 35 were age 1 (Table 5). Most rainbow trout were recaptured in the river section in which they were marked (224, or 91.4%), 15 (6.1%) were recaptured in a different river section downstream, and 6 (2.4%) were recaptured in a different river section upstream.

No movement out of a river section was detected for most age-0 rainbow trout marked in summer and recaptured in autumn (Table 5). We did, however, detect limited summer-to-autumn downstream and upstream movement of marked fish. Two age-0 rainbow trout marked in Box Canyon were recaptured downstream in Harriman East, and one marked in Last Chance was recaptured downstream in Pinehaven–Riverside. One age-0 fish marked in Harriman State Park was recaptured upstream in Last Chance, and two marked in Last Chance were recaptured upstream in Box Canyon.

No movement out of Box Canyon or Pinehaven–Riverside was detected for most age-0 rainbow trout marked in autumn and recaptured in spring (Table 5). No fish marked before winter in Last Chance, Harriman State Park, and Harriman East was recaptured after winter in the same river section. Prewinter-to-postwinter downstream movement was detected from all river sections to Pinehaven–Riverside (Table 5). Prewinter-to-postwinter upstream movement was also detected from Last Chance to Box Canyon (Table 5).

Movement among river sections was not detected for most rainbow trout that had been marked at age 0 in summer, autumn, or spring and were recaptured at age 1 the following summer, autumn, or spring (Table 5). Four fish were recaptured at age 1 in river sections downstream from the section in which they were marked at age 0. Two fish moved from Box Canyon to Last Chance, and one trout from Box Canyon and one from Last Chance moved to Pinehaven–Riverside.

Immigration of Hatchery Rainbow Trout

We found no indication that age-0 rainbow trout stocked in Island Park Reservoir were contributing significantly to recruitment in the Henrys Fork. Despite inspecting more than 30,000 age-0 rainbow trout from summer 1995 to spring 1998, we identified only one age-0 rainbow trout marked with an adipose clip.

Habitat Use

Summer and autumn.—The mean number of age-0 rainbow trout captured per transect indicated that more age-0 fish used bank habitat rather than center channel habitat in summer and autumn in Box Canyon (Figure 4). In Last Chance, more age-0 fish used center channel habitat than used bank

TABLE 4.—Autumn-to-spring apparent survival estimates (95% confidence intervals) of age-0 rainbow trout by river section and year.

River section	Autumn-to-spring apparent survival		
	1995–1996	1996–1997	1997–1998
Box Canyon	0.23 (0.19–0.34)	0.18 (0.12–0.29)	0.21 (0.14–0.32)
Last Chance		0.11	0.03
Harriman State Park	0.003	0.001	0.004
Harriman East	0.005	0	0.014
Pinehaven–Riverside	0.24	1.10	1.35

TABLE 5.—Movement of juvenile rainbow trout between seasons (summer, autumn, and spring) and between sections within a season. Age-0 fish were marked in 9 seasons from spring 1995 to autumn 1997 and recaptured at age 0 or age 1 in 10 seasons from spring 1995 to spring 1998. The first column shows the number of recaptured fish. In subsequent columns, the first number is the section in which the fish were marked, the second the section in which they were recaptured (the numbers in the same column that are separated by a comma represent intraseasonal movement). Sections are numbered as follows: Box Canyon = 1, Last Chance = 2, Harriman State Park = 3, Harriman East = 4, and Pinehaven–Riverside = 5. A vertical dashed line indicates the overwintering period.

	Recaptured at age 0			Recaptured at age 1		
Recaptures	Summer	Autumn	Spring	Summer	Autumn	Spring
Box Canyon						
53	1	1				
2	1	4				
1	1	1	1			
3	1		1			
1	1		5			
1	1			1		
43		1	1			
1		1	5			
7		1		1		
1		1		2		
1		1			1	
4			1	1		
1			1	2		
1			1		1	
3			1			1
1			1			5
Last Chance						
77	2	2				
2	2	1				
1	2	5				
1	2		5			
1		2, 1				
2		2	1			
1		2	5			
1		2		5		
1			2, 5			
1			2	2		
1			2		2	
Harriman State Park						
10	3	3				
1	3	2				
2		3	5			
Harriman East						
1		4	5			
Pinehaven–Riverside						
5	5	5				
1		5	5			
1		5		5		
9			5	5		
1			5		5	
1			5			5

habitat. More age-0 fish used bank habitat in Box Canyon than in Last Chance, and more age-0 rainbow trout inhabited center habitat in Last Chance than in Box Canyon. In Harriman State Park, most age-0 fish were using center channel habitat, the number of fish using bank habitat in autumn not differing significantly from zero.

