



Sampling and analysis techniques and their application for estimating recruitment of juvenile rainbow trout in the Henrys Fork of the Snake River, Idaho
by Matthew George Mitro

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in
Fish and Wildlife Biology
Montana State University
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Abstract:

Juvenile rainbow trout were sampled to quantify production and recruitment processes in the Henrys Fork, to identify factors limiting the trout population, and to propose management actions to improve natural recruitment. The study area was a 25-km river reach that varied in width from 50 to 150 m. I used distance sampling to identify spawning areas in the Henrys Fork and to quantify spawning activity therein. I developed and evaluated mark-recapture and removal techniques to address the inherent difficulties in the sampling and analysis of large abundances of age-0 salmonids over a large spatial scale. Mark-recapture data were collected from 100-m long sample areas. I found the Chao Mt estimator for mark-recapture data to have minimal bias and interval coverage close to the nominal level in simulations with mean capture probabilities (0.02-0.106) and rates of emigration (0-10%) based on actual Henrys Fork data sets. Three-pass removal data were collected along the banks in 15-m units. I developed and rigorously evaluated simple linear regression and mean capture probability models to predict abundance from the first-pass catch. These models worked particularly well for estimating abundance over a large spatial scale, allowing effort to be reallocated from intensively sampling few areas to sampling many areas with reduced effort, resulting in gains in estimate precision. These techniques were used to provide a comprehensive analysis of age-0 rainbow trout recruitment in the Henrys Fork. There was suitable habitat throughout the study area to support the yearly production of 150,000 to 250,000 age-0 trout through summer and autumn. Recruitment to the fishery was limited by poor survival during their first winter. I identified a flow-survival relation for age-0 trout in a river section with complex bank habitat. The number of age-0 trout that survived their first winter was related to higher discharge during the latter half of winter. The higher discharge during the latter half of winter created more available habitat in the section with complex bank habitat and coincided with the loss of age-0 trout from non-bank areas. Movement of age-0 trout was detected from river sections with simple bank habitat to sections with complex bank habitat. I recommended that winter discharge be managed to increase the availability of complex bank habitat, thereby improving recruitment of age-0 rainbow trout.

**SAMPLING AND ANALYSIS TECHNIQUES AND THEIR APPLICATION
FOR ESTIMATING RECRUITMENT OF JUVENILE RAINBOW TROUT
IN THE HENRYS FORK OF THE SNAKE RIVER, IDAHO**

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in

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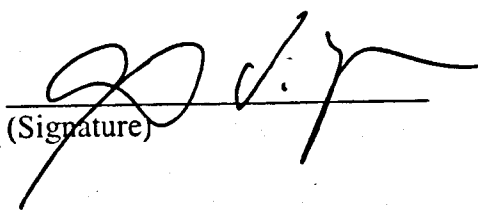
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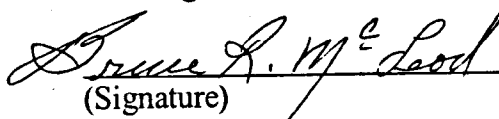
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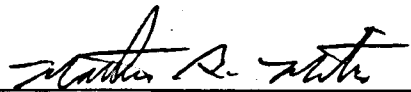

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ABSTRACT

Juvenile rainbow trout were sampled to quantify production and recruitment processes in the Henrys Fork, to identify factors limiting the trout population, and to propose management actions to improve natural recruitment. The study area was a 25-km river reach that varied in width from 50 to 150 m. I used distance sampling to identify spawning areas in the Henrys Fork and to quantify spawning activity therein. I developed and evaluated mark-recapture and removal techniques to address the inherent difficulties in the sampling and analysis of large abundances of age-0 salmonids over a large spatial scale. Mark-recapture data were collected from 100-m long sample areas. I found the Chao Mt estimator for mark-recapture data to have minimal bias and interval coverage close to the nominal level in simulations with mean capture probabilities (0.02-0.106) and rates of emigration (0-10%) based on actual Henrys Fork data sets. Three-pass removal data were collected along the banks in 15-m units. I developed and rigorously evaluated simple linear regression and mean capture probability models to predict abundance from the first-pass catch. These models worked particularly well for estimating abundance over a large spatial scale, allowing effort to be reallocated from intensively sampling few areas to sampling many areas with reduced effort, resulting in gains in estimate precision. These techniques were used to provide a comprehensive analysis of age-0 rainbow trout recruitment in the Henrys Fork. There was suitable habitat throughout the study area to support the yearly production of 150,000 to 250,000 age-0 trout through summer and autumn. Recruitment to the fishery was limited by poor survival during their first winter. I identified a flow-survival relation for age-0 trout in a river section with complex bank habitat. The number of age-0 trout that survived their first winter was related to higher discharge during the latter half of winter. The higher discharge during the latter half of winter created more available habitat in the section with complex bank habitat and coincided with the loss of age-0 trout from non-bank areas. Movement of age-0 trout was detected from river sections with simple bank habitat to sections with complex bank habitat. I recommended that winter discharge be managed to increase the availability of complex bank habitat, thereby improving recruitment of age-0 rainbow trout.

CHAPTER 1

INTRODUCTION

The Henrys Fork of the Snake River has long been renowned as one of the world's best rainbow trout *Oncorhynchus mykiss* fly fishing rivers. Since 1978, the river section from Island Park Dam to Riverside Campground has been managed under special regulations to protect the fishery, including catch-and-release since 1988. However, rainbow trout abundances there have generally declined since 1988, but with large, unexplained annual fluctuations according to Idaho Department of Fish and Game population estimates and angler surveys. An increase in numbers of rainbow trout occurred in 1993 following the 1992 drawdown of Island Park Reservoir, but the fishery began to decline again thereafter. The causes of these fluctuations in the rainbow trout fishery are not well understood. Recruitment may have been limited by the loss of concealment cover resulting from overgrazing of aquatic macrophytes by trumpeter swans *Cygnus buccinator* and siltation and dewatering of interstitial spaces from drawdowns of Island Park Reservoir. Prior to the screening of most of the discharge from the dam beginning in 1993 to prevent fish migration downstream to the river, recruitment may have been augmented by rainbow trout escaping from Island Park Reservoir.

Adult abundance estimates, such as those obtained for the Henrys Fork, tell us how many fish were recruited to the adult life stage, and a time series of such data may identify whether or not a recruitment problem exists. However, adult abundance estimates cannot tell us why a particular recruitment pattern exists or at what life stage

recruitment is limited. Recruitment is defined as the cumulative outcome or survival through a series of life stages (Trippel and Chambers 1997). The abundance of adult rainbow trout will necessarily depend on the survival of rainbow trout through early life stages beginning with spawning and fertilization and extending through the juvenile life stage. The study of these early life history stages is critical to the understanding of year-class formation and changes in fish populations (Elliott 1994; Trippel and Chambers 1997).

Sampling methods used by the Idaho Department of Fish and Game and by Angradi and Contor (1988) to obtain data for abundance estimation have precluded making inferences on abundances of juvenile rainbow trout in the Henrys Fork. Rainbow trout less than 150 mm were consistently underrepresented in samples collected in successive years by Angradi and Contor (1988). The failure to capture small trout is often a result of the sampling method; electrofishing is widely recognized as a size-selective sampling technique that favors capture of larger individuals (e.g., White et al. 1982; Bohlin et al. 1989; Jones and Stockwell 1995). Juvenile rainbow trout are also ecologically distinct from adults in their habitat requirements. Juvenile salmonids tend to occupy shallow, low velocity stream areas and may move to deeper habitat as they grow (Bohlin 1977; Gatz et al. 1987; Maki-Petays et al. 1997). Therefore, sampling must be directed specifically at juvenile rainbow trout if inferences concerning juvenile abundances are to be made.

Studies that have been directed at juvenile rainbow trout in the Henrys Fork have been limited in scope such that inferences on river-wide recruitment could not be made. We know that cobble-boulder concealment cover along banks is used by juvenile rainbow

trout during winter (Contor 1989; Griffith and Smith 1995). Movement of juvenile rainbow trout from macrophyte cover to cobble-boulder cover along banks has been observed (Griffith and Smith 1995). Experimental studies indicated that winter survival of age-0 rainbow trout was higher in cages with cobble-boulder substrate than in cages without cover (Smith and Griffith 1994) and survival was higher with warmer water temperatures (3.1-4.3 °C versus 1.5-4.3 °C; Meyer and Griffith 1997). Most mortality in cages has been observed in early winter (95%; Smith and Griffith 1994). Size-dependent mortality (age-0 rainbow trout < 90-100 mm total length) occurred in cages with no cover or with colder water temperatures (Smith and Griffith 1994; Meyer and Griffith 1997). Angradi and Contor (1988) estimated age-0 rainbow trout density by sampling along one bank in each of four river sections in summer. However, these estimates could not be extrapolated to both banks of the river because sampling was not representative of both banks. Studies of juvenile rainbow trout in the Henrys Fork must include multiple time periods and sampling areas representative of a large river reach such that recruitment can be quantified.

Estimates of temporal and spatial abundances of juvenile rainbow trout are essential to the evaluation of recruitment in the Henrys Fork. The estimation of survival and movement rates complements abundance estimation by aiding in the interpretation of temporal and spatial differences in abundances. Seasonal survival rates may be related to environmental changes in temperature and discharge, and spatial changes may be related to the movement of juvenile rainbow trout as habitat availability and habitat requirements change. The quantification of movement may also delineate the upper bound on the portion of a loss rate attributable to actual mortality. Therefore, a comprehensive study

of juvenile rainbow trout to evaluate recruitment limitations should include the estimation of abundance, survival, movement, and habitat use across time and space.

Inferences concerning fish abundance, survival, movement, and habitat use are inherently difficult to make because individuals are not readily observable and information is only available on fish that are captured (Otis et al. 1978; Burnham et al. 1987; Gowan et al. 1994; Hilborn and Mangel 1997). Additional difficulties with juvenile fish are the typically large abundances and low capture probabilities that result in large variances and wide interval estimates (Cormack 1992). The yearly production of age-0 trout in the Henrys Fork may exceed 100,000. The size of the management area of interest, which is 25 km long with an average width of 90 m, poses additional sampling problems concerning sampling efficiency (Kennedy and Strange 1981; Bohlin et al. 1989). Obviously, only a small percentage of such a population could ever be sampled given typical personnel and equipment constraints. However, sampling strategies and methods of analysis can be tailored and improved to meet the demands of a recruitment study in a river such as the Henrys Fork.

I developed and evaluated sampling methodologies to obtain data to quantify spawning activity and seasonal abundance, survival, movement, and habitat use of age-0 rainbow trout in the Henrys Fork. Existing methods of analysis for collected data were evaluated and adapted, and new methods of analysis were developed, to improve inference on salmonid recruitment at the juvenile life stage. The methods of analysis were applied to the collected data to produce a comprehensive analysis of age-0 rainbow trout recruitment in the Henrys Fork.

The results of my study are organized into five chapters. Each chapter is written in a format suitable for journal publication and is self-contained. Chapters two to four describe the development and evaluation of sampling methodologies and their application to the Henrys Fork study. In Chapter two I describe the evaluation and adaptation of distance sampling techniques to identify spawning areas in river sections of the Henrys Fork and to quantify spawning activity therein. In Chapter three I describe a sampling methodology I developed to obtain mark-recapture data to estimate abundances of age-0 rainbow trout in the Henrys Fork. I evaluated the utility of closed and open population models for such data and recommended an appropriate estimator. In Chapter four I describe the development and evaluation of competing predictive models for obtaining abundance estimates from single-pass removal data along bank areas in the Henrys Fork. The models were developed for use in the Henrys Fork, but can be calibrated for use in other streams or rivers or anywhere removal sampling is appropriate.

Chapters five and six describe the application of the sampling methodologies developed and evaluated in Chapters two to four. Chapter five constitutes a comprehensive analysis of the production and recruitment of age-0 rainbow trout in the Henrys Fork. I identified spawning areas and quantified spawning activity therein and I quantified seasonal abundance, survival, movement, and habitat use of age-0 rainbow trout. In Chapter six I describe a flow-survival relation identified for age-0 rainbow trout in the Box Canyon section of the Henrys Fork and a winter discharge experiment, based on this relation, to improve natural recruitment of age-0 rainbow trout in the Henrys Fork.

The results of this study improved our understanding of the processes affecting rainbow trout recruitment rates in the Henrys Fork downstream of Island Park Reservoir.

Whereas past studies in the Henrys Fork have been limited in scope such that inferences on river-wide recruitment could not be made, this study provided detailed information on river-wide production, survival, movement, and habitat use of rainbow trout at the age-0 life stage. These results were used to assist management policy for maintaining and improving the Henrys Fork wild rainbow trout fishery. Sampling and analysis techniques developed and evaluated in this study provided the tools necessary to study the recruitment process for age-0 trout and can be used to efficiently monitor age-0 trout recruitment and evaluate the effects of management actions in the future.

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CHAPTER 2

USE OF DISTANCE SAMPLING TO ESTIMATE RAINBOW TROUT REDD ABUNDANCES IN THE HENRYS FORK OF THE SNAKE RIVER, IDAHO

Introduction

Redds are spawning nests of salmonids constructed by digging a depression in gravel substrate, depositing eggs, and covering the eggs with loose gravel. Redd counts are typically conducted to identify spawning areas, to confirm that spawning has occurred, and to obtain a total number of redds present in an area. Redd counts are obtained by censusing an area or stream and it is generally assumed that all redds are detected. Redd censusing may be conducted on foot or by canoe in small streams (e.g., Beland 1996) or by aerial observation in larger streams (e.g., Heggberget et al. 1986). However, it may be unreasonable to assume that all redds can be detected, especially when searching large areas. Censusing may yield biased results if some redds remain undetected.

Distance sampling (Buckland et al. 1993) can be used to systematically search a large area of interest and to obtain an abundance estimate of objects within that area. Distance sampling theory allows for the detectability of objects to decrease as the distance of the object from a line transect increases (Buckland et al. 1993). Therefore, objects can remain undetected without undermining the validity of the estimate. Perpendicular distances from a transect to a detected object are "sampled" and the distances are modeled so that detectability and density can be estimated. As distance

from the transect increases, detectability decreases, allowing estimation of the effective area sampled. The use of distance sampling has received little attention in the study of fish populations (for exceptions see Bergstedt and Anderson 1990; Ensign et al. 1995). Distance sampling has not been used in the estimation of redd abundance although it appears to be well suited to this problem. Three assumptions necessary for reliable estimation from line transect sampling are: 1. Objects on a transect are detected with certainty; 2. Objects are detected at their initial location before any movement in response to the observer; and 3. Distances between objects and the transect are measured accurately (Buckland et al. 1993). It is reasonable to assume that redds on a transect will be detected with certainty. Redds are immobile objects; therefore, redds detected off a transect will be detected in their initial location and the distance from a transect to a redd can be measured accurately.

I used distance sampling to identify spawning areas in study sections of the Henrys Fork of the Snake River, Idaho, and to quantify spawning activity therein.

Study Area

The Henrys Fork is a medium-sized river that had a mean annual discharge of $24.3 \text{ m}^3/\text{s}$ in 1995-1997 at Island Park Dam (range, 6.9 to $78.4 \text{ m}^3/\text{s}$). The Henrys Fork at Island Park Dam is at 1,897 m in elevation and drains a $1,246\text{-km}^2$ area. I divided the Henrys Fork from Island Park Dam to Osborne Bridge into the following five sections for sampling rainbow trout redds: 1. Island Park Dam to the United States Geological Survey (USGS) gauging station (length (L) = 250 m; mean width $\bar{w}$ = 56 m); 2. USGS gauging station to the Buffalo River (L = 350 m; $\bar{w}$ = 42 m); 3. Box Canyon (L = 4 km; $\bar{w}$ = 70

m); 4. Last Chance ($L = 4$ km; $\bar{w} = 95$ m); and 5. Harriman State Park ($L = 8$ km; $\bar{w} = 125$ m) (Figure 2.1).

The Buffalo River joins the Henrys Fork about 0.6 km downstream of Island Park Dam (Figure 2.1). The Buffalo River is spring-fed and has a relatively constant discharge of $6 \text{ m}^3/\text{s}$. A dam at the mouth of the Buffalo River prevented upstream migration of rainbow trout, except during spring runoff, prior to the installation of a fish ladder in October 1996.

The river section from Island Park Dam to the Buffalo River has an intermediate gradient (0.3%) with boulder substrate in the thalweg and gravel substrate in the adjacent shallow areas; there is a larger-gravel substrate area upstream of the USGS gauging station. Box Canyon has a high gradient (0.45%) with cobble-boulder substrate and Last Chance has an intermediate gradient (0.3%) with cobble substrate. Harriman State Park has a low gradient (0.1%) with a highly embedded sand-gravel substrate.

Methods

Replicate transects perpendicular to flow were systematically traversed by a combination of wading and snorkeling, with a random first start within each river section. Locations of redds on either side of a transect of known length were recorded to estimate the effective area sampled and the density of redds. Locations were identified by perpendicular distance (m) from the transect to the redd center. Redd densities were estimated using the computer program DISTANCE (Laake et al. 1994). An estimate of the total number of redds in a section was obtained by extrapolating the estimate of density across the total area within the section. I also searched for redds along alternating

sides of the river between transects in Box Canyon, Last Chance, and Harriman State Park to verify that transects were representative of sections (i.e., that there were not many more or less redds between transects versus on or near transects).

Distance sampling was conducted once in 1995 from Island Park Dam to the Buffalo River, in Box Canyon, and in Last Chance. The section between Island Park Dam and the USGS gauging station was sampled on four dates in 1996 and on six dates in 1997. Last Chance and Harriman State Park were each sampled once in 1997. I sampled 10-15 transects on each date in sections between the dam and the Buffalo River and 20 transects on each date in the remaining sections.

The first spawning activity of each season in each river section was verified by digging into suspected redds until eggs were found. Thereafter, depressions in the substrate were identified as redds based on characteristics including a decreasing gravel size-gradient from the redd pit through the redd tail, gravel in a redd that were cleaned of periphyton compared to surrounding gravel, and gravel in a redd pit-area that were loose to the touch.

Results

Rainbow trout spawning activity was concentrated in the section between Island Park Dam and the USGS gauging station on sampling dates in 1995 and 1996 and was limited in other sections. Spawning was limited in all sections of the Henrys Fork on sampling dates in 1997.

Twenty-two redds were observed on 27 April 1995 between the dam and the USGS gauging station, yielding an estimate of 28 redds (95% confidence interval (CI),

12-67; Table 2.1). (See Appendix Table A.1 for detection function model specification, encounter rate, and effective strip width.) The discharge was $17.0 \text{ m}^3/\text{s}$. Redds were scattered throughout the shallow areas adjacent to the thalweg. There was an insufficient number of redd observations in the other sampled sections to estimate redd density using program DISTANCE (Table 2.2). One redd was observed near the west bank between the USGS gauging station and the Buffalo River on 27 April and one redd was observed near the east bank in Last Chance on 18 April. No redds were observed in Box Canyon on 17 April and no redds were observed along alternating sides of the river between transects in Box Canyon and Last Chance.

There was an increasing trend in the total number of redds between Island Park Dam and the USGS gauging station between 30 March and 21 April 1996 (Table 2.1). An estimate could not be obtained for 30 March because only two redds were observed. The maximum number of redds observed was 11 on 14 April, yielding an estimate of 11 redds (95% CI, 4-30). Visibility was reduced by 21 April because of an increase in discharge to $19.7 \text{ m}^3/\text{s}$ from $16.0 \text{ m}^3/\text{s}$ on 14 April; 9 redds were observed, yielding an estimate of 16 redds (95% CI, 6-42) (Appendix Table A.1). Thereafter, it was not feasible to wade or snorkel to sample redds because of an additional increase in discharge.

An increasing trend in the total number of redds between Island Park Dam and the USGS gauging station was not observed between 11 March and 19 April 1997 (Table 2.1). Discharge was $26.2 \text{ m}^3/\text{s}$ on 11 March and about $21.3 \text{ m}^3/\text{s}$ from 31 March to 19 April. One redd was first observed on 31 March and no additional redds were identified thereafter. No redds were observed in Last Chance on 20-21 April or in Harriman State

Park on 21 April (Table 2.2); no redds were observed along alternating sides of the river between transects. Visibility was reduced because of an increase in discharge by the last week of April 1997 and it was not feasible to wade or snorkel to sample redds thereafter.

Discussion

A ground-based method of searching for redds in the Henrys Fork was necessary because trumpeter swans *Cygnus buccinator* left depressions in the substrate after feeding on macrophytes and the depressions could be mistaken for redds when viewed from far away (e.g., from an airplane). Distance sampling provided an unbiased approach to identifying spawning areas and to quantifying spawning activity therein. Traditional redd counts are not robust to changes in detectability and therein lies the advantage of distance sampling—detectability can change without affecting the validity of the estimates.

The robustness of distance sampling to changes in detectability was demonstrated when sampling the river section between Island Park Dam and the USGS gauging station on multiple dates in 1996. As discharge increased between sampling dates, the distance at which redds could be detected from a transect decreased. Consequently, fewer redds were detected for a given number of transects. However, the shorter distances of detected redds from transects indicated an increase in redd density and hence an increase in spawning activity. A traditional redd count would have required more effort to detect an increase in spawning activity given the decrease in detectability, and the increase in spawning activity may not have been observed if redds remained undetected.

There was an increasing trend in spawning activity in the river section between Island Park Dam and the USGS gauging station from 30 March to 21 April 1996. This

trend was not observed in 1997. The installation of the Buffalo River fish ladder in October 1996 provided access to spawning areas in the Buffalo River in spring 1997 that were previously inaccessible to rainbow trout in the Henrys Fork prior to spring runoff. Spawning rainbow trout that may have formerly used the area near Island Park Dam could have spawned in the Buffalo River instead. The Henrys Fork Foundation reported that 224 rainbow trout greater than 400 mm total length (TL) migrated upstream through the fish ladder during spring 1997 prior to runoff (R. Van Kirk, Henrys Fork Foundation, personal communication). This may explain the estimated differences in redds between 1996 and 1997.

The detectability of redds may depend on stream discharge and light conditions. Increased discharge may decrease the distance at which redds can be detected from a transect. Distance sampling is robust to this situation provided that redds on a transect are still detected with certainty (Buckland et al. 1993). Light may affect visibility by creating a glare on the water surface. If a glare occurs on one side of the transects, observations will be asymmetric about the transects, but estimation will not be adversely affected (Buckland et al. 1993). If a glare occurs in the direction a transect is being traversed, the observer can turn around and look back to make observations (Buckland et al. 1993).

A random and independent distribution of redds is not required for distance sampling if the transects are randomly located in a river section or if a systematic grid of transects in a river section begins with a random first start (Buckland et al. 1993). Therefore, it is important that transects extend from bank to bank perpendicular to the current such that transects are representative of river habitat across a channel. If redds

are clustered along a bank, transects that follow the bank will overestimate redd abundance when used to make inference on the river as a whole. However, I do think it is useful to search for redds while moving along the bank from one transect to the next. This additional information cannot be used to calculate redd density, but it can be used to judge the effectiveness of a systematic sampling grid at representing a river section. For example, no redds were observed between transects in Box Canyon, thereby supporting the assumption that the transects were representative of Box Canyon (where no redds were observed on or near the transects).

An estimation problem encountered in this study was small sample size, which led to large confidence intervals on abundance estimates. Buckland et al. (1993) suggest a minimum sample size of 60 to 80 detected objects; my largest sample was 22 redds. Confidence intervals for abundance estimates also had lower bounds less than the actual number of distinct redds observed. Program DISTANCE computes confidence intervals based on the $\log_e$ approach of Burnham et al. (1987), but unlike the $\log_e$ approach used to construct intervals for mark-recapture and removal estimates of abundance, intervals constructed in DISTANCE do not guarantee lower bounds equal to or greater than the number of objects observed.

Distance sampling was particularly useful for sampling large-scale areas such as Box Canyon, Last Chance, and Harriman State Park, where a traditional census was not feasible. This method provided an objective approach to searching large-scale areas for spawning activity and quantifying spawning activity therein. Distance sampling is not useful for sampling redds in small tributaries and streams because of their narrow width. For example, a stream 5 m wide can usually be adequately searched from the bank and a

census taken while walking along the stream length would be more efficient and likely more accurate compared to a distance sampling approach. However, distance sampling may be useful for quantifying spawning activity in ponds and lakes, such as for centrarchid nests.

Summary

Distance sampling was used, as an alternative to a census, to sample large-scale areas of the Henrys Fork of the Snake River, Idaho, for rainbow trout spawning redds. Replicate transects perpendicular to flow were traversed by a combination of wading and snorkeling. Perpendicular distances from transects to detected redds were "sampled" and these data were analyzed using the computer program DISTANCE to estimate redd detectability and density. As discharge increased between sampling dates, detectability of redds decreased and most observations were closer to the transects. The effective area sampled was smaller, but an increase in redd density was observed, indicating increased spawning activity and demonstrating the robustness of distance sampling to changes in detectability. Distance sampling provided an unbiased approach to sampling large-scale areas in a river for redds, and may be useful for quantifying nesting spawning activity in similarly large-scale areas in lakes or ponds.

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Table 2.1.—Estimates of redd abundance ($\hat{N}$) and 95% confidence intervals (CI) in the Henrys Fork from Island Park Dam to the United States Geological Survey gauging station (13,750 m²) in 1995, 1996, and 1997. Estimates were obtained using the computer program DISTANCE; effort equaled the sum of transect lengths; ne = no estimate.

Date	Transects	Effort	Observed		
		(m)	redds	$\hat{N}$	95% CI
1995					
27 Apr	13	716.7	22	28	[12, 67]
1996					
30 Mar	10	537.5	2	ne	ne
9 Apr	10	520.6	6	12	[3, 44]
14 Apr	10	551.0	11	11	[4, 30]
21 Apr	10	575.0	9	16	[6, 42]

Table 2.1.—Continued.

Date	Transects	Effort	Observed	$\hat{N}$	95% CI
		(m)	redds		
1997					
11 Mar	10	565.0	0	ne	ne
31 Mar	10	579.0	1	ne	ne
6 Apr	10	608.5	1	ne	ne
13 Apr	15	839.0	0	ne	ne
18 Apr	11	660.5	1	ne	ne
19 Apr	11	606.0	1	ne	ne

Table 2.2.—Summary statistics for sampling of redds in the Henrys Fork from the United States Geological Survey (USGS) gauging station to Harriman State Park. Effort equaled the sum of transect lengths; additional effort included the section length for observations made along banks between transects.

Section	Date	Area (m ²)	Transects	Effort (m) (additional)	Observed redds
USGS gauging station to Buffalo River	27 Apr 1995	14,700	10	421.5 (350)	1 (0)
Box Canyon	17 Apr 1995	270,000	20	1,394 (4,000)	0 (0)
Last Chance	18 Apr 1995	336,800	20	1,946 (4,000)	1 (0)
	20-21 Apr 1997		20	1,820 (4,000)	0 (0)
Harriman State Park	21 Apr 1997	1,013,000	20	2,532 (8,000)	0 (0)

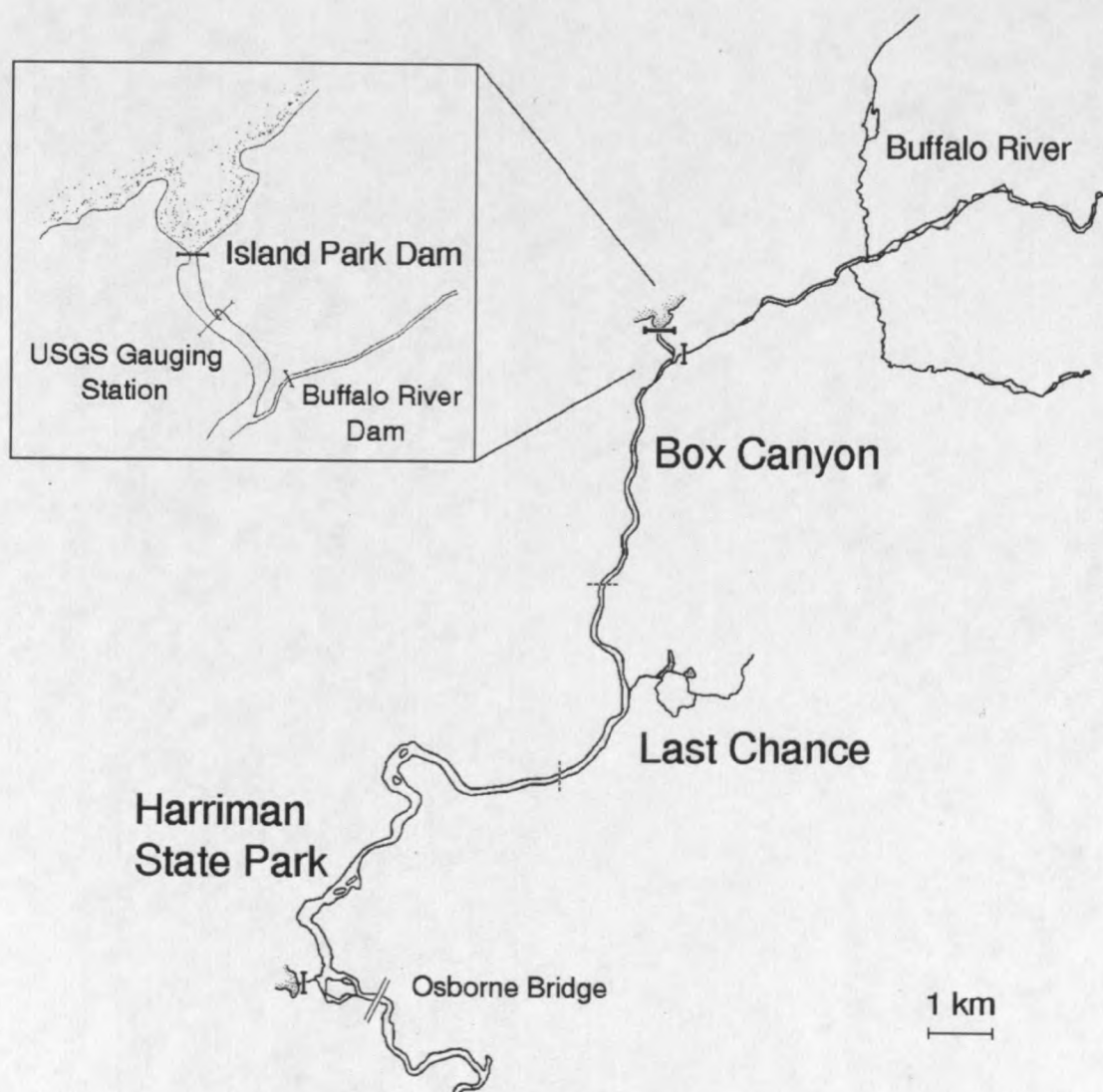


Figure 2.1.—Study sections of the Henrys Fork: 1. Island Park Dam to the United States Geological Survey (USGS) gauging station, 2. USGS gauging station to the Buffalo River, 3. Box Canyon, 4. Last Chance, and 5. Harriman State Park. Lines with end-caps = dams, dashed lines = river section boundaries, and parallel lines = bridge.

CHAPTER 3

A SAMPLING METHODOLOGY TO OBTAIN MARK-RECAPTURE DATA AND AN EVALUATION OF ANALYSIS TECHNIQUES FOR ESTIMATING ABUNDANCES OF AGE-0 RAINBOW TROUT IN A MEDIUM-SIZED RIVER

Introduction

The juvenile component of a fish population is inherently difficult to sample and quantify in large river systems and over large spatial scales. Estimates of juvenile fish abundance in such rivers are often required to quantify the production of juvenile fish, to quantify the recruitment of juvenile fish to successive life stages, and to determine the effects of management actions on juvenile fish survival. I was interested in estimating juvenile rainbow trout *Oncorhynchus mykiss* abundance in an area of the Henrys Fork of the Snake River, Idaho, about 25 km in length and varying from about 50 to 150 m in width.

Many studies of riverine salmonid abundance have been limited to streams less than 10 m wide and have used the removal method to estimate abundance (e.g., Kennedy and Strange 1981; Riley and Fausch 1992; Kruse et al. 1998). Quantitative sampling in rivers of greater width is more difficult. Smaller capture efficiencies necessitate the use of mark-recapture instead of the removal method to estimate abundance. However, abundances of juvenile (i.e., age 0) salmonids can be large in such rivers, rendering capture probabilities too small to get precise abundance estimates when sampling long (e.g., ≥ 1 km) river sections by electrofishing. A 1-km section of the Henrys Fork may contain 20,000 juvenile trout or about 20 trout per 100 m². Sampling such an abundance

of juvenile trout in a river area of this size would result in a very small capture efficiency and possibly no trout recaptured.

A sampling methodology was needed to improve capture efficiency and recapture rate and hence improve estimates of juvenile rainbow trout abundance in the Henrys Fork, to aid the management of the river's trout fishery. I developed and evaluated a sampling methodology to obtain mark-recapture data to estimate abundances of age-0 rainbow trout in the Henrys Fork. Sampling was concentrated in river sample areas that were 100 m long and extended from bank to bank. A greater proportion of juvenile rainbow trout could be marked, and thus recaptured, in sample areas as compared to longer river sections.

Sample areas were physically open because the use of blocking nets in a river such as the Henrys Fork was impractical. However, contingent on a short study period, physically open populations can sometimes be treated as closed (Pollock 1982). If juvenile rainbow trout restrict their activities to a defined area, sample areas may be considered biologically closed (Bohlin et al. 1989).

The assumptions of population closure and equal catchability of individual fish are important to consider when developing and evaluating a sampling methodology. If the assumption of population closure is satisfied, a set of closed-population abundance estimators can be considered for estimating abundance from the sample data. This set of estimators included the Lincoln-Peterson estimator for two capture occasions and the Schumacher-Eschmeyer and Schnabel estimators for multiple capture occasions (Ricker 1975). If the closure assumption is not satisfied, the Jolly-Seber estimator for open populations can be used (Ricker 1975). There is also a set of closed-population

abundance estimators for multiple capture occasions included in program CAPTURE (Otis et al. 1978; Rexstad and Burnham 1991). This set includes estimators for models that are parameterized for various violations of the equal catchability assumption.

I address in the methods section the mark-recapture sampling methodology, the separation of age classes for analysis, the key assumptions associated with abundance estimation, abundance estimators and estimator selection, extrapolation of abundance estimates to areas not sampled, and variables affecting capture probability. In the results section, I first address the simulation results for estimator selection and I then address the analysis of the Henrys Fork data sets.

Study Area

The Henrys Fork is a medium-sized river that had a mean annual discharge of $24.3 \text{ m}^3/\text{s}$ during 1995-1997 at Island Park Dam (range, 6.9 to $78.4 \text{ m}^3/\text{s}$). The Henrys Fork at Island Park Dam is at 1,897 m elevation and drains a $1,246\text{-km}^2$ area. The Buffalo River joins the Henrys Fork about 0.6 km downstream of Island Park Dam (Figure 3.1). The Buffalo River is spring-fed and has a relatively constant discharge of $6 \text{ m}^3/\text{s}$. I divided the Henrys Fork from the confluence with the Buffalo River to Osborne Bridge into the following three sections for sampling juvenile rainbow trout: 1. Box Canyon (length $L = 4 \text{ km}$, mean width $\bar{w} = 70 \text{ m}$), 2. Last Chance ($L = 4 \text{ km}$, $\bar{w} = 95 \text{ m}$), and 3. Harriman State Park ($L = 8 \text{ km}$, $\bar{w} = 125 \text{ m}$) (Figure 3.1). Box Canyon was further divided into upper Box Canyon ($L = 1.5 \text{ km}$) and lower Box Canyon ($L = 2.5 \text{ km}$).