When age-0 rainbow trout were observed in Harriman East in autumn, the fish were using habitat throughout the center channel and not along the banks. Although few age-0 fish were captured in Pinehaven–Riverside in summer and autumn, those that were captured were using both bank and center channel habitat.

Age-0 rainbow trout using bank habitat and center channel habitat in Box Canyon and Last Chance

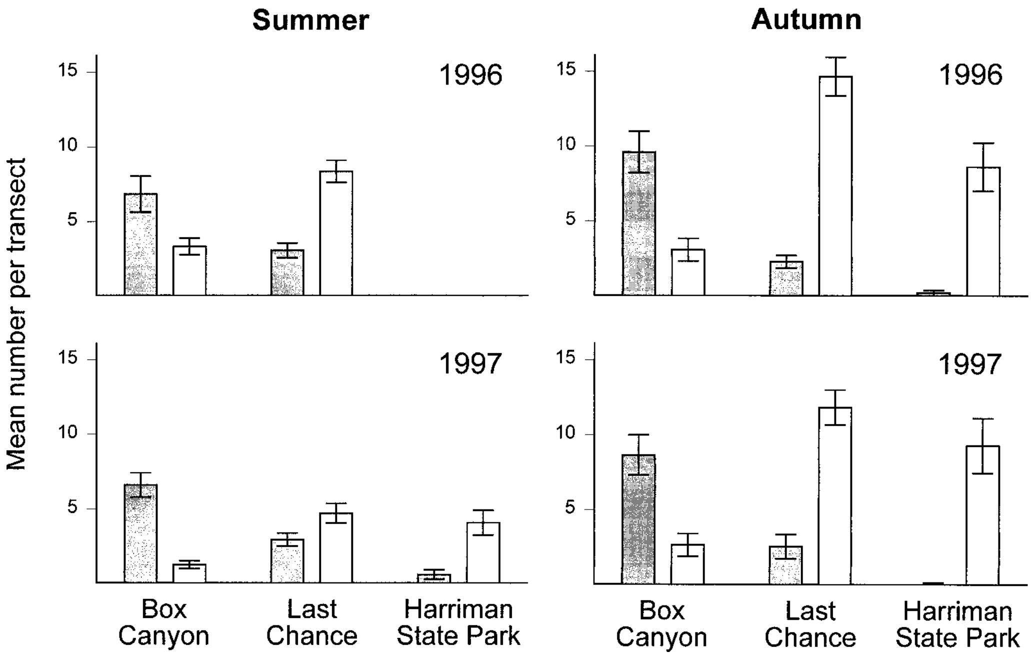

FIGURE 4.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals for bank areas (shaded) and center channel habitat (open) in Box Canyon, Last Chance, and Harriman State Park in summer and autumn 1996 and 1997. No habitat use data were available for Harriman State Park in summer 1996.