Box Canyon has a high gradient (0.45%) with cobble-boulder substrate and is characterized by an abundance of rocks and woody debris along the banks and sparse

macrophytes across the channel. It was only possible to safely wade across the channel in lower Box Canyon. Upper Box Canyon has areas of rapids, deep holes (i.e., > 1 m deep), and large, uneven substrate. Last Chance has an intermediate gradient (0.3%) with cobble substrate and is characterized by dense macrophyte beds across the channel and a lack of cover along the banks. Harriman State Park has a low gradient (0.1%) with a highly embedded sand-gravel substrate and is characterized by a patchy distribution of dense macrophyte beds, but a general lack of cover in the channel and along the banks. The channel depth is usually less than 1 m in lower Box Canyon, Last Chance, and Harriman State Park.

Methods

Sampling Methodology

Twenty nine mark-recapture data sets were obtained by intensively resampling multiple sample areas in each river section on 3 to 5 capture occasions within 3 to 17-d periods in summer (August) and autumn (October) 1995-1998. A unique fin clip indicated capture histories for each capture occasion. Fin clips were minimal in size to allow mark recognition within the summer or autumn sampling periods and regeneration thereafter. Sample areas were defined as bank-to-bank areas about 100 m long. Limiting the length of the sampling period may have minimized additions or losses to the sample area and allowed for the collection of multiple samples to increase the proportion of juvenile trout captured. I generally sampled every other day to reduce behavioral response to electrofishing (Mesa and Schreck 1989).

A stratified random procedure was used to select the sample areas; sample areas were separated by at least 1 km to reduce the likelihood of trout marked in one sample area moving to another sample area within a season. I sampled two sample areas in Box Canyon, two in Last Chance, and one in Harriman State Park. The same sample areas were used in each season and year.

Juvenile rainbow trout were collected along eight transects perpendicular to the current in each 100-m sample area by wading with boat-mounted electrofishing gear (continuous DC, 175-250 V). One person operated the electrical on-off switch, held the bow of the drift boat, and waded across the river with the boat parallel to the current. An electrode ring was suspended port or starboard in the direction that the boat was moving. Another person, positioned downstream of the electrode ring, netted fish. The amount of effort in each sample area was equal among sampling dates. This sampling method could only be used in areas and seasons in which discharge allowed wading across the width of the river.

Separation of Age-0 and Age-1 Rainbow Trout

Scales were collected from up to 10 juvenile rainbow trout in each 10-mm size class, ranging from 60 to 260 mm total length, in each river section in summer and autumn from 1995 to 1997. Three scales from each trout were pressed onto cellulose acetate slides. I read each set of scales counting the number of annual rings and retained sets for further analysis if age readings were obtained for all three scales. Each fish was assigned the maximum age read from the set of three scales.

Logistic regression was used to partition trout into age classes based on length when the range of lengths for age-0 trout overlapped the range for age-1 trout. The length at which a logistic regression function (fitted to length and age data for a particular river section, season, and year) equaled 0.5 was used as the classification length. Any rainbow trout in the mark-recapture data (for that river section, season, and year) with total length less than the classification length was classified age 0. Logistic regression analyses were performed using the categorical data modeling procedure in SAS (PROC CATMOD; SAS Institute 1994).

Abundance Estimators

An appropriate abundance estimator was selected for each Henrys Fork mark-recapture data set to estimate the abundance of age-0 rainbow trout in a sample area. Estimators were selected from a candidate list of closed-population and open-population abundance estimators. Closed-population estimators included the following estimators in the computer program CAPTURE: Null M_0 , Darroch M_1 , Chao M_1 , Chao M_h , and Chao M_{th} (Otis et al. 1978; Chao 1989; Rexstad and Burnham 1991; Chao et al. 1992). The Null estimator for model M_0 assumes a constant capture probability for each fish on all capture occasions. The Darroch and Chao estimators for model M_1 assume capture probabilities vary with time (i.e., capture occasion). The Chao estimator for model M_h assumes capture probabilities vary for each fish. The Chao estimator for model M_{th} assumes capture probabilities vary for each fish and with time. Closed-population estimators also included the Schumacher-Eschmeyer and Schnabel estimators for multiple censuses and the Lincoln-Petersen estimator for two capture occasions (Ricker

1975). Mark-recapture data were pooled into early (i.e., sampling dates 1, 2, and 3) and late (i.e., sampling dates 4 and 5) samples to use the Lincoln-Petersen estimator. These estimators assume a constant capture probability for each fish. No assumption is made about a constant capture probability with time. The Lincoln-Petersen estimator is actually a special case of the Darroch and Chao M_t estimators for two capture occasions (Otis et al. 1978; Chao 1989). The open-population estimator was the Jolly-Seber estimator (Ricker 1975), which estimates abundance for capture occasions 2, 3, and 4 for a data set including 5 capture occasions.

Model and Estimator Selection

I evaluated the utility of the model selection procedure in CAPTURE for analyzing juvenile rainbow trout mark-recapture data from the Henrys Fork. I performed simulations using the model selection procedure to determine whether or not the procedure can detect known violations of the equal catchability assumption when capture probabilities were small (i.e., < 0.10) and varied with time. Four capture probability scenarios that included temporal variation were examined: 1. $\bar{p} = 0.02$ ($p_1 = 0.01, p_2 = 0.04, p_3 = 0.02, p_4 = 0.02, p_5 = 0.01$), 2. $\bar{p} = 0.046$ ($p_1 = 0.03, p_2 = 0.03, p_3 = 0.05, p_4 = 0.05, p_5 = 0.07$), 3. $\bar{p} = 0.078$ ($p_1 = 0.08, p_2 = 0.07, p_3 = 0.10, p_4 = 0.06, p_5 = 0.08$), and 4. $\bar{p} = 0.106$ ($p_1 = 0.10, p_2 = 0.13, p_3 = 0.08, p_4 = 0.10, p_5 = 0.12$). Simulations were performed for each scenario for 5 population sizes ($N = 1,000; 1,500; 2,000; 2,500; \text{ and } 3,000$) and 1,000 replications. Capture probabilities and population sizes used in all simulations were based on actual Henrys Fork data sets for age-0 rainbow trout.

The model selection procedure in CAPTURE does not select between competing estimators for a particular model (e.g., the Darroch and Chao estimators for model M_1) and does not consider the Lincoln-Petersen, Schumacher-Eschmeyer, Schnabel, or Jolly-Seber estimators. I performed simulations to evaluate the performance of each closed-population and open-population estimator listed earlier. These results were used to identify bias and coverage problems for estimators when capture probabilities were small, and therefore aid in the selection of an estimator.

Simulations were programmed in MATLAB® version 5 (MathWorks, Inc. 1998). Five population sizes (1,000; 1,500; 2,000; 2,500; and 3,000) were sampled under each of the four capture probability scenarios listed earlier (1,000 replications). A capture probability p_{unif} was randomly selected from $\text{uniform}(0, 1)$ for each individual in a population on each capture occasion. If $p_{unif} \leq p_t$ for $t = 1$ to 5, then the individual was considered captured and marked. After five capture occasions, each individual had a capture history indicating on which occasions it was captured. Each sample comprised the capture histories of individuals that were captured at least once. These data were analyzed with each closed-population and open-population estimator to provide an abundance estimate and 95% confidence interval. Confidence intervals for Null M_0 , Darroch M_1 , Chao M_1 , Chao M_h , and Chao M_{th} were constructed assuming the $\log_e$ transformation of the estimated number of animals not captured has an approximate normal distribution (Chao 1989; Rexstad and Burnham 1991). Confidence intervals for the Lincoln-Petersen and Schnabel estimators were constructed assuming the number of recaptures has a Poisson distribution (Ricker 1975). Confidence intervals for the Schumacher-Eschmeyer and Jolly-Seber estimators were constructed assuming

normality. The following statistics were computed: average abundance estimate and standard error, average interval length and standard error, percent interval coverage, and average bias and interval length each expressed as a percentage of the true abundance.

I also examined diagnostic statistics for Henrys Fork data to identify patterns consistent with models M_0 , M_t , and M_h . Diagnostic statistics included the total number of individuals captured in each sample, the number of first captures in each sample, and recapture frequencies. Data consistent with models M_0 and M_h have on average the same number of individuals captured on each occasion and a steady decline from the average sample size in the number of first captures. Frequencies of multiple recaptures are considerably higher for model M_h versus model M_0 . Data consistent with model M_t show erratic changes in the total number of individuals captured and the number of first captures.

Population Closure

Henrys Fork Study

The closure assumption was tested for sample areas for within-season sampling periods. That is, I wanted to determine how much movement upstream or downstream out of a 100-m sample area occurred within a seasonal sampling period. Juvenile rainbow trout were marked and recaptured in 50-m areas upstream and downstream adjacent to sample area 1 in Last Chance in summer 1996 and 1997 and in autumn 1996. A unique fin clip was assigned to each adjacent area to identify movement into and out of the sample area. Adjacent 50-m areas were sampled on the last capture occasion for all 100-m sample areas in Box Canyon and Last Chance in both summer and autumn 1997 to

Henrys Fork Abundance Estimates, Indices, and Extrapolation

Seasonal estimates of age-0 rainbow trout abundance were obtained for sample areas using an estimator selected as described earlier. I calculated capture efficiency and recapture rate for each sample area abundance estimate. Capture efficiency was equal to the total number of captures as a percentage of the estimated abundance. Seventeen mark-recapture data sets that included five capture occasions were analyzed using the first three occasions, the first four occasions, and all five occasions to determine how increasing the number of capture occasions improved capture efficiency and estimate precision.

I calculated average abundance estimates for sample areas in Box Canyon and Last Chance in each season and year to use as indices of abundance for river sections. Average abundance estimates included within- and among-sample area error terms.

Average abundance estimates obtained for 100-m sample areas in lower Box Canyon and Last Chance were extrapolated for each river section to estimate total abundance; extrapolated abundance estimates for Harriman State Park were only obtained for the 1-km area downstream of the Railroad Bridge (Figure 3.1). Confidence intervals for total abundance estimates included within-sample area, among-sample area, and extrapolation error terms.

Variables Affecting Capture Probability

I investigated how the following variables were related to capture probability in the Henrys Fork data sets: discharge, season, river section, and relative sampling date.

Relative sampling date was a standardized measure of the sequence of sampling dates in which the first sampling date for a sample area in each season is assigned 1. (For example, five capture occasions that occurred every other day would be assigned dates 1, 3, 5, 7, and 9.) I computed Pearson correlation coefficients (r) and coefficients of determination (r^2) using PROC CORR in SAS (SAS Institute, 1994).

Results

Model and Estimator Selection

Model Selection in Program CAPTURE

The model selection procedure in program CAPTURE did not provide results for simulations under the capture probability scenario of model M_t with $\bar{p}=0.02$. The data-generating model M_t was correctly selected with greater frequency as population size increased from 1,000 to 3,000 and as $\bar{p}$ increased from 0.046 to 0.106 (Table 3.3). Model $M_{t_{bh}}$ was selected most frequently at $\bar{p}=0.046$ (52.0% to 78.3%). (There is no estimator in CAPTURE for model $M_{t_{bh}}$.) Model M_t was selected most frequently at $\bar{p}=0.078$ (49.5% to 86.5%) and $\bar{p}=0.106$ (66.5% to 89.3%). The model selection procedure did not select between the Darroch and Chao estimators for model M_t .

Model Selection by Simulation

The Chao M_t estimator performed best overall, in terms of bias and interval coverage, for the simulated capture scenarios and population sizes (Appendix Tables A.2-A.4). Average bias, expressed as a percentage of the true abundance, was generally

smaller than $\pm 1\%$ for closed populations (Figure 3.2). There was increasing positive bias as the emigration rate increased; average bias was about 4 to 5% at a 5% emigration rate and about 9 to 10% at a 10% emigration rate. Average bias gradually decreased at all levels of emigration as $\bar{p}$ increased from 0.02 to 0.106. Percent interval coverage was about 93% at $\bar{p}=0.02$ and increased to the nominal level of 95% for an emigration rate of 10% (Figure 3.3). Percent interval coverage was about 94% at $\bar{p}=0.046$ for 0%, 5%, and 10% emigration. The nominal coverage level was achieved at $\bar{p}=0.078$ and 0.106 for a closed population, but coverage decreased to as low as 67.9% as N increased to 3,000 and the emigration rate increased to 10%. Average interval length, expressed as a percentage of the true abundance, decreased as N and $\bar{p}$ increased and increased as the emigration rate increased (Figure 3.4). The greatest decreases in average interval length occurred with increases in $\bar{p}$; average interval length decreased by 62%, 79%, and 85% as $\bar{p}$ increased from 0.02 to 0.046, 0.078, and 0.106.

The Darroch M_t estimator performed about as well as the Chao M_t estimator at $\bar{p}=0.046$ to 0.106, but performed poorly at $\bar{p}=0.02$. The Darroch M_t estimator had a large negative bias that was greater than 10% at $\bar{p}=0.02$ and decreased to about 8% as N and the emigration rate increased (Figure 3.2). Percent interval coverage exceeded the nominal level of 95% at $\bar{p}=0.02$; coverage was greater at larger N and emigration rates (Figure 3.3). Average interval length was shorter than that of the Chao M_t estimator at $\bar{p}=0.02$ (Figure 3.4).

The Null M_o estimator performed about as well as the Chao M_t estimator at $\bar{p}=0.078$ and 0.106, but performed poorly at $\bar{p}=0.02$ and 0.046. The Null M_o estimator

had a large negative bias that was greater than 8% at $\bar{p}=0.02$ and decreased to about 6% as N and the emigration rate increased (Figure 3.2). Average bias was positive at $\bar{p}=0.046$; bias was about 5% for a closed population, about 10% for an emigration rate of 5%, and about 15% for an emigration rate of 10%. Percent interval coverage exceeded the nominal level of 95% at $\bar{p}=0.02$, similar to the Darroch M_t estimator (Figure 3.3). Coverage was about at the nominal level at higher values of $\bar{p}$ for closed populations, but decreased to a greater extent compared to the Chao M_t estimator for emigration rates of 5% and 10%. Average interval length was shorter than that of the Chao M_t estimator and about the same as that of the Null M_0 estimator (Figure 3.4).

The Chao M_h estimator performed poorly, having large positive bias and poor interval coverage. Abundance estimates were not obtained for $N = 1,000, 1,500$, and $2,000$ at $\bar{p}=0.02$. Positive bias decreased from about 50% at $\bar{p}=0.02$ to about 15% at $\bar{p}=0.106$ for closed populations and increased as emigration rate increased. Percent interval coverage was 88% at $\bar{p}=0.02$ for closed populations and decreased to as low as 2.1% as N , $\bar{p}$, and emigration rate increased.

The Chao M_{th} estimator performed poorly at $\bar{p}=0.02$ but improved as $\bar{p}$ increased to 0.106. Abundance estimates were not obtained for $N = 1,000, 1,500$, and $2,000$ at $\bar{p}=0.02$. Positive bias decreased from about 33% at $\bar{p}=0.02$ to about 3% at $\bar{p}=0.106$ for closed populations and increased as emigration rate increased. Percent interval coverage and average interval length changed in a pattern similar to the Chao M_t estimator with smaller coverage and larger interval length.

The Lincoln-Petersen estimator performed satisfactorily at small values of $\bar{p}$ and an emigration rate of 10% (Figures 3.2-3.4), but performed poorly at smaller values of $\bar{p}$ for closed populations and at larger values of $\bar{p}$. Unlike the estimators in program CAPTURE, negative bias increased as $\bar{p}$ increased, bias decreased and percent interval coverage increased as emigration rate increased, and average interval length increased as N increased at $\bar{p}=0.02$ (Figure 3.4).

The Schumacher-Eschmeyer estimator performed poorly at $\bar{p}=0.078$ and 0.106 and no abundance estimates were obtained at $\bar{p}=0.02$ and 0.046 . Average bias was negative and exceeded 30% for closed populations. Like the Lincoln-Petersen estimator, bias increased as $\bar{p}$ increased and bias decreased and percent interval coverage increased as emigration rate increased. Percent interval coverage exceeded the nominal level of 95% and average interval length was about four times greater than for other estimators.

The Schnabel estimator performed poorly, having negative bias that exceeded 40% for closed populations and having poor interval coverage. Abundance estimates were not obtained for $N = 1,000, 1,500, 2,000,$ and $2,500$ at $\bar{p}=0.02$. Like the Lincoln-Petersen and Schumacher-Eschmeyer estimators, bias decreased as emigration rate increased. Percent interval coverage decreased as N , $\bar{p}$, and emigration rate increased. Coverage was less than 20% at $\bar{p}=0.078$ and less than 10% at $\bar{p}=0.106$. Average interval length was about two times greater than for other estimators.

Abundance estimates were not obtained for the Jolly-Seber estimator at all values of N , $\bar{p}$, and emigration rates.

Henry's Fork Study

Separation of Age-0 and Age-1 Rainbow Trout

There was no overlap in length ranges of age-0 and age-1 rainbow trout, as identified by reading scales, in Box Canyon and Last Chance in summer 1995 and 1996, in Last Chance in autumn 1996, and in Harriman State Park in all sampling seasons and years (Table 3.1). There were zero or one age-1 rainbow trout identified in seven of nine sections, seasons, and years for which there was no overlap in length ranges identified (Table 3.1). A classification length separating age-0 and age-1 rainbow trout was estimated using logistic regression for Box Canyon and Last Chance in autumn 1995 and summer and autumn 1997, and for Box Canyon in autumn 1996 (Table 3.2). The probability of correctly classifying a rainbow trout as age 0 ranged from 0.93 to 1 and the probability of correctly classifying a rainbow trout as age 1 ranged from 0.60 to 0.97 (Table 3.2).

Population Closure

Most age-0 rainbow trout that were recaptured in sample areas in Box Canyon and Last Chance, or in areas upstream or downstream adjacent to sample area 1 in Last Chance, were in the area they were marked (Table 3.4). About 85% (44 of 52) of trout recaptured on the last sampling occasion (when adjacent areas were only sampled on the last occasion) were in the area they were marked; about 15% were recaptured outside of a sample area (5 upstream and 3 downstream). There was no consistent pattern of emigration direction (i.e., upstream versus downstream) when considering all samples; however, more trout were recaptured downstream (23) than upstream (14). There was a

decreasing trend in the number of recaptured trout as the distance from the marking area (i.e., areas adjacent to sample area 1 in Last Chance) increased, both upstream and downstream.

Capture Diagnostics

There were erratic changes by sampling occasion in the total number of individuals captured and the number of first captures for all mark-recapture data sets from sample areas in the Henrys Fork (Appendix Table A.5). These patterns of captures were consistent with model M_t . Most age-0 rainbow trout were captured one time (93.8%; sample size = 9,247); 5.8% were captured two times, 0.4% were recaptured three times, and none were recaptured four or five times (Appendix Table A.5). These small frequencies of multiple recaptures were not consistent with model M_h .

Representative Sample Areas

There was no significant difference between the number of age-0 rainbow trout captured per transect within and outside of sample areas for Box Canyon in summer 1997 and for Last Chance in summer and autumn 1997 (Table 3.5). There were more trout captured per transect within versus outside of sample areas for Box Canyon in autumn 1997 (Table 3.5).

Abundance Estimates

Abundance estimates for sample areas were obtained using the Chao M_t estimator because the Chao M_t estimator performed best in simulations based on Henrys Fork data sets, with minimal bias and interval coverage near or at the nominal level. Abundance

estimates ranged from 778 to 8,175 with a median of 2,383 (Appendix Table A.5). The mean capture probability ranged from 0.01 to 0.126 with a median of 0.036 (Appendix Table A.5). The capture efficiency ranged from 4.2 to 62.4% with a median of 16.7% and the recapture rate ranged from 0.7 to 22.4% with a median of 5.4% (Appendix Table A.5).

The average capture efficiency increased from 14.2% to 17.4% and 20.0% as the number of capture occasions increased from 3 to 4 and 5; the average standard error for abundance estimates decreased from 817.4 to 551.8 and 468.4.

Box Canyon and Last Chance indices of abundance (i.e., the average of two sample areas) and extrapolated abundance estimates for 1995-1997 indicated that the highest abundances of age-0 rainbow trout occurred in 1996 and the lowest abundances occurred in 1995 for each season (Tables 3.6 and 3.7). Indices of abundance and extrapolated abundance estimates showed either no change or decreases between summer and autumn of each year. Age-0 rainbow trout density (i.e., number per 100-m sample area) was higher in Last Chance versus Box Canyon in all seasons and years (Table 3.6); density was lowest in Harriman State Park (Appendix Table A.5).

Variables Affecting Capture Probability

Season, discharge, river section, and relative sampling date did not explain much of the variation in capture probability. Capture probability was weakly correlated with season ($r^2 = 0.30$) and discharge ($r^2 = 0.18$); capture probability was not correlated with river section ($r^2 = 0.03$) and relative sampling date ($r^2 = 0.03$). The correlation between capture probability and season was positive ($r = 0.55$), indicating a trend towards

increased capture probability in autumn versus summer. The correlation between capture probability and discharge was negative ($r = -0.42$), indicating a trend towards decreased capture probability at higher levels of discharge.

Discussion

Sampling Methodology

Abundances of age-0 trout can be large in rivers the size of the Henrys Fork. A small proportion of marked trout is recaptured in studies of large populations, resulting in wide confidence intervals (Cormack 1992). The precision of abundance estimates depends on the number of trout captured (i.e., capture efficiency) and the number recaptured. I showed that mark-recapture sampling of age-0 rainbow trout in the Henrys Fork can be concentrated in 100-m sample areas, thereby improving capture efficiency and recapture rate. Capture efficiency and estimate precision improved as the number of capture occasions increased from three to five. The resultant mark-recapture data could then be analyzed using a closed-population abundance estimator that has minimal bias and interval coverage near or at the nominal level.

Population Closure

Sample areas were physically open because the use of blocking nets in a river as wide as the Henrys Fork was impractical. However, contingent on a short study period, physically open populations can sometimes be treated as closed (Pollock 1982). I could not conduct a statistically valid test for population closure based only on the mark-

recapture data for a sample area because such a test cannot be constructed (White et al. 1982). A test for closure is included in program CAPTURE and assumes model M_h as the null model. However, the test has low power, true failure of the closure assumption cannot be differentiated from behavioral variation in capture probabilities or from certain patterns of temporal variation, and temporary emigration cannot be detected.

Mark-recapture data for sample areas and adjacent areas upstream and downstream indicated that most marked trout remained in the area they were marked through a series of capture occasions. If juvenile rainbow trout restrict their activities to a defined area, sample areas may be considered biologically closed (Bohlin et al. 1989). Koenig and Coleman (1998) observed low rates of juvenile gag *Mycteroperca microlepis* movement in sea grass in 150-m square sampling stations in St. George Sound in the northeastern Gulf of Mexico; they suggested that for future studies sampling stations be considered closed for purposes of abundance estimation. Similarly, juvenile rainbow trout in the Henrys Fork tended to conceal themselves in the interstitial space of the rocky substrate, in woody debris, and in macrophytes. The slow, methodical process of electrofishing along transects across the river was particularly effective at capturing juvenile trout because of this tendency towards concealment, even when disturbed.

Biological closure of sample areas was not absolute as indicated by the recapture of trout in areas adjacent to the area in which they were marked. Trout that were captured and marked were removed from their home range; upon release, these trout had to move to locate the area from which they were removed or relocate to a new home range. Cutthroat trout *Oncorhynchus clarki* subjected to electrofishing mark-recapture in

streams immediately seek cover upon release (Mesa and Schreck 1989). Some marked juvenile rainbow trout may have left a sample area in their search for cover.

The emigration of unmarked fish may have occurred, but such movement could not be measured. Fish that are stunned by electrofishing and not captured will drift before regaining control and seeking cover. Some may drift out of a sample area (in particular, those stunned near the downstream end of a sample area) and all will be induced to move in order to locate the area from which they were removed or to relocate to a new home range. Observations made by both personnel while electrofishing indicated that few juvenile trout were stunned and drifted downstream. Therefore, such movement may be negligible.

Mark-recapture data for juvenile rainbow trout in the Henrys Fork indicated that capture probabilities were small (e.g., the median capture probability was 0.036). This special nature of the data may render minor violations of the closure assumption insignificant in relation to abundance estimation. I showed by simulation that 95% confidence intervals achieved a coverage level of about 92-95% for the Chao M_t estimator when $N = 1,000$ to $3,000$, $\bar{p} = 0.046$ and the emigration rate was 10%.

Equal Catchability of Individuals

The assumption of equal catchability of individuals often conflicts with biological reality (Bohlin and Sundstrom 1977). Intraspecific variation in behavioral dominance, feeding behavior, predator avoidance, and habitat use is common (Magurran 1986; Elliott 1994). Trout may also exhibit a behavioral (trap-shy) response to electrofishing (Cross and Stott 1975; Mesa and Schreck 1989). Effort was taken to reduce temporal variation,

behavioral variation, and individual heterogeneity in capture probabilities in order to reduce model parameterization such that the simplest model possible is the most appropriate model for the data (White et al. 1982; Pollock et al. 1990). However, the small capture probabilities encountered limit how much we can parameterize a model. That is, a violation of the equal catchability assumption may occur, but may not be detectable in the data.

Temporal variation was limited by expending equal effort in a sample area on each sampling occasion. However, the data did exhibit erratic changes by sampling occasion in the total number of individuals captured and the number of first captures. Discharge and season explained some of the variation in capture probability, but much of the variation remained unexplained. Changes in discharge may obscure the netter's visibility of juvenile trout and change the probability that an individual trout is susceptible to electrofishing. The cooler water temperature in autumn may slow trout response time, thereby increasing susceptibility to capture. This was evident in the increased capture of larger trout in autumn (i.e., trout > 200 mm total length). Age-0 trout were larger in autumn than they were in summer and therefore may have been more susceptible then.

Fish have been observed to respond behaviorally to electrofishing mark-recapture. Capture probabilities decreased in subsequent capture periods at 2-h intervals for marked roach *Rutilus rutilus*, gudgeon *Gobio gobio*, and rudd *Scardinius erythrophthalmus*, and such a behavioral response is also likely for rainbow trout (Cross and Stott 1975). However, at intervals greater than 24 h, marked fish did not appear to be less catchable. A similar behavioral response to electrofishing mark-recapture occurred in cutthroat trout

(Mesa and Schreck 1989). At least 24 h was required for wild trout to return to normal behavior such that capture probability would not be reduced. Capture occasions for juvenile rainbow trout in the Henrys Fork were usually at least every other day in order to reduce the effects of behavioral variation on capture probability. There was no correlation between capture probability and relative sampling date, which suggests that there was no significant behavioral response to electrofishing.

Heterogeneity in individual capture probabilities is likely to occur to some degree in all mark-recapture studies (Chao 1989; Pollock et al. 1990). Electrofishing is widely recognized as a size-selective sampling technique that favors capture of larger individuals (e.g., White et al. 1982; Bohlin et al. 1989; Jones and Stockwell 1995). Length-frequency data from the Henrys Fork indicated that the electrofishing method used in sample areas was not biased toward capturing large trout. On the contrary, the capture of large trout appeared to be less likely. This may have resulted from the slow, methodical approach to electrofishing these areas. Larger trout tended to react to the slowly approaching intermittent electric field by attempting to escape it while juvenile trout sought or remained concealed in cover.

Model and Estimator Selection

Multiple-recapture data sets for age-0 rainbow trout in the Henrys Fork were characterized by a large number of individuals captured once and very few individuals captured two or three times. No individuals were captured more than three times. Estimated abundances were usually greater than 2,000 and capture probabilities were usually less than 0.05, even in intensively sampled areas of reduced size (i.e., 100-m

sample areas). Such data is termed “sparse” (Chao 1988, 1989). Preferred estimators should be robust to departures from catchability assumptions because it is usually impossible to test such assumptions with sparse data.

Program CAPTURE contains an objective procedure for selecting the most appropriate model for a given data set. However, the procedure is not very reliable (Menkens and Anderson 1988; Pollock et al. 1990; Seber 1992). I found that the linear discriminant classifier in CAPTURE frequently selected the wrong generating model for simulated sparse data sets analogous to field-collected data from the Henrys Fork.

Stanley and Burnham (1998) developed new classifiers to select a best estimator, rather than a best generating model, but found that the new classifiers also performed poorly.

Other approaches to model or estimator selection, such as the information theoretic approach (Burnham and Anderson 1998) and the use of likelihood ratio tests, are not practical. Some models in CAPTURE have likelihood equations with non-identifiable parameters, some estimators do not have a likelihood form, and some models are not nested.

We cannot know or identify the true generating model for field-collected data because such a model may have an effectively infinite number of parameters and the data set that is used to select a model is finite. The goal is to select a parsimonious model that is supported by the data. A parsimonious model achieves a balance between bias and variance and parameterizes effects supported by the data (Burnham and Anderson 1998). A sparse data set cannot support a highly parameterized model.

I used a simulation approach with sparse data sets (based on actual Henrys Fork data sets) to evaluate the performance of the estimators for the models in CAPTURE.

This approach, while not an objective means to select the likely generating model for a data set, identifies estimators that perform well in terms of bias and coverage properties for data simulated under a known generating model. This approach also allowed us to evaluate estimators not in CAPTURE, but commonly used by fisheries professionals (i.e., the Lincoln-Petersen, Schumacher-Eschmeyer, and Schnabel estimators). Simulated data were generated under the temporal variation model M_t because diagnostic statistics for Henrys Fork data were consistent with temporal variation in capture probability and did not suggest behavioral variation or individual heterogeneity in capture probability.

I found that the Chao M_t estimator performed best for sparse data generated under model M_t with N ranging from 1,000 to 3,000, $\bar{p}$ ranging from 0.02 to 0.106, and emigration rate ranging from 0% to 10%. The Chao M_t estimator was developed for sparse data sets and is based on lower-order capture frequency counts (i.e., the number of individuals captured exactly once or twice) (Chao 1989). This estimator is suitable for Henrys Fork data sets because few trout were ever captured more than two times.

The Null M_0 and Darroch M_t estimators performed about as well as the Chao M_t estimator for certain simulated capture scenarios. However, I do not recommend their use when abundances are large and capture probabilities are small and when the possibility exists for low levels of emigration because these estimators did not perform consistently as well as the Chao M_t estimator. I also do not recommend the use of estimators for heterogeneity models for such data. Capture diagnostic statistics were not consistent with individual heterogeneity in capture probability. I also do not recommend the use of the Schumacher-Eschmeyer, Schnabel, and Jolly-Seber estimators. These estimators require high capture rates for precise estimates and generally did not produce

estimates for sparse data sets. Osmundson and Burnham (1998) also found that the Jolly-Seber estimator was inappropriate for sparse data sets for adult Colorado squawfish *Ptychocheilus lucius* (estimates of capture probability ranged from 0.074 to 0.194).

The Darroch and Chao M_t estimators both reduce to the Lincoln-Petersen estimator for the special case of two capture occasions (Otis et al. 1978; Chao 1989). Multiple capture data can be pooled into two capture occasions to use the Lincoln-Petersen estimator. Menkins and Anderson (1988) found the Lincoln-Petersen estimator to be preferable when model selection is poor. The Lincoln-Petersen estimator generally performed poorly in my simulations of sparse data. One reason for such poor performance may be the loss of information when pooling capture occasions. For example, if a trout is marked on occasion 1 and recaptured on occasion 3 and capture occasions 1, 2, and 3 are pooled into one occasion, that recapture information is lost and not used in analysis. The use of the Lincoln-Petersen estimator is also subjective when there are more than two capture occasions. The researcher or manager has to decide how to partition multiple capture occasions into one occasion in which fish were marked and one occasion in which fish were inspected for marks. I recommend analyzing multiple capture data as multiple capture data and not pooling capture occasions for use with the Lincoln-Petersen estimator.

Representative Sample Areas

Mark-recapture is a labor-intensive sampling process. I could only sample a small percentage of the total area in a river section because one electrofishing crew could only sample two sample areas per day. Therefore it was important that the areas sampled

were representative of the river section as a whole if I was to use the data as indices of abundance or extrapolate the data to areas not sampled.

A comparison of the number of age-0 rainbow trout captured per transect within and outside of sample areas in Last Chance indicated that the sample areas were representative of the river section as a whole. The habitat was generally uniform in Last Chance. There was a lack of cover along the banks and dense macrophyte beds across the channel throughout the section. Therefore it was unlikely that a sample area would contain much more or less cover than other areas of the river section and hence be biased towards a high or low abundance.

A comparison of catch per effort for transects in Box Canyon indicated that the catch was greater in sample areas in one season but not in another. However, this does not necessarily mean that abundances were sometimes greater in the sample areas. Box Canyon was characterized by an abundance of rocks and woody debris along the banks. Many age-0 trout were often captured near fallen trees. Transects in the sample areas were selected such that concentrations of age-0 trout would be captured, thereby improving capture efficiency. Transects outside of sample areas in Box Canyon were random and were not selected to include concentrations of age-0 trout. Therefore, comparisons of transects in Box Canyon may not have been an appropriate method to determine whether or not sample areas were representative of the river section.

Henrys Fork Abundance Estimates

Indices of abundance and extrapolated abundance estimates showed the same year-to-year trends for Box Canyon and Last Chance in summer and autumn 1995-1997.

Abundances were highest in 1996 and lowest in 1995. These trends indicated that changes in abundances over time occurred throughout the river sections and did not result from a redistribution of fish. These trends also suggested that sampling multiple 100-m sample areas was an effective methodology to monitor changes in age-0 trout abundance in a river such as the Henrys Fork. Similar methodologies have been used to estimate abundance of juvenile fishes in other systems. Koenig and Coleman (1998) sampled juvenile gag in 150-m square sampling stations (divided into six sampling lanes) and extrapolated abundance estimates to sea grass areas not sampled.

Summary

I developed and evaluated a sampling methodology to obtain mark-recapture data to estimate abundances of age-0 rainbow trout in an area of the Henrys Fork of the Snake River, Idaho, that varied in width from 50 to 150 m. Sampling by electrofishing was concentrated in river sample areas that were 100 m long and extended from bank to bank. The assumptions of population closure and equal catchability of individuals were addressed with field-collected data and simulation. I evaluated closed population (Null M_0 , Darroch M_t , Chao M_t , Chao M_h , Chao M_{th} , Schumacher-Eschmeyer, Schnabel, and Lincoln-Petersen) and open population (Jolly-Seber) abundance estimators by simulation. Simulated abundances ranged from 1,000 to 3,000, average capture probabilities (incorporating temporal variation) ranged from 0.02 to 0.106, and emigration rates were 0%, 5%, or 10% for marked fish. The Chao M_t estimator performed best with minimal bias and interval coverage near or at the nominal level; this estimator was also robust to minor violations of the closure assumption. The Chao M_t estimator was developed for

sparse data sets and is based on lower-order capture frequency counts (i.e., the number of individuals captured exactly once or twice). Capture diagnostic statistics for Henrys Fork data indicated temporal variation in capture probabilities. The median capture probability was 0.036, the median capture efficiency was 16.7%, and the median recapture rate was 5.4%. Sample areas were found to be representative of river sections based on comparisons of catch per effort within and outside of sample areas. Therefore, average abundance estimates for sample areas provided indices of abundance and extrapolated estimates provided total abundance estimates for a river section.

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Table 3.1.—Number and length range of age-0 and age-1 rainbow trout identified by reading scales.

Sampling		Number of	Number of	Age-0 length	Age-1 length
Season	River section	age-0 trout	age-1 trout	range (mm)	range (mm)
1995					
Summer	Box Canyon	76	1	44-120	160
	Last Chance	69	0	50-133	--
Autumn	Box Canyon ^a	129	8	49-195	169-217
	Last Chance ^a	119	3	52-199	188-220
	HSP	38	0	75-196	--
1996					
Summer	Box Canyon	76	25	60-139	155-221
	Last Chance	107	7	61-139	171-216
	HSP	38	0	52-103	--
Autumn	Box Canyon ^a	111	5	62-183	180-216
	Last Chance	83	7	65-171	196-217

Table 3.1.—Continued.