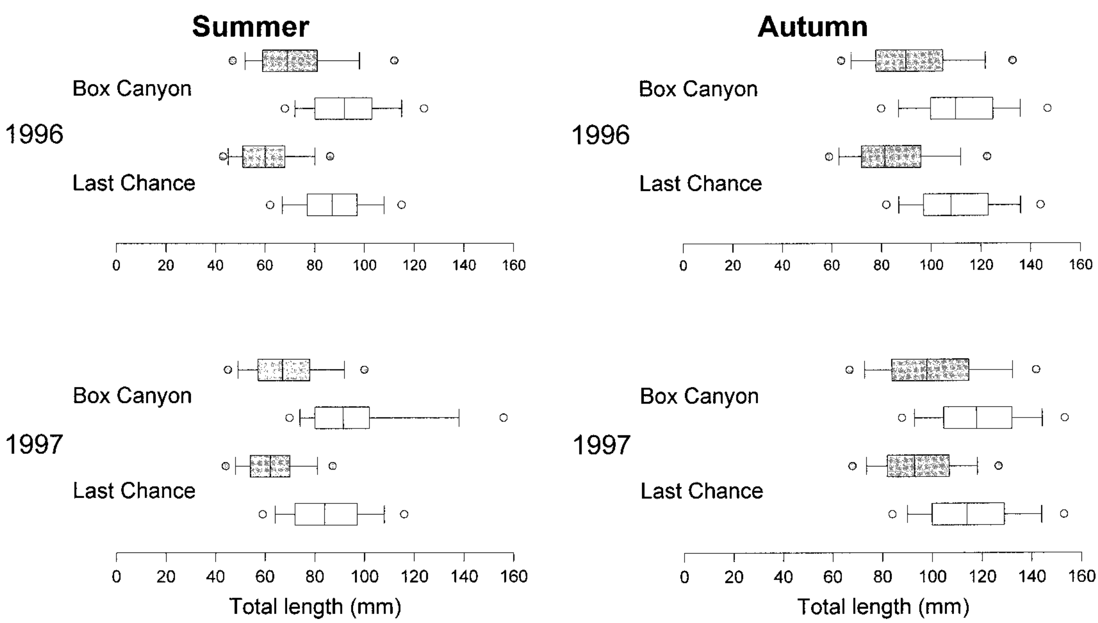

FIGURE 5.—Box plots showing the size distribution of age-0 rainbow trout in bank areas (shaded) and center channel habitat (open) in Box Canyon and Last Chance in summer and autumn 1996 and 1997. The ends of the box mark the 25th and 75th percentiles, the line inside the box marks the 50th percentile or median, the capped bars mark the 10th and 90th percentiles, and the circles mark the 5th and 95th percentiles.

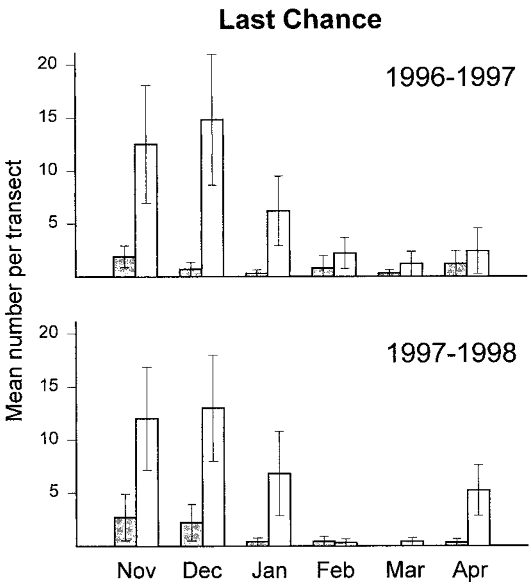

FIGURE 6.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals for bank areas (shaded) and center channel habitat (open) in Last Chance from November to April 1996–1997 and 1997–1998.