Sampling Season	River section	Number of age-0 trout	Number of age-1 trout	Age-0 length range (mm)	Age-1 length range (mm)
1997					
Summer	Box Canyon ^a	51	64	90-170	160-253
	Last Chance ^a	59	73	90-159	151-248
	HSP	19	1	60-102	193
Autumn	Box Canyon ^a	123	22	74-199	174-258
	Last Chance ^a	85	5	93-193	170-217
	HSP	118	0	72-181	--

^a Logistic regression used to estimate length for classifying rainbow trout as age 0 or age

1. -

Table 3.2.—Number of age-0 and age-1 rainbow trout identified by reading scales and estimated total length (mm) separating these age classes (i.e., classification length). Classification length was estimated using logistic regression (β_0 = intercept; β_1 = slope). $P(\text{age } 0 \mid \text{age } 0)$ = probability of classifying a trout as age 0 given that the trout is age 0 ($P(\text{age } 1 \mid \text{age } 1)$ = probability of classifying a trout as age 1 given that the trout is age 1) using the logistic regression equation and classification length.

Sampling		Number of	Number of	Parameter					Classification	
Season	River section	age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
1995										
Autumn	Box Canyon	129	8	β_0	-22.7532	(7.1184)	0.0014	0.98	0.88	182 mm
				β_1	0.1242	(0.0400)	0.0019			
	Last Chance	119	3	β_0	-34.7767	(17.2950)	0.0443	1	0.67	200 mm
				β_1	0.0443	(0.0906)	0.0551			

Table 3.2—Continued.

Sampling		Number of	Number of	Parameter						Classification
Season	River section	age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
1996										
Autumn	Box Canyon	111	5	β_0	-72.8275	(52.1161)	0.1623	0.99	0.80	183 mm
				β_1	0.3983	(0.2878)	0.1664			
1997										
Summer	Box Canyon	51	64	β_0	-50.3360	(16.6355)	0.0025	0.94	0.95	165 mm
				β_1	0.3049	(0.1006)	0.0024			
	Last Chance	59	73	β_0	-54.1926	(18.2134)	0.0029	0.93	0.97	156 mm
				β_1	0.3480	(0.1157)	0.0026			

Table 3.2—Continued.

Sampling		Number of	Number of	Parameter					Classification	
Season	River section	age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
Autumn	Box Canyon	123	22	β_0	-26.4600	(7.0017)	0.0002	0.97	0.82	183 mm
				β_1	0.1435	(0.0384)	0.0002			
	Last Chance	85	5	β_0	-23.6526	(8.8096)	0.0073	0.99	0.60	180 mm
				β_1	0.1304	(0.0518)	0.0118			

Table 3.3.—Percent selection of models M_o , M_h , M_b , M_{bh} , M_t , M_{th} , M_{tb} , and M_{tbh} by the model selection procedure in program CAPTURE. Mark-recapture data were simulated under model M_t for four capture probability scenarios ($\bar{p}$ ranged from 0.02 to 0.106) and five population sizes ranging from 1,000 to 3,000; $t=5$ capture occasions, 1,000 replications. Note: The model selection procedure in CAPTURE does not select among competing estimators for a particular model (e.g., the Darroch and Chao estimators for model M_t) and there is no estimator for model M_{tbh} .

Model	Population size				
	1,000	1,500	2,000	2,500	3,000
1. $p_1=0.01, p_1=0.04, p_1=0.02, p_1=0.02, p_1=0.01; \bar{p}=0.02$					
No model selection results					
2. $p_1=0.03, p_1=0.03, p_1=0.05, p_1=0.05, p_1=0.07; \bar{p}=0.046$					
M_o	1.8	0	0	0	0
M_h	2.9	0.5	2.2	3.1	3.3
M_b	0	0	0	0	0
M_{bh}	0	0	0	0	0
M_t	11.5	19.5	25.8	31.0	36.8
M_{th}	5.5	6.6	7.4	7.5	7.9
M_{tb}	0	0	0	0	0
M_{tbh}	78.3	73.4	64.6	58.4	52.0

Table 3.3.—Continued.

Model	Population size				
	1,000	1,500	2,000	2,500	3,000
3. $p_1=0.08, p_1=0.07, p_1=0.10, p_1=0.06, p_1=0.08; \bar{p}=0.078$					
M_o	20.7	6.5	1.4	0.6	0
M_h	4.1	1.8	0.3	0	0
M_b	0.4	0.3	0	0	0
M_{bh}	0.3	0	0	0	0
M_t	49.5	71.1	80.2	84.3	86.5
M_{th}	18.7	13.1	11.1	7.7	5.7
M_{tb}	4.1	6.5	6.2	7.1	7.6
M_{tbh}	2.2	0.7	0.8	0.3	0.2
4. $p_1=0.10, p_1=0.13, p_1=0.08, p_1=0.10, p_1=0.12; \bar{p}=0.106$					
M_o	10.4	1.7	0.1	0.1	0
M_h	0.9	0.3	0	0	0
M_b	0	0	0	0	0
M_{bh}	0	0	0	0	0
M_t	66.5	83.4	86.9	88.7	89.3
M_{th}	18.4	10.1	8.0	6.5	6.4
M_{tb}	3.1	4.0	4.7	4.4	4.2
M_{tbh}	0.7	0.5	0.3	0.3	0.1

Table 3.4.—Total number of captures of age-0 rainbow trout and the distribution of recaptures in sample areas (100 m) and the adjacent areas upstream (50 m) and downstream (50 m) in summer and autumn 1996 and 1997. In parentheses are numbers on trout marked and recaptured only on day(s) adjacent areas were sampled

Capture area	Total captured	d	Recapture area		
			Upstream	Sample area	Downstream
Box Canyon					
Summer 1997					
Upstream	44	1	--	--	--
Sample area 1	331	5	1 (0)	18 (7)	0
Downstream	44	1	--	--	--
Autumn 1997					
Upstream	43	1	--	--	--
Sample area 2	267	5	1 (0)	9 (2)	0
Downstream	26	1	--	--	--

Table 3.4.—Continued.

Capture area	Total captured	d	Recapture area		
			Upstream	Sample area	Downstream
Autumn 1997					
Upstream	53	1	--	--	--
Sample area 1	419	4	2	43 ^a (23)	1
Downstream	54	1	--	--	--
Last Chance					
Summer 1996					
Upstream	280	5	7	4	0
Sample area 1	510	5	2	13 ^b	3
Downstream	219	5	0	0	7
Autumn 1996					
Upstream	223	3	12 (0)	6 (1)	0
Sample area 1	927	5	0	68 ^a (24)	6 ^c (5)
Downstream	222	3	0	5 (2)	12 (0)

Table 3.4.—Continued.

Capture area	Total captured	d	Recapture area		
			Upstream	Sample area	Downstream
Summer 1997					
Upstream	148	5	3	1	0
Sample area 1	387	5	1	13 ^b	0
Downstream	150	5	1	0	9 ^b
Upstream	25	1	--	--	--
Sample area 2	207	5	0	5 ^b (2)	1 (0)
Downstream	19	1	--	--	--
Autumn 1997					
Upstream	75	1	--	--	--
Sample area 1	502	4	1 (0)	23 ^b (10)	1 ^c (0)
Downstream	58	1	--	--	--

^a Three trout were recaptured twice.

^b One trout was recaptured twice.

^c One trout captured on day 1 and 3 in sample area 1.

Table 3.5.—Average number of age-0 rainbow trout captured per transect (n) within and outside of sample areas for the first capture occasion in Box Canyon and Last Chance in summer and autumn 1997 ($N = 16$).

River section	Within sample areas		Outside of sample areas		<i>P</i>
	<i>n</i>	(SE)	<i>n</i>	(SE)	
Summer 1997					
Box Canyon	18.1	(2.4)	14.9	(2.3)	0.33
Last Chance	15.2	(2.4)	17.8	(2.3)	0.43
Autumn 1997					
Box Canyon	22.8	(1.8)	10.3	(1.7)	0.0001
Last Chance	16.0	(2.2)	16.9	(2.5)	0.80

Table 3.6.—Average abundance estimates for two sample areas within a river section for age-0 rainbow trout in the Henrys Fork. LB and UB = lower and upper bounds of normal 95% confidence intervals including within- and among-sample area error.

Year	$\bar{N}$	(SE)	[LB—UB]
Summer			
Box Canyon			
1995	1,880	(744.3)	[421—3,339]
1996	2,807	(929.3)	[985—4,629]
1997	2,422	(679.6)	[1,089—3,754]
Last Chance			
1995	2,742	(1,752.8)	[-693—6,178]
1996	5,547	(1,763.8)	[2,089—9,005]
1997	4,372	(1,703.5)	[1,032—7,711]
Autumn			
Box Canyon			
1995 ^a	1,205	(210.3)	[877—1,716]
1996	2,793	(448.3)	[1,914—3,672]
1997	1,615	(277.5)	[1,071—2,159]
1998	900	(92.1)	[719—1,081]

Table 3.6.—Continued.

Year	$\bar{N}$	(SE)	[LB—UB]
Last Chance			
1995	2,283	(352.6)	[1,591—2,975]
1996	3,865	(529.7)	[2,826—4,903]
1997	3,255	(730.0)	[1,824—4,686]

^a One sample area.

Table 3.7.—Extrapolated abundance estimates for age-0 rainbow trout in river sections of the Henrys Fork (lower Box Canyon (2.5 km), Last Chance (4 km), and Harriman State Park (1 km)). LB and UB = lower and upper bounds of normal 95% prediction intervals including within- and among-sample area error and extrapolation error.

Year	$\bar{N}$	(SE)	[LB—UB]
Summer			
Box Canyon			
1995	47,000	(9,932)	[27,534—66,466]
1996	70,175	(8,766)	[52,993—87,357]
1997	60,537	(7,859)	[45,135—75,940]
Last Chance			
1995	109,680	(31,420)	[48,100—171,260]
1996	221,880	(103,060)	[19,870—423,890]
1997	174,860	(15,800)	[143,890—205,830]
Harriman State Park			
1995 ^a			
1996 ^a	10,080	(1,556)	[7,030—13,130]
1997 ^a	12,520	(1,268)	[10,033—15,006]

Table 3.7.—Continued.

Year	$\bar{N}$	(SE)	[LB—UB]
Autumn			
Box Canyon			
1995 ^a	30,125	(1,052)	[28,064—32,186]
1996	69,825	(6,131)	[57,807—81,843]
1997	40,375	(2,791)	[34,904—45,846]
1998	22,500	(2,961)	[16,696—28,304]
Last Chance			
1995	91,320	(4,490)	[82,520—100,120]
1996	154,580	(32,940)	[90,020—219,140]
1997	130,200	(29,600)	[72,180—188,220]
Harriman State Park			
1995 ^a	13,290	(1,026)	[11,278—15,302]
1996 ^a			
1997 ^a	13,800	(1,132)	[11,580—16,020]

^a One sample area.

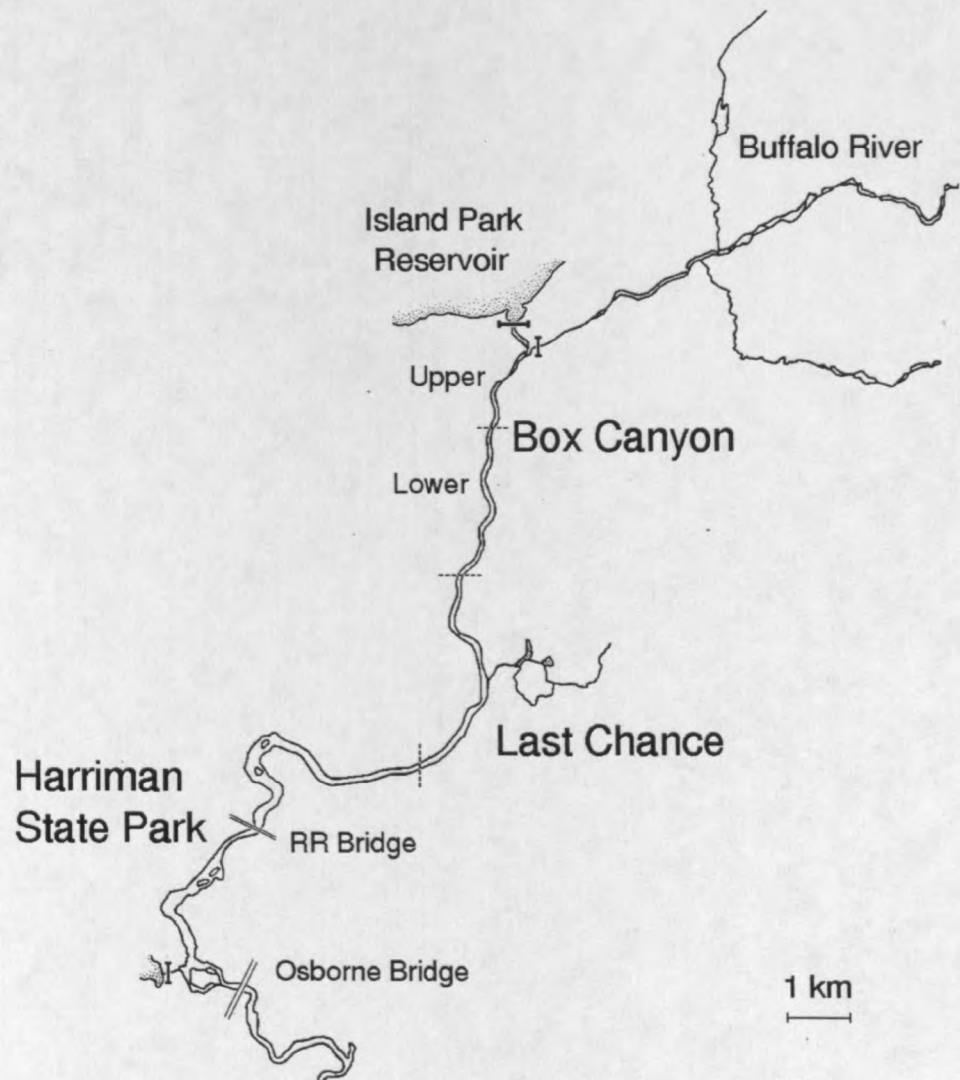


Figure 3.1.—Study sections of the Henrys Fork downstream of Island Park Reservoir and the Buffalo River: Box Canyon (upper and lower), Last Chance, and Harriman State Park. Lines with end-caps = dams, dashed lines = river section boundaries, and parallel lines = bridges.

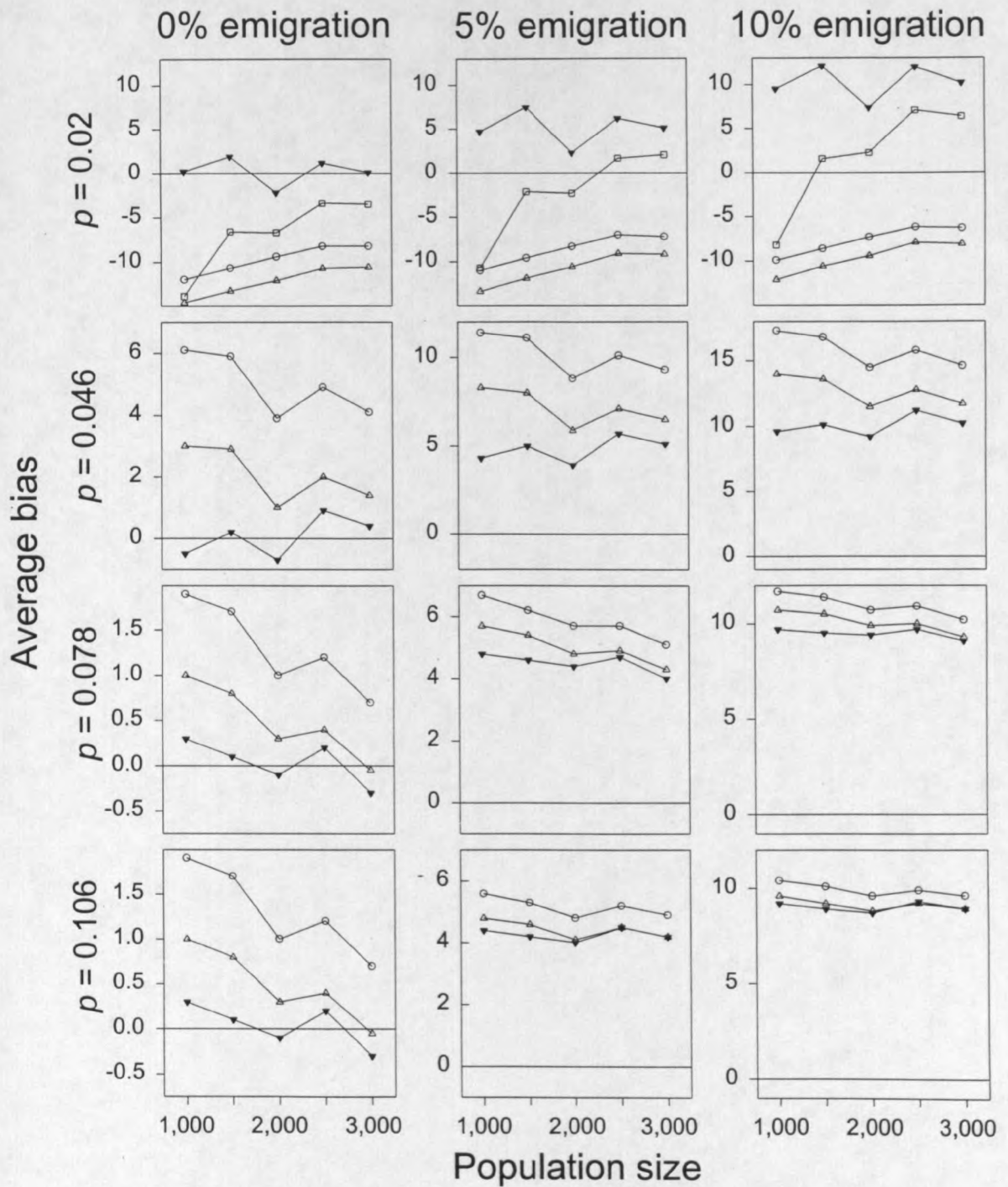


Figure 3.2.—Average bias expressed as a percentage of the true abundance for closed-population abundance estimators (black triangles = Chao M_t , open triangles = Darroch M_t , circles = Null M_o , and squares = Lincoln-Petersen). Mark-recapture data were simulated under model M_t for four populations with permanent emigration of 0%, 5%, or 10% of marked fish. Average capture probabilities ranged from 0.02 to 0.106; $t=5$ capture occasions; 1,000 replications.

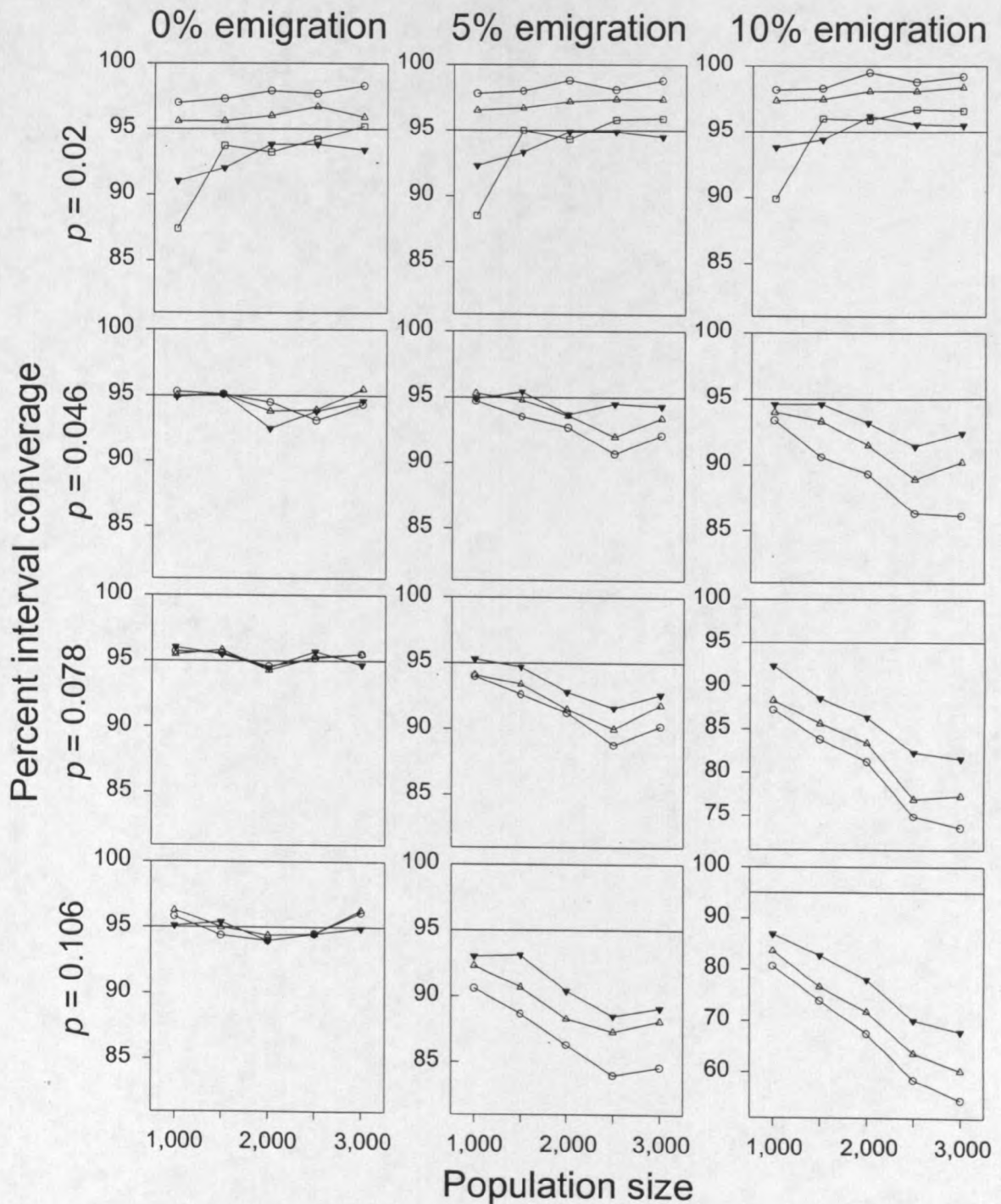


Figure 3.3.—Percent coverage of the true abundance for 95% confidence intervals for closed-population abundance estimators (black triangles = Chao M_t , open triangles = Darroch M_t , circles = Null M_0 , and squares = Lincoln-Petersen). Mark-recapture data were simulated under model M_t for four populations with permanent emigration of 0%, 5%, or 10% of marked fish. Average capture probabilities ranged from 0.02 to 0.106; $t=5$ capture occasions; 1,000 replications.

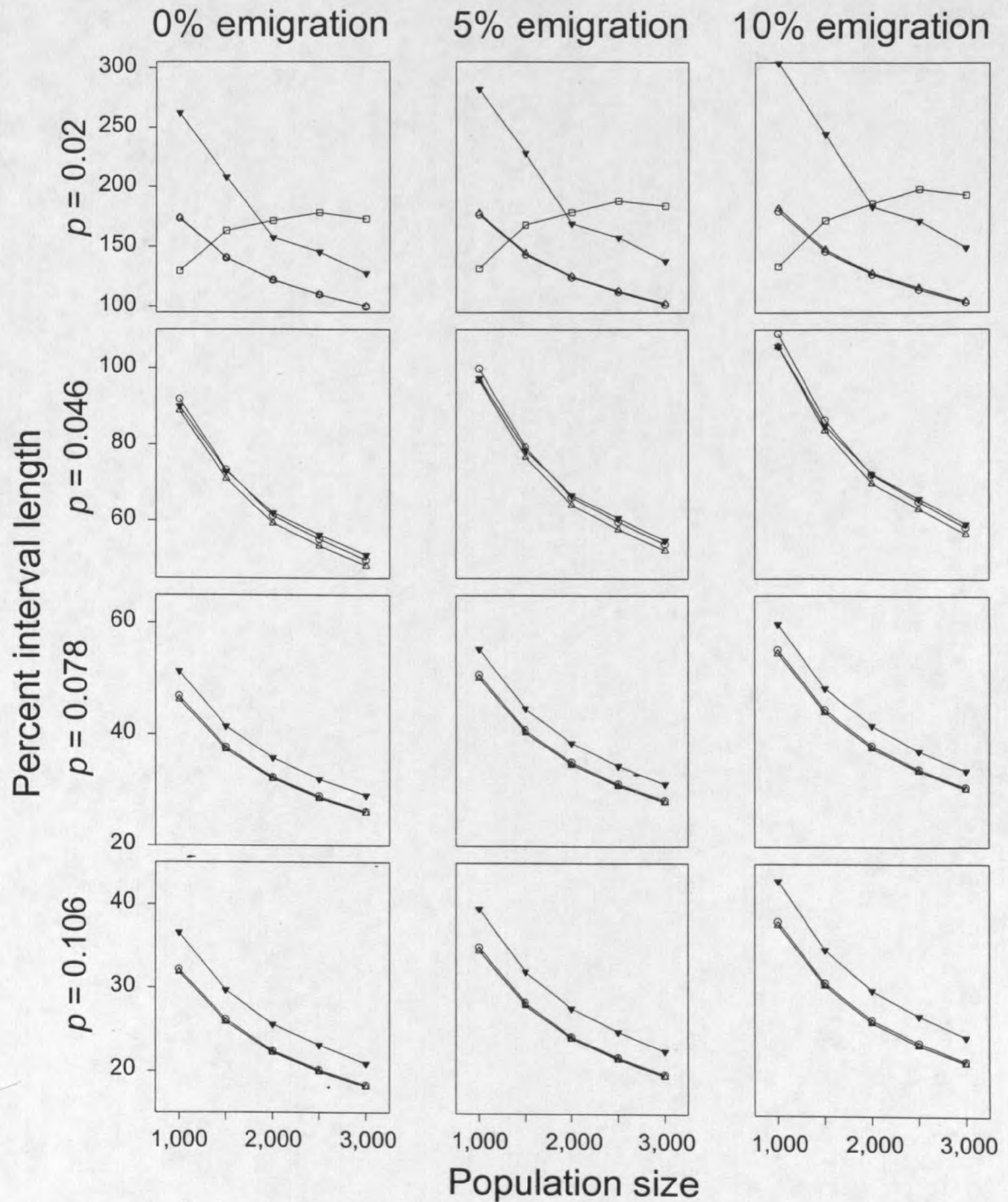


Figure 3.4.—Average interval length expressed as a percentage of the true abundance for closed-population abundance estimators (black triangles = Chao M_t , open triangles = Darroch M_t , circles = Null M_o , and squares = Lincoln-Petersen). Mark-recapture data were simulated under model M_t for four populations with permanent emigration of 0%, 5%, or 10% of marked fish. Average capture probabilities ranged from 0.02 to 0.106; $t=5$ capture occasions; 1,000 replications.

CHAPTER 4

PREDICTING FISH ABUNDANCE USING SINGLE-PASS REMOVAL SAMPLING

Introduction

Three-pass removal sampling is a common methodology used to estimate fish abundances in streams. A group of fish is numerically depleted by physical removal or marking on successive capture occasions such that catch per unit effort decreases proportionately to the number of fish remaining. An estimate of abundance is obtained using a maximum likelihood estimator (Zippin 1956; Otis et al. 1978; Rexstad and Burnham 1991).

Three-pass removal sampling can be labor intensive and costly when applied to many areas in a watershed or to a random selection of sampling units for the purpose of estimating abundance for a larger area. For example, I used three-pass removal sampling to estimate juvenile rainbow trout (*Oncorhynchus mykiss*) abundance along the banks of a 4-km section of the Henrys Fork of the Snake River, Idaho. The river section was divided into bank sampling units from which a subset was randomly selected to sample. The overall precision of an abundance estimate for such an area depends on the number of units sampled and the precision of the estimate from each sample. The abundance estimate should include measures of within-unit and among-unit variability and an extrapolation error term. Extrapolation error is related to the percentage of units sampled out of the total population of units in the area of interest. This error can be quite large when a small subset of units is sampled.

Some interest has been directed at reducing, from three to two, the number of passes required to obtain an abundance estimate (Seber 1982; Heimbuch et al. 1997). If the effort required to obtain an abundance estimate for a sampling unit could be reduced, the overall effort could be directed towards sampling more units to reduce among-unit variability and extrapolation error. However, if large proportions of fish are captured on the first pass, then we should be able to reduce sampling effort to a single pass.

However, this would require additional information to predict abundance from the single-pass catch; i.e., if a statistical relation could be developed between total abundance and a single-pass removal sample, it could be used to predict abundance. We could then, for example, sample 60 units by single-pass removal with the same effort required to sample 20 units by three-pass removal. The loss in estimate precision would be compensated by a gain in precision among sample units and in the extrapolation error term for estimating total abundance in a larger area. Strange et al. (1989) proposed such a relation to predict abundances of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in small streams. They first obtained a "semi-quantitative" sample by electrofishing a single pass through a 50-m blocknetted stream section, excluding 10 m near each net. The entire section was subsequently sampled by three-pass removal and the "quantitative" estimate was the sum of the "semi-quantitative" single-pass catch and the three-pass removal estimate. Predictions were made from a model of the "quantitative" estimate as a function of the "semi-quantitative" sample. Crozier and Kennedy (1994) used a similar method for juvenile salmonids in streams but only excluded 5 m near each net for their "semi-quantitative" single-pass sample.

Lobon-Cervia and Utrilla (1993) proposed estimating abundance of trout in streams by relating a three-pass abundance estimate to the catch in the first pass. Kruse et al. (1998) used such a relation to predict trout abundance in mountain streams with sparse habitat. Jones and Stockwell (1995) proposed the same method and compared it to a relation between a single-pass sample and an independent three-pass abundance estimate obtained three to five weeks later. Jones and Stockwell (1995) stated that a comparison between a three-pass abundance estimate and the catch from the first pass is not statistically valid because the abundance estimate and first-pass catch were not measured independently. This statement does not make sense. There is no violation of the Gauss-Markov conditions for least squares regression (Sen and Srivastava 1990) in a comparison of a three-pass abundance estimate and the first-pass catch. The response variable (the three-pass abundance estimate) is assumed to be dependent on the predictor variable (the first-pass catch) in least squares regression.

An alternate approach is the use of an estimate of capture probability from a previous multiple-pass removal sample(s) to estimate abundance from a single-pass catch (Seber and Le Cren 1967). Here it is assumed that the estimate of capture probability from the previous sample is similar to the expected capture probability for the new sample. Capture probability is also assumed to remain constant as a population is depleted. Abundance is estimated by dividing a single-pass catch by the estimate of capture probability.

I constructed and evaluated competing predictive models for obtaining abundance estimates from single-pass catch data. Three-pass removal data for juvenile rainbow trout along bank areas of the Henrys Fork were used to construct models either using a

linear relation between estimated abundance and single-pass catch or using a mean capture probability for all bank units sampled by three-pass removal. Cross-validation was used to compare the predictive ability of each model. Simulation was used to evaluate bias and interval coverage properties for predicting abundance in a bank sampling unit, mean abundance per bank sampling unit, and total abundance in a river section.

Methods

Henrys Fork Study

Three-pass removal sampling in bank sampling units was used to collect data for the estimation of juvenile rainbow trout (i.e., ≤ 200 mm total length) abundance in the Box Canyon section of the Henrys Fork. Box Canyon is a 4-km long river section that has an average width of 75 m, a high gradient (0.45%), and a cobble-boulder substrate. Bank areas are characterized by an abundance of rocks and woody debris. A bank sampling unit (hereafter referred to as bank unit) was defined as a known-length section of bank extending out into the channel a minimum of 2 m, or further to encompass any structure associated with the bank, such as a fallen tree. Bank units were about 15 m in length. Juvenile trout were immobilized using a hand-held probe operated from boat-mounted electrofishing gear (continuous DC, 250 V) and collected with a dip net. Each removal pass was performed by wading upstream from the boat. All habitat was thoroughly sampled on each pass such that effort remained constant. Blocking nets were not used to physically close bank units; I assumed bank units were biologically closed

such that juvenile rainbow trout were not entering or leaving the area. Unlike adult trout, which typically fled outside a bank unit as I approached, juvenile trout moved to nearby cover within a unit during electrofishing. A subset of the total population of bank units in the river section was randomly selected and sampled. Maximum likelihood estimates of abundance were obtained using the Zippin removal estimator in program CAPTURE (Rexstad and Burnham 1991). Bank unit estimates were used to obtain an estimate of the mean number of juvenile rainbow trout per bank unit and an extrapolated estimate of total abundance for the river section. Samples were collected from 154 bank units during nine seasons (spring, summer, or autumn) from summer 1995 to spring 1998.

Simple Linear Regression Model

A simple linear regression (SLR) model was constructed relating the three-pass abundance estimate $\hat{n}$ as a function of the first-pass catch c_1 :

$$\hat{n} = \beta_0 + \beta_1 \cdot c_1.$$

Model adequacy was checked by analyzing residuals and an appropriate transformation was selected from the Box-Cox family of transformations. Two types of prediction intervals were constructed: (1) 95% prediction intervals assuming normality:

$$\left[\hat{n}_{pred} \pm 1.96 \cdot \sqrt{\hat{var}(SLR)_{pred}} \right]$$

where

$$\hat{var}(SLR)_{pred} = s \cdot (1 + m + 2 \cdot c_{1pred} \cdot \sum_i^m c_i + c_{1pred}^2 \cdot \sum_i^m c_i^2),$$

$$s = \frac{\sum_i^m (n_i - \hat{n})}{m - 2},$$

c_{1pred} is a first-pass catch for which a prediction is to be made,

$\hat{n}_{pred}$ is a model prediction of abundance at c_{1pred} ,

$\hat{var}(SLR)_{pred}$ is the estimated variance for the SLR model, including an error term for making a prediction,

and m is the total number of observations in the SLR model and (2) 95% prediction intervals assuming the $\log_e$ transformation of the number of animals not captured has an approximate normal distribution:

$$\left[c_{1pred} + f / g_{pred}, c_{1pred} + f \cdot g_{pred} \right]$$

where

$$f = \hat{n}_{pred} - c_{1pred}$$

and

$$g_{pred} = \exp \left[1.96 \cdot \sqrt{\log_e \left(1 + \frac{\hat{var}(SLR)_{pred}}{f^2} \right)} \right]$$

(Chao 1989; Rexstad and Burnham 1991). All models and prediction intervals were programmed in MATLAB® version 5 (MathWorks, Inc. 1998).

Mean Capture Probability Model

A mean capture probability (MCP) model was constructed in which the mean capture probability $\hat{p}$ for all bank units sampled by three-pass removal was used to estimate abundance from single-pass removal data:

$$\hat{n} = \frac{c_1}{\hat{p}}$$

(Seber and Le Cren 1967). Two types of prediction intervals were constructed: (1) 95% prediction intervals assuming normality:

$$\left[\hat{n}_{pred} \pm 1.96 \cdot \sqrt{\text{var}(MCP)_{pred}} \right]$$

where

$$\text{var}(MCP)_{pred} = \left(\hat{n}_{pred}^2 \cdot \hat{p}^2 + \hat{n}_{pred} \cdot \hat{p} \cdot (1 - \hat{p}) \right) \cdot \left(\frac{1 - \hat{p}}{\sum_i^m \hat{n}_{pred_i} \cdot \hat{p}^2 \cdot (1 - (1 - \hat{p})^3)} \right) + \frac{\hat{n}_{pred} \cdot (1 - \hat{p})}{\hat{p}}$$

is the estimated variance for the MCP model (Seber and Le Cren 1967) and (2) 95% prediction intervals assuming a log-odds transformation:

$$\left[\frac{c_{1pred}}{\hat{P}_{\log\text{-odds}(upper)}}, \frac{c_{1pred}}{\hat{P}_{\log\text{-odds}(lower)}} \right]$$

where

$$\hat{P}_{\log\text{-odds}(lower)} = \frac{\hat{p}}{\hat{p} + (1 - \hat{p}) \cdot d},$$

$$\hat{p}_{\log\text{-odds}(\text{upper})} = \frac{\hat{p}}{\hat{p} + \frac{(1 - \hat{p})}{d}},$$

$$d = \exp\left[\frac{1.96 \cdot SE(\hat{p})}{\hat{p} \cdot (1 - \hat{p})}\right],$$

$\hat{p}_{\log\text{-odds}(\text{lower})}$ is the lower bound of the log-odds 95% confidence interval for $\hat{p}$,

$\hat{p}_{\log\text{-odds}(\text{upper})}$ is the upper bound of the log-odds 95% confidence interval for $\hat{p}$,

and $SE(\hat{p})$ is the standard error of $\hat{p}$ (Burnham et al. 1987).