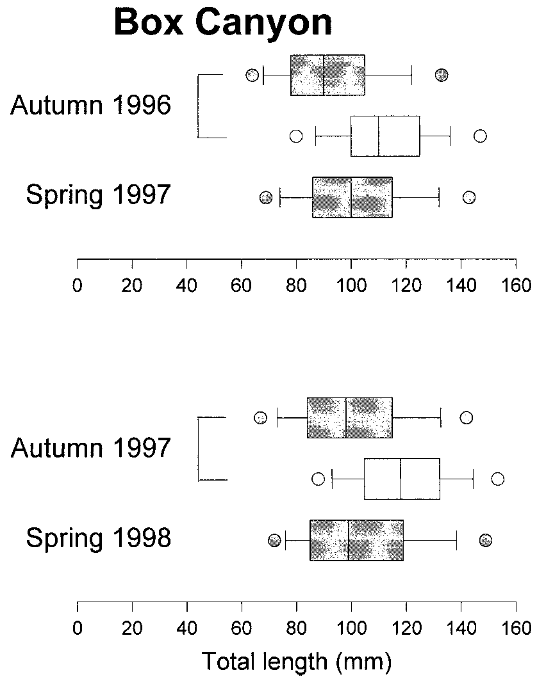

FIGURE 7.—Box plots showing the size distribution of age-0 rainbow trout in bank areas (shaded) and center channel habitat (open) in Box Canyon in autumn 1996 and 1997 and in bank areas in spring 1997 and 1998. (Boxes constructed as in Figure 6.)

in summer and autumn exhibited some overlap in size distributions (Figure 5). However, the smaller trout consistently tended to use the bank habitat.

Winter.—Use of bank habitat in Last Chance was low but consistent throughout the winter, whereas use of center channel habitat was high but more variable (Figure 6). The mean number of age-0 rainbow trout captured per transect in Last Chance indicated that trout were primarily using center channel habitat in November and December as they were in October of our autumn samples (Figure 4). The use of center channel habitat decreased by about 50% in January, but the fish using the center channel were still significantly more than those using the bank habitat. No significant difference existed in the use of center channel habitat versus bank habitat in February and March. The numbers of rainbow trout per transect increased in April, and the number of rainbow trout in the center channel significantly exceeded those in the bank habitat in April 1998.

Spring.—We sampled along the banks in Box Canyon in each spring when discharge was at the highest levels recorded during a year; the high discharge levels precluded effective sampling of center channel habitat for age-0 rainbow trout. We sampled the other river sections about 2 to 3 weeks later when discharge had decreased. However, discharge levels were still high enough that we could not sample bank-to-bank transects in Last Chance and Harriman State Park because of unsafe wading conditions. Some age-0 rainbow trout were captured in the center channel in Last Chance by drifting and electrofishing, indicating that this habitat was being used. Some age-0 fish were captured in three-pass removal samples along the banks in Last Chance. The few age-0 fish captured in Harriman State Park and Harriman East were in the center channel, and most age-0 fish captured in Pinehaven–Riverside were in the center channel.

Sizes of age-0 rainbow trout using bank habitat in Box Canyon in spring were slightly greater than in autumn (Figure 7). However, the age-0 fish along the banks in spring were generally smaller than the age-0 fish in the center channel in autumn. About 50% of the age-0 rainbow trout sampled in spring were shorter than 100 mm TL.

Discussion

Natural production of rainbow trout occurred in the Henrys Fork in each year of this study and yearly production ranged from 158,000 to 306,000 in the 25-km reach downstream from Island Park

Dam. We saw no evidence of recruitment from rainbow trout stocked in Island Park Reservoir. Suitable rearing habitat was present in the five river sections to support these abundances of age-0 fish through summer and autumn. However, only Box Canyon and to a lesser extent Pinehaven–Riverside—river sections with complex bank habitat, higher gradients, and larger substrates—supported appreciable abundances of age-0 rainbow trout through their first winter. The highest overwinter survival occurred in Box Canyon. The remote location of Pinehaven–Riverside relative to the spawning and rearing areas in Box Canyon and Last Chance probably contributed to the limited number of age-0 fish found there. Overwinter loss of age-0 rainbow trout from Harriman State Park and Harriman East was almost complete. Some fish overwintered in Last Chance, but the loss from this river section (primarily from center channel habitat) was great, considering the abundances present at the beginning of each winter. Use of available bank habitat in Last Chance was relatively consistent through winter and movement was detected from river sections with simple bank habitat to river sections with complex bank habitat.

Apparent Survival

The period between summer and autumn was a time of high apparent survival for age-0 rainbow trout in the Henrys Fork. We used the term ''apparent survival'' because any loss of age-0 fish could be attributable to both mortality and movement. Recruitment may also have continued from summer to autumn, through the growth of recently emerged rainbow trout. The greatest loss of age-0 fish occurred during winter. After having thoroughly sampled river sections such as Last Chance, Harriman State Park, and Harriman East, we were confident that the large abundances of age-0 rainbow trout in those sections in autumn were not there in spring, indicating large changes in abundance and low apparent survival rates.