Model Evaluation

Cross-Validation

The predictive ability of the SLR and MCP models was evaluated by cross-validation. Cross-validation was conducted by removing one observation from the data, fitting the model to the remaining observations, and using the model to predict abundance from the first-pass catch for the removed observation. This procedure was repeated for all observations in the data set using the shortcut available for least squares fitting (Efron and Tibshirani 1993 p. 256). Model performance was evaluated by calculating the mean prediction sum of squares. This statistic was used to compare the predictive performance of each model, and hence select the best model.

Simulation

Simulated data were used to construct SLR and MCP models and to evaluate the bias of model predictions and the coverage properties of prediction intervals. All simulations were programmed in MATLAB version 5 (MathWorks, Inc. 1998). A simulated 4-km river section was divided into 533 15-m bank units. Ten populations of known size were randomly selected and distributed among the bank units following a normal distribution with a standard deviation equal to 50% of the mean number of individuals per bank unit (i.e., $\text{normal}(\mu_j, \sigma_j^2)$) where $\mu_j = \frac{N_j}{533}$, N_j = size of population j , and $\sigma_j = 0.50 \cdot \mu_j$ for $j = 1$ to 10). A subset of 150 bank units (i.e., 15 per population) were randomly selected and sampled using three-pass removal.

A capture probability p_{beta} was randomly selected from a $\text{beta}(\alpha = 11.14, \beta = 4.0341)$ distribution for each bank unit sampled. The estimated parameters of the beta distribution were maximum likelihood estimates obtained by fitting the distribution to the capture probability estimates for field data (excluding observations of $\hat{p} = 1$). The capture probability p_{beta} remained constant for each removal occasion. A capture probability p_{unif} was randomly selected from $\text{uniform}(0,1)$ for each individual in the bank unit. If $p_{\text{unif}} \leq p_{\text{beta}}$ then the individual was considered captured and removed from the bank unit; otherwise, the individual was not captured and remained in the bank unit. This procedure was repeated for second- and third-pass removals for individuals remaining in the bank unit. The three-pass removal data were checked to determine if the group of individuals in a bank unit was sufficiently depleted

(i.e., the number of fish captured in the third pass was less than the number captured in the first pass (Seber and Whale 1970; Otis et al. 1978)). If a group was not sufficiently depleted, the sampling failed and an estimate of abundance could not be obtained for that bank unit; another bank unit was then sampled in its place. The three-pass removal data were analyzed using the Zippin maximum likelihood removal estimator to estimate abundance $\hat{n}_i$ for $i = 1$ to 150. The capture probability $\hat{p}_i$ was estimated from the catch data and $\hat{n}_i$ (Zippin 1956).

The 150 observations were used to construct SLR and MCP models as described earlier. SLR models for simulated data and for Henrys Fork data were compared using the general linear models procedure in SAS (PROC GLM; SAS Institute 1994) to compare intercepts and slopes. MCP models were compared by analysis of variance on ranked capture probabilities (SAS Institute 1994). Single-pass catch data were simulated from bank units and river sections of known abundance to evaluate the ability of the models to predict: (1) abundance in a bank unit, (2) mean abundance per bank unit, and (3) abundance in a river section. Second- and third-pass catch data were also simulated to evaluate the Zippin removal estimator and compare it to the model predictions.

Abundance in a bank unit.—One hundred groups of known size ranging from 1 to 100 were each sampled by three-pass removal using a randomly selected p_{beta} for a group and p_{unif} for each individual in a group on each removal pass as described earlier. The three-pass removal data were used to estimate group size using the Zippin removal estimator and to construct normal and log_e-based confidence intervals. (Three-pass removal samples that failed to sufficiently deplete the group could not be analyzed using

the Zippin removal estimator.) The first-pass catch data were used in the SLR and MCP models to estimate group size and to construct normal and log_e-based prediction intervals for the SLR model and normal and log-odds prediction intervals for the MCP model. This procedure was replicated 1,000 times for each group size. The following bias and interval statistics were computed: mean bias, bias standard error, percent interval coverage, mean lower bound, mean upper bound, mean interval length, and interval length standard error. I also compared the interval lower bound to the total number of individuals captured for each bank unit to determine the number of times the interval lower bound was less than the actual number of individuals captured. (The total number of individuals captured was obtained from three passes for three-pass removal estimates, and from a single pass for SLR and MCP model predictions.)

Mean abundance per bank unit.—A population of known size $N=10,000$ was distributed normal($\mu = \frac{10,000}{533}$, $\sigma^2 = (0.50 \cdot \mu)^2$) in a 4-km river section comprising 533 15-m bank units. Two hundred bank units were randomly selected for sampling by three-pass removal. A randomly selected p_{beta} was used for each bank unit and p_{unif} for each individual in a bank unit on each removal pass as described earlier. The three-pass removal data were used to estimate abundance and its associated variance for each bank unit using the Zippin removal estimator. (Three-pass removal samples that failed to sufficiently deplete the group could not be analyzed using the Zippin removal estimator.) The first-pass catch data were used in the SLR and MCP models to estimate abundance and its associated variance (including an error term for making a prediction). These data

were used to estimate the mean abundance per bank unit for 191 sample sizes ranging from 10 to 200. Normal confidence intervals were constructed for three-pass removal estimates and normal prediction intervals were constructed for SLR and MCP model predictions. This sampling and evaluation procedure was replicated 1,000 times. Bias and interval statistics were computed as described earlier.

Abundance in a river section.—The procedure to estimate mean abundance per bank unit for a population of known size $N=10,000$ was extended to estimate abundance for the river section as a whole. Estimates of river section abundance were obtained by multiplying the mean abundance per bank unit times the total number of bank units in the river section. Prediction intervals assuming normality were constructed for three-pass removal and SLR and MCP model predictions. Variance estimates included error terms for within-bank unit error (i.e., variation associated with making an estimate or model prediction), among-bank unit error (i.e., spatial variation), and extrapolation error:

$$\hat{v}ar_{total} = \frac{U}{m} \cdot (U - m) \cdot \hat{v}ar_{among} + \frac{U}{m} \cdot \hat{v}ar_{within}$$

where

$$\hat{v}ar_{among} = \frac{\sum_i^m (\hat{n}_i - \hat{\bar{n}})^2}{m - 1},$$

$$\hat{v}ar_{within} = \sum_i^m \hat{v}ar(\square)_i,$$

$\text{var}(\_)_{est}$ is var_{est} for three-pass estimates, $\text{var}(SLR)_{pred}$ for SLR model predictions, and $\text{var}(MCP)_{pred}$ for MCP model predictions,

U is the total number of bank units in the river section,

and m is the sample size

(Bohlin et al. 1989). This procedure was also performed for the 1,000 replicates. Bias and interval statistics were computed as described earlier.

Bank unit size.—I also investigated the effect of bank unit length on sample size (i.e., the number of bank units sampled) and the estimation of abundance in a river section. SLR and MCP models were constructed from three-pass removal data from 150 30-m bank unit samples from the ten simulated populations of known size described earlier. A population of known size $N=10,000$ was distributed $\text{normal}(\mu = \frac{10,000}{266}, \sigma^2 = (0.50 \cdot \mu)^2)$ in a 4-km river section comprising 266 30-m bank units. One hundred bank units were randomly selected and sampled by three-pass removal as described earlier. These data were used to estimate the abundance in a river section for 91 sample sizes ranging from 10 to 100.

SLR and MCP models were also constructed from three-pass removal data from 150 60-m bank units samples. A population of known size $N=10,000$ was distributed $\text{normal}(\mu = \frac{10,000}{133}, \sigma^2 = (0.50 \cdot \mu)^2)$ in a 4-km river section comprising 133 60-m bank units. Fifty bank units were randomly selected and sampled by three-pass removal.

These data were used to estimate abundance in a river section for 41 sample sizes ranging from 10 to 50.

Each procedure was replicated 1,000 times. Bias and interval statistics were computed as described earlier.

Results

Henry's Fork Study

Maximum likelihood estimates of abundance were obtained for 147 bank units; 5 bank units were not sufficiently depleted and abundance could not be estimated (3.4% failure rate) and no trout were captured in 2 samples. Five observations were considered influential points (Sen and Srivastava 1990) and were excluded from the data set for model construction (Figure 4.1A). Therefore, models were constructed using 142 observations (Figure 4.1B).

SLR Model

A plot of the data (Figure 4.1B) and plots of the residuals against the predictor variable 'first-pass catch' and the response variable 'estimated abundance' indicated that there was increasing variation with increasing first-pass catch and estimated abundance (i.e., heteroscedasticity). A square root transformation of both the predictor variable and the response variable was used to stabilize the variance. The mean prediction sum of squares of the SLR model (Table 4.1) was 20.39. Normal and log_e-based prediction intervals for the SLR model are displayed in Figure 4.1C, D.

MCP Model

Sixteen observations of $\hat{p} = 1$ were removed from the data set containing 142 observations to estimate $\bar{\hat{p}}$ for the MCP model (Table 4.2). The mean prediction sum of squares of the MCP model was 20.32.

Model Evaluation by Simulation

Simulating Capture Probabilities

There was no linear relation between capture probability $\hat{p}$ and estimated abundance $\hat{n}$ for the 142 observations from the Henrys Fork ($r^2=0.16$; Figure 4.2A). Most observations of $\hat{p}$ were between 0.6 and 0.9. A beta distribution fit to the 142 observations (including 16 observations of $\hat{p} = 1$) was strictly increasing on the interval (0,1) (beta($\alpha=2.4884$, $\beta=0.6675$); Figure 4.2B). (The observations of $\hat{p} = 1$ were in practice analyzed as values close to 1, i.e., 0.9999, when fitting the beta distribution.) This indicated that there was a higher probability of selecting random values of $\hat{p}$ greater than 0.9 than values of $\hat{p}$ between 0.6 and 0.9 from this beta distribution. A beta distribution fit to 126 observations (excluding the 16 observations of $\hat{p} = 1$) was not strictly increasing on the interval (0,1) and indicated a higher probability of selecting random values of $\hat{p}$ between 0.6 and 0.9 (beta($\alpha=11.14$, $\beta=4.0341$); Figure 4.2C). A plot of $\hat{p}$ and $\hat{n}$, each estimated from simulated three-pass removal data collected using p_{beta} , showed no linear relation and estimates of $\hat{p} = 1$ were observed as in data from the Henrys Fork ($r^2=0.14$; Figure 4.2D).

Models for 15-m, 30-m, and 60-m Bank Unit Samples

Plots of simulated data from 15-m, 30-m, and 60-m bank units (Figures 4.3A, 4.4A, and 4.5A) and plots of the residuals against the predictor variable c_1 and the response variable $\hat{n}$ indicated that for each SLR model there was increasing variation with increasing first-pass catch and estimated abundance (i.e., heteroscedasticity). A square root transformation of both the predictor variable and the response variable was used to stabilize the variance for each SLR model. There was no significant difference among SLR models for Henrys Fork data and data simulated for 15-, 30-, and 60-m bank units (intercept, $P=0.95$; slope, $P=0.53$) (Table 4.1). The mean prediction sum of squares was 62.2 for the 15-m bank unit model, 160.4 for the 30-m bank unit model, and 771.6 for the 60-m bank unit model. Normal and $\log_e$ -based prediction intervals for the SLR models are displayed in Figures 4.3B, C; 4.4B, C; and 4.5B, C.

Thirty-four observations of $\hat{p} = 1$ were removed from the data set containing 150 observations to estimate $\bar{\hat{p}}$ for the 15-m bank unit MCP model; 24 and 21 observations were removed for the 30-m and 60-m bank unit MCP models (Table 4.2). There was no significant difference among mean capture probabilities used in MCP models ($P=0.53$). The mean prediction sum of squares for the MCP models were 61.4 for the 15-m bank unit model, 161.9 for the 30-m bank unit model, and 770.5 for the 60-m bank unit model.

Sample Failures

There were 755 failures out of 100,000 samples for estimating abundance in a bank unit. Three-pass removal estimates could not be calculated for failed samples.

Most failures occurred for samples of smaller abundances: 608 failures for abundances less than or equal to 5 and 703 failures for abundances less than or equal to 10.

There were 7,228 failures out of 200,000 samples of 15-m bank units. The failure rate was about 3.6% for a given sample size ranging from 10 to 200. Therefore, actual sample sizes used for three-pass removal estimates of mean abundance per bank unit or abundance in a river section were on average about 3.6% less than the stated sample size.

There were 3,817 failures out of 100,000 samples of 30-m bank units. The failure rate was about 3.8% for a given sample size ranging from 10 to 100. There were 1,586 failures out of 50,000 samples of 60-m bank units. The failure rate was about 3.2% for a given sample size ranging from 10 to 50.

Abundance in a Bank Unit

Normal and $\log_e$ -based confidence intervals for three-pass removal estimates of abundance achieved a coverage level of 93-95% (Figure 4.6A, B). The percent coverage of both intervals remained relatively constant with increasing abundance. Normal prediction interval coverage for the SLR model was at or above the nominal level for abundances up to about 40 and coverage decreased thereafter to about 85% at abundances of 90 to 100 (Figure 4.7A). $\log_e$ -based prediction interval coverage was at or above the nominal level for abundances up to about 50 and coverage decreased thereafter to about 87% at abundances of 90 to 100 (Figure 4.7B). Normal prediction interval coverage for the MCP model occasionally achieved the nominal level for abundances up to about 10 and coverage decreased thereafter to less than 60% at abundances of 90 to 100 (Figure 4.8A). Log-odds prediction intervals achieved a coverage level between about 90 and

95% for abundances up to about 40 and achieved the nominal coverage level thereafter (Figure 4.8B). (See Appendix Table A.6 for interval statistics for 10 sample sizes ranging from 10 to 100.)

The lower interval bound was less than the total number of individuals sampled for 96% of three-pass removal normal intervals ($N=99,245$), 70% of SLR model normal intervals ($N=100,000$), and 22% of MCP model normal intervals ($N=100,000$). The lower interval bound was not less than the total number of individuals sampled for three-pass and SLR model $\log_e$ -based intervals and for MCP model log-odds intervals.

Mean bias (expressed as a percentage of known abundance) for three-pass removal estimates and SLR and MCP model predictions was negative and was relatively small for most abundances (Figure 4.9). Percent mean bias was large for small abundances and rapidly declined asymptotically to a stable level as abundance increased. The average percent mean bias for abundances between 20 and 100 was -1.2% for three-pass estimates, -4.3% for SLR model predictions, and -3.6% for MCP model predictions. (See Appendix Table A.6 for bias statistics for 10 sample sizes ranging from 10 to 100.)

Mean interval length and the standard error of interval length (each expressed as a percentage of known abundance) were large for small abundances and rapidly declined asymptotically to stable levels as abundance increased (Figure 4.10A-F). Percent mean interval length for three-pass removal normal and $\log_e$ -based confidence intervals decreased asymptotically to about 10% for abundances up to 100 (Figure 4.10A, B). The percent standard error of interval length was slightly greater than percent mean interval length and was more variable for $\log_e$ -based confidence intervals (Figure 4.10A, B).

Percent mean interval length was greater than 100% for abundances less than 20 for SLR model normal prediction intervals and for abundances less than 30 for log_e-based prediction intervals (Figure 4.10C, D). Percent mean interval length decreased asymptotically to about 40% for each SLR model prediction interval as abundance increased to 100. The percent standard error of interval length was less than percent mean interval length and decreased asymptotically to about 3% for each SLR model prediction interval (Figure 4.10C, D).

Percent mean interval length for MCP model normal prediction intervals was greater than 80% for abundances less than 10 and decreased asymptotically to about 22% for abundances up to 100 (Figure 4.10E). The percent standard error of interval length was less than percent mean interval length and decreased asymptotically to about 2% (Figure 4.10E). Percent mean interval length for MCP log-odds prediction intervals was greater than 90% for abundances less than 5 and decreased asymptotically to about 75% for abundances up to 100 (Figure 4.10F). The percent standard error of interval length was less than percent mean interval length and decreased asymptotically to about 12% (Figure 4.10F).

Log-odds prediction intervals for the MCP model achieved the nominal coverage level of 95% when percent mean interval length was greater than 75% (Figures 4.8B and 4.10F). The nominal coverage level was less than 95% when percent mean interval length was less than 75% for SLR model normal (Figures 4.7A and 4.10C) and log_e-based (Figures 4.7B and 4.10C) prediction intervals and for MCP model normal prediction intervals (Figure 8A and 10E).

Mean Abundance per Bank Unit

The mean abundance per 15-m bank unit for a population of 10,000 in a 4-km river section was 18.762. Three-pass removal estimates had a positive bias and SLR and MCP model predictions had a negative bias. Percent mean bias for three-pass removal estimates decreased from 7% (N=10) to 0.2% (N=200). Percent mean bias for SLR model predictions decreased from -4.5% (N=11) to -0.3% (N=200). Percent mean bias was least for MCP model predictions and decreased from -5% (N=12) to -0.35% (N=200).

Normal confidence intervals for three-pass removal estimates of mean abundance per 15-m bank unit achieved the nominal coverage level of 95% at a sample size of about 190 (Table 4.3). Normal prediction intervals for the SLR model achieved the nominal coverage level at a sample size of about 40. Normal prediction intervals for the MCP model achieved the nominal coverage level at a sample size of about 75. Mean interval length for three-pass removal estimates gradually increased with sample size from 5 at N=10 to 6.6 at N=200 (Table 4.3). Mean interval length was larger for model predictions and remained relatively constant as sample size increased (13.9-14.0 for the SLR model; 9.3-9.4 for the MCP model). The standard error of interval length decreased for all intervals as sample size increased and was largest for three-pass removal intervals (Table 4.3).