The first-winter apparent survival rates of rainbow trout in the Henrys Fork were consistently low from year to year within each river section. More annual variation in first-winter survival of salmonids is common (Needham et al. 1945; Hunt 1969; Seelbach 1993; Ward and Slaney 1993; Quinn and Peterson 1996) and may be caused by variable production or weather. Low annual variation in the Henrys Fork probably results from stable and consistent physical and chemical conditions produced by spring and dam discharges.

Apparent survival rate estimates for Pinehaven–Riverside were high and variable, ranging from 0.24 to 1.35. We consider these estimates to be better described as measures of recruitment rather than measures of survival. Few age-0 rainbow trout were observed in Pinehaven–Riverside before winter, and the recapture of marked fish indicated that some age-0 rainbow trout from all river sections were moving to Pinehaven–Riverside between spring and autumn. Therefore, a significant increase in age-0 trout abundance in Pinehaven–Riverside would be expected, which would confound survival with recruitment or immigration when comparing abundances.

The loss of age-0 rainbow trout from Last Chance occurred in the latter half of each winter, from January to March, contrary to the experimental results of Smith and Griffith (1994) and Meyer and Griffith (1997), which indicated that most age-0 rainbow trout mortality in cages occurred in early winter, in October and November. Their cage experiments may not have been representative of riverwide phenomena.

The loss of age-0 trout from Last Chance was primarily from the center channel, because age-0 trout were captured along the bank throughout winter. This consistent capture of age-0 rainbow trout in bank areas through winter suggested that the decrease in captures in the center channel was not a result of change in capture efficiency but rather a change in abundance and therefore in apparent survival.

We observed no significant size-dependent loss of age-0 rainbow trout in Box Canyon in winter. Overlap in size distributions was considerable for age-0 trout in bank areas of Box Canyon in autumn and spring, with no indication of a greater loss of small fish. Smith and Griffith (1994) observed 100% mortality of rainbow trout shorter than 100 mm TL in October in cages in the Henrys Fork. Meyer and Griffith (1997) found no significant difference in survival of rainbow trout shorter and longer than 90 mm TL at warm sites (3.1–4.3°C); moreover, all mortality at cold sites (1.5–4.3°C) occurred in rainbow trout less than 90 mm TL. However, we found that about 50% of age-0 rainbow trout were shorter than 100 mm TL in spring 1997 and 1998 samples in Box Canyon. The median size of age-0 trout did increase from autumn to spring (Figure 7)—perhaps as a result of limited size-dependent mortality or of the movement of larger age-0 fish from the center channel to bank areas during winter or during spring runoff. Movement to more suitable habitat could have counteracted any temperature effect on survival.

Movement

Movement is an integral variable in defining the use of time and space by fishes (Wootton 1990). Movement is common in resident stream salmonids and may result from seasonal changes in the stream environment, the presence of conspecifics, or behaviors such as fry dispersal and ontogenetic shifts in habitat use or diet (Gowan et al. 1994). Temporal and spatial changes in the abundance of juvenile salmonids may be attributable to movement as well as to mortality or recruitment. Therefore, detection and quantification of juvenile salmonid movement are important to understanding population dynamics.

Identifying the movement of stream salmonids over large spatial scales is inherently difficult (Gowan et al. 1994). By repeatedly sampling areas in Box Canyon, Last Chance, and Harriman State Park and sampling throughout Harriman East and Pinehaven–Riverside, we were able to detect movement patterns of juvenile rainbow trout by recapturing marked fish. Because recapture rates of marked trout that moved among river sections were low, multiple years of seasonal sampling were required to obtain the evidence of movement: recaptured marked rainbow trout.

We were also able to detect movement by using catch data, which was corroborated by recapturing marked fish. For example, the juvenile rainbow trout catch-per-day in Harriman East was often zero in spring and summer but more than 150 in autumn, suggesting movement into Harriman East between summer and autumn and movement out of Harriman East between autumn and spring. Mark–recapture data confirmed that such movement had occurred (Table 5).

Most movement of age-0 rainbow trout was from rearing habitat to overwinter habitat and took place between autumn and spring; rainbow trout moved upstream from Last Chance to Box Canyon and downstream from all river sections to Pinehaven–Riverside. Age-0 trout were not detected moving into Last Chance, Harriman State Park, or Harriman East to overwinter, but they were detected moving out of these sections. Although all river sections supported age-0 rainbow trout at some time during summer or autumn, only Box Canyon and Pinehaven–Riverside supported age-0 trout year-round.

Habitat Use

Age-0 rainbow trout had no shortage of rearing habitat in the Henrys Fork in summer and autumn. They were found throughout Box Canyon, Last Chance, and Harriman State Park and to a lesser extent in Pinehaven–Riverside in summer and autumn, primarily in complex bank habitat and in macrophytes in the center channel. Harriman East was not used by age-0 trout during summer; on the basis of catch data, we concluded that abundances in this section were negligible. This river section was deep (1–2 m) and devoid of cover. Age-0 trout did move to Harriman East in autumn but these were likely transient.

The greatest densities and abundances of age-0 rainbow trout in the Henrys Fork were in Last Chance in summer and autumn. Most age-0 trout in Last Chance were captured in the extensive macrophyte beds that occurred across the channel and throughout the river section. Habitat use by brown trout *Salmo trutta* was similar in a third-order river in northern Finland (Maki-Petays et al. 1997).

Winter habitat was limiting in the Henrys Fork. Cover and interstitial space are the most important factors regulating river salmonid populations in winter (Cunjak 1996). Harriman State Park and Harriman East were nearly devoid of instream cover such as macrophytes by spring, and the substrate was embedded such that interstitial space was not available. Age-0 rainbow trout did not use these sections throughout winter and into spring. Age-0 rainbow trout in spring occupied complex bank habitat in Box Canyon and to a lesser extent Pinehaven–Riverside.

Center-channel macrophytes did not provide winter habitat for age-0 rainbow trout (Griffith and Smith 1995). Although macrophyte cover decreased through winter because of grazing and senescence, some persisted but was not used by age-0 fish. The loss of age-0 rainbow trout from Last Chance was from the vegetated center channel, whereas the simple bank habitat available was consistently used through each winter.

Conclusions

The abundance of juvenile rainbow trout in streams and rivers can be limited by a lack of suitable spawning habitat, summer rearing habitat, or overwinter habitat (Waters 1995). Although only a limited amount of spawning activity has been observed in the Henrys Fork (Mitro and Zale 2000b), the abundances of age-0 rainbow trout present during summer and autumn suggested that spawning was not a limiting factor. The abundance of age-0 trout observed through autumn also suggested that summer rearing habitat was not a limiting factor. However, interstitial space necessary for overwinter habitat is largely confined to the river margins of Box Canyon. Consequently, overwinter survival was greatest in Box Canyon, and rainbow trout observed in other sections in autumn were absent the following spring.

Our original goal was to discern what factor limited recruitment in this population such that it could be manipulated to duplicate the fishery of the 1970s, when abundances in Box Canyon approximated 4,500 adults per kilometer (Van Kirk and Gamblin 2000). Our conclusion that complex bank winter habitat limits this population failed to meet this intent, given that the amount or quality of such habitat in the Henrys Fork is not much different now than it was in the 1970s. Rather, our findings lend credence to the hypothesis that abundances in the 1970s were maintained at artificially high levels by direct hatchery stocking and immigration of hatchery fish from Island Park Reservoir during frequent drawdowns (Van Kirk and Gamblin 2000). Current management of this reach as a designated wild trout fishery precludes stocking, and less frequent and extreme drawdowns of Island Park Reservoir, combined with a screened intake on the dam, limit emigration from the reservoir. Thus, our original premise that natural recruitment of this population declined in recent decades was in error; instead, natural recruitment has not declined but hatchery contributions have, leading to fewer adults. In fact, natural recruitment may well be improved in the Henrys Fork now that potential deleterious effects of hatchery supplementation (Einum and Fleming 2001) have been eased.

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