Abundance in a River Section

Three-pass removal estimates of abundance in a river section from sampling 15-m bank units had a positive bias; the mean estimate of abundance $\bar{N}$ was 10,253 (Figure

4.12A). There was a negative bias in SLR model predictions ($\bar{N} = 9,687$; Figure 4.13A) and in MCP model predictions ($\bar{N} = 9,652$; Figure 4.14A).

Three-pass removal and SLR and MCP model predictions performed about equally well at a given sample size (Figures 4.12, 4.13, and 4.14 and Table 4.4). Prediction interval coverage for three-pass removal increased from about 90% at $N=10$ to about 94-95% at $N=25$ to 200 (Figure 4.12B and Table 4.4). Prediction interval coverage for SLR and MCP models increased from about 90% at $N=10$ to about 93-95% at $N=25$ to 135 and decreased to about 90% at $N=200$ (Figures 4.13B and 4.14B and Table 4.4). Mean interval length decreased as sample size increased (e.g., from about 6,150 at $N=50$ to about 3,200 at $N=150$; Figures 4.12A, 4.13A, and 4.14A and Table 4.4).

The reallocation of an equal amount of effort applied to three-pass removal sampling to single-pass sampling and the use of the SLR or MCP model increased the precision of prediction intervals (Table 4.4). Sampling with 150 removal passes as single passes rather than as 50 sets of three-pass samples resulted in a 48% increase in prediction interval precision (i.e., mean interval length decreased from 6,279 to 3,166 (SLR model) and 3,134 (MCP model)).

Bank Unit Size

Doubling or quadrupling the area sampled by doubling or quadrupling the length of bank units provided a marginal increase in prediction interval precision. Precision increased by about 6% when sampling 50 30-m bank units and by about 16% when sampling 50 60-m bank units versus sampling 50 15-m bank units (Table 4.4).

Doubling the number of bank units sampled by halving the length of bank units (while total length of bank sampled remained constant) provided a large increase in prediction interval precision. Sampling 1,500 m of bank as 100 15-m bank units increased precision by about 28% versus sampling 50 30-m bank units and by about 50% versus sampling 25 60-m bank units. Precision also increased by about 28% and 50% when sampling 3,000 m of bank as 200 15-m bank units versus 100 30-m bank units and 50 60-m bank units.

Discussion

Abundance in a River Section

The precision of total abundance estimates for a river section can be significantly improved by allocating a given amount of effort to sampling more bank units by single-pass removal and using either the SLR or MCP model to predict abundance. The loss of precision by predicting abundance for a given bank unit was more than compensated for by reductions in among-bank unit variability and extrapolation error. Strange et al. (1989) and Crozier and Kennedy (1994) proposed using such a sampling strategy along with a regression model to construct indices of abundance for a large area. Jones and Stockwell (1995) went further in stating that actual abundance estimates could be obtained. I explicitly showed by simulation that abundance estimates for a large area, with prediction intervals that achieved the nominal level of coverage, could be obtained using either a SLR or MCP model.

There was also little loss of precision for three-pass removal versus single-pass removal when there was no change in the number of bank units sampled. This was likely an effect of sampling a large number of bank units to obtain the abundance estimate. For example, consider a data set that includes 5 samples each with a first-pass catch of 50. Three-pass removal estimates may include capture probabilities ranging from 0.4 to 0.9 and associated abundance estimates ranging from 125 to 55, each with a different variance estimate. Model predictions of abundance would be equal for each of the 5 samples (e.g., 67 for a MCP model using a mean capture probability of 0.75) and variance would not differ. Therefore, among-unit variation would be greater for three-pass removal than for single-pass removal.

The actual sample size for three-pass removal estimates of total abundance was on average 3.6% less than the stated sample size. If 200 three-pass removal samples were taken, maximum likelihood estimates of abundance could be calculated for about 196 of those samples. Sample failures often occur in field situations. About 3.4% of bank samples from the Henrys Fork failed. Time constraints may preclude obtaining additional field samples in the event of sample failure; the simulation procedure mimicked that scenario. This type of sample failure is not a problem for SLR and MCP models because the models only use the catch from the first pass to predict abundance. Failures cannot be identified because second and third passes are not performed. Therefore, if 200 single-pass samples were taken, 200 samples were used to predict total abundance.

Lobon-Cervia and Utrilla (1993) expressed caution concerning the use of a mean capture probability to predict abundance from single-pass catch, but no one has explicitly

considered a MCP model as an alternative to a SLR model. I found that SLR and MCP models performed about equally well for predicting total abundance in a river section. Cross-validation showed little difference in mean prediction sum of squares, also indicating that SLR and MCP model performances were about the same. However, the MCP model was easier to construct and to use because no data transformations were needed. I would therefore recommend the use of the MCP model for predicting total abundance in a river section. The MCP model (and the SLR model) could also be used in watershed-wide monitoring programs. A network of small streams in a watershed could be divided into segments, of which a subset is sampled. If three-pass removal sampling had previously been used, sampling effort in the future could be allocated to sampling more stream segments by single-pass removal. If single-pass sampling had previously been used for collecting presence and absence data, the model could be used to now obtain abundance estimates.

The SLR and MCP models constructed for Henrys Fork data will be used in the future for monitoring juvenile rainbow trout recruitment in the Henrys Fork. These models may or may not be robust such that they can be used in other systems. I recommend constructing and calibrating models for rivers or watersheds in which they will be used. This entails randomly selecting and sampling by three-pass removal a subset of bank units or stream segments in a system to obtain data to construct models. Parameter estimates for SLR and MCP models for simulated data stabilized at a sample size of about 30, which can therefore be considered a minimum number of valid three-pass removal samples for constructing a model. After models have been constructed, a

hybrid sampling strategy may be used that includes both three-pass and single-pass removal. Three-pass samples can be used for model validation and calibration while using single-pass sampling to increase the number of areas sampled.

Bank Unit Size

There was no significant difference among SLR models (comparisons of intercepts and slopes) or MCP models (comparisons of $\hat{p}$) constructed from samples from 15-, 30-, and 60-m bank units. Sampling larger bank units resulted in sampling some larger groups of fish and hence obtaining some larger values of $\hat{n}$ and c_1 . There was a marginal increase in precision for predictions of total abundance in a river section when sampling an equal number of larger bank units, e.g., 50 30-m bank units (i.e., 1,500 m of bank) versus 50 15-m bank units (i.e., 750 m of bank; Table 4.4). This increase in precision results from sampling a larger portion of the bank in a river section, thereby decreasing extrapolation error. Precision was actually lost for abundance estimates for individual bank units when using a SLR or MCP model constructed from samples of larger bank units. Capture probability tends to vary more when sampling larger groups of fish, resulting in larger variation in plots of c_1 versus $\hat{n}$ (SLR model) and larger variation in the estimate of $\hat{p}$ (MCP model).

Precision increased greatly when sampling a larger number of small bank units versus a smaller number of large bank units (e.g., 100 15-m bank units (1,500 m of bank) versus 50 30-m bank units (1,500 m of bank); Table 4.4). In this case the gain in precision is a result of a reduction in among-bank unit variation. Sampling smaller bank

units means encountering a smaller size range of groups of fish. This reduces the size of the difference between any abundance estimate and the mean estimate of abundance for all bank units sampled, which is squared and summed in calculating $\text{var}_{\text{among}}$.

Mean Abundance per Bank Unit

SLR and MCP models were also useful for obtaining an estimate of mean abundance per bank unit. Such an estimate is a precursor to estimating total abundance in a river section, but may also be used by itself as an index. The nominal coverage level was achieved at relatively small sample sizes: about 40 for the SLR model and about 75 for the MCP model. Three-pass removal estimation required a sample size of about 190 to achieve the same nominal coverage level. This was a result of small interval length rather than bias (Table 4.3).

Abundance in a Bank Unit

Lobon-Cervia and Utrilla (1993) and Jones and Stockwell (1995) suggested that a regression model and single-pass removal data could be used as an alternative to three-pass removal sampling for predicting site-specific abundance. My simulation results for predicting abundance in a single bank unit were not encouraging, because of the great loss in precision (bias was minimal and about equal for each model). These results were in accordance with Crozier and Kennedy's (1994) recommendation not to use a regression model and single-pass removal data to predict site-specific abundance. I considered both SLR and MCP models and normal, log_e-based, and log-odds prediction intervals and found their performance to be unsatisfactory. The MCP model with log-

odds prediction intervals performed best in terms of achieving the nominal level of coverage at all abundances between 1 and 100. However, log-odds prediction intervals were large—about 7.5 times those of three-pass removal intervals.

There was a relation between the percent mean interval length (expressed as a percentage of the known abundance) and the percent coverage of prediction intervals. Percent coverage was about 95% for percent mean interval length equal to about 75%. Log-odds prediction intervals for the MCP model performed best because percent mean interval length was at this 75% level across abundances (Figures 4.10F and 4.8B). Percent coverage was greater than (less than) 95% for percent mean interval length greater than (less than) about 75%. SLR model normal and $\log_e$ -based prediction intervals and MCP model normal prediction intervals crossed this threshold, resulting in over-coverage at small abundances and under-coverage at large abundances (Figures 4.10C, D, and E; 4.7A and B; and 4.8A). Therefore, poor prediction interval coverage (not bias) was related to short interval length.

The threshold between over-coverage at small abundances and under-coverage at large abundances existed for SLR models because there was a pattern of increasing variation with increasing abundance (e.g., Figure 4.3A). The square root transformation reduced this variation but did not eliminate it. If a transformation had not been used, the threshold would have occurred at a larger abundance and interval width would have been greater for abundances less than that threshold value.

Simulating Capture Probabilities

A beta distribution fit to a set of capture probability estimates excluding all $\hat{p} = 1$ better represented the observed capture probabilities. Likewise, estimates of $\hat{p} = 1$ were excluded from calculations of a mean capture probability for a MCP model. Estimates of $\hat{p} = 1$ were an artifact of small abundances. If the actual probability of capture is high, all individuals in a small group are often captured, sometimes in the first pass. We see this in the fan-shaped pattern of plots of first-pass catch versus estimated abundance, in which there is increasing variation with increasing abundance (e.g., Figure 4.1B). The concept is similar to that of demographic stochasticity: stochastic effects decrease in magnitude with increasing population size (Nations and Boyce 1997). Simulations showed that estimates of $\hat{p} = 1$ could be obtained from analyses of sample data collected using a $p_{\text{beta}} \neq 1$.

Linear Regression Models

The response variable in a linear regression model is considered a random variable, but the predictor values are usually considered known constants (i.e., the predictor variable is not a random variable) (Sen and Srivastava 1990; Neter et al. 1996). However, first-pass catch (i.e., the predictor variable) is a random variable. If we could obtain many independent samples of fish in a bank unit, there is reason to believe that the first-pass catch would vary. Previous studies have not acknowledged that the first-pass catch is a random variable (Strange et al. 1989; Lobon-Cervia and Utrilla 1993; Crozier

and Kennedy 1994; Jones and Stockwell 1995). This raises a concern about the validity of a regression model of total abundance as a function of first-pass catch.

All results on estimation, testing, and prediction obtained for the regression model are still valid if first-pass catch is a random variable, but only if two conditions are met (Neter et al. 1996). For discussion purposes, let Y_i be a random variable for estimated total abundance and let X_i be a random variable for the corresponding first-pass catch, where $i=1, \dots, n$ and n is the sample size. The conditions require that (1) the conditional distributions of the Y_i given X_i are normal and independent and (2) the probability distribution of the X_i does not involve the regression coefficients (Neter et al. 1996). Condition (2) is satisfied because first-pass catch is not a function of estimated total abundance. First-pass catch is a function of the true total abundance and unknown variables affecting catchability. Condition (1) is more troublesome because estimated total abundance is non-normally distributed (Rexstad and Burnham 1991). The scatter plots of first-pass catch versus estimated abundance do not suggest that estimated abundance is non-normal. Therefore, it can be assumed for the purpose of regression analysis that the conditional distributions of total abundance estimates given first-pass catch were approximately normal. If condition (1) was not satisfied, I would have expected $\log_e$ -based prediction intervals to perform better than normal prediction intervals, but they performed about equally well (Figure 4.7A, B).

Five observations in the Henrys Fork data set were identified as influential points because they were located far away from the other observations. These observations, if included in the SLR model, would artificially reduce the variability of the regression (their residual values were small). Model prediction intervals would then be too precise

and coverage of the true abundance would be much less than the nominal level. Therefore these observations were not included in the models. There were some observations in the Henrys Fork data and in the simulated data that had large residuals and were not far away from other observations. These observations were not considered outliers and were included in the models. Such observations are encountered in the field and their variability should be included in predictive models.

Prediction Intervals

Prediction intervals constructed assuming normality were inappropriate for model predictions of abundance. The lower bound of a normal interval for abundance estimates may be less than the number of individuals sampled (Rexstad and Burnham 1991). This occurred in simulations of normal intervals for 96% of three-pass removal estimates, 70% of SLR model predictions, and 22% of MCP model predictions. It was not surprising that this was less of a problem for model predictions because models use only the first-pass catch, which is smaller than the sum of a three-pass sample (unless no individuals were captured on the second and third passes). Nevertheless, an interval lower bound less than the number of individuals sampled is problematic. We know the abundance in a sampled area is at least as large as the number of individuals captured.

Truncating an interval lower bound to the number of individuals captured has no basis in statistical theory and results in interval coverage less than the nominal level (by an unknown amount). Chao (1989) and Rexstad and Burnham (1991) used an approach to constructing confidence intervals for abundance estimates that assumes the $\log_e$ transformation of the number of animals not captured has an approximate normal

distribution. The lower bound of a $\log_e$ -based interval cannot be less than the number of individuals sampled (the upper bound tends to be larger than the normal interval upper bound). This approach was used to construct prediction intervals for the SLR model. Simulations confirmed that the lower bound of the $\log_e$ -based prediction interval was never less than the number of individuals captured (i.e., first-pass catch).

Normal prediction intervals are also inappropriate because of the non-normal distribution of estimated abundance, which leads to poor coverage of the true abundance (Rexstad and Burnham 1991). This was not the case for simulations of three-pass removal estimates for abundances ranging from 10 to 100, for which normal (as well as $\log_e$ -based) confidence intervals achieved the nominal coverage level of 95% (Figure 4.6A, B). Normal and $\log_e$ -based prediction intervals for the SLR model achieved similar levels of coverage (Figure 4.7A, B). $\log_e$ -based intervals had lower bounds that were not less than the total number of individuals sampled, but did not improve upon interval coverage of the true abundance.

Removal Methodology Assumptions

Population Closure

Population closure is an important condition for the use of the removal methodology. The loss or addition of juvenile trout during sampling could bias estimates of abundance (Otis et al. 1978; White et al. 1982; Pollock et al. 1990). Bank units in the Henrys Fork were physically open when sampled because the use of blocking nets was impractical. The installation and maintenance of efficient blocking nets would be labor intensive, and any advantage of a physically closed system may have been offset by the

disturbance of fish while installing the nets (Bohlin et al. 1989). However, physically open populations can sometimes be treated as closed, contingent on a short study period (Pollock 1982). It can also be argued that the sample areas are biologically closed when the species of interest restricts its activities to a defined area (Bohlin et al. 1989). When disturbed, juvenile rainbow trout in the Henrys Fork concealed themselves in the interstitial space of the rocky substrate, in woody debris, and in macrophytes. The slow, methodical process of electrofishing upstream was particularly effective at capturing juvenile trout because of this tendency towards concealment. (Such an approach to sampling large trout would not work because large trout were typically observed fleeing sample areas, except when water temperatures were low and fish response time was slow.) Any loss of juvenile trout from bank units during sampling was likely minimal. Movement of juvenile trout into bank units during the short sampling duration (e.g., 1 h) was also likely minimal, as groups of fish in bank units were consistently depleted.

A statistically valid test of the closure assumption based only on multiple-recapture data cannot be constructed (White et al. 1982). A test for closure assuming the heterogeneity model M_h as the null model (Otis et al. 1978) is included in program CAPTURE. However, this test cannot detect temporary emigration, and true failure of the closure assumption cannot be differentiated from behavioral variation in capture probability or certain patterns of temporal variation. The use of a three-pass removal methodology explicitly assumes the use of the behavioral model M_b and the Zippin removal estimator. Removed individuals obviously have a zero probability of being recaptured. Otis et al. (1978) observed strong rejection of the closure test when model M_b was true for simulated data.

Equal Catchability of Individuals

Equal catchability of individuals is another important condition for the use of the removal methodology. However, the assumption of equal catchability often conflicts with biological reality (Bohlin and Sundstrom 1977). Fish may exhibit temporal variation, behavioral variation, and individual heterogeneity in capture probabilities.

Temporal variation was controlled because effort was equal for each pass. Effort remained constant by thoroughly sampling all habitat in a bank unit on each pass (Riley and Fausch 1992). Trout may exhibit a behavioral response to electrofishing (Cross and Stott 1975; Mesa and Schreck 1989). This was not a concern for juvenile trout that were captured because they were removed from bank units and not subject to recapture.

However, trout that escape capture in the electric field should be subject to recapture during a subsequent pass. The probability of recapture would decrease if these trout leave the bank unit or better conceal themselves. I cannot say that this never occurred, but some juvenile trout were observed concealing themselves in the rocky substrate and were recaptured during the subsequent pass. Temporal and behavioral variation are of concern when sampling multiple passes and using these data to construct models, but become irrelevant when using single-pass catch to predict abundance.

Heterogeneity in individual capture probabilities occurs when sampling methods are size-selective. Electrofishing is widely recognized as a size-selective sampling technique that favors capture of larger individuals (e.g., White et al. 1982; Bohlin et al. 1989; Jones and Stockwell 1995). The slow, methodical approach to sampling bank units was very effective at capturing juvenile trout and reduced the likelihood of capturing large trout (i.e., > 200 mm total length). Larger fish tended to react to the slowly

approaching intermittent electric field by attempting to escape it while smaller fish sought or remained concealed in cover. Therefore, heterogeneity in capture probabilities was likely not a problem, as I was interested only in the juveniles.

Decreasing catchability in multiple-pass removal sampling of fish populations is common and may result in the underestimation of abundance if catchability is modeled as remaining constant (Cross and Stott 1975; Bohlin and Sunderstrom 1977; Peterson and Cederholm 1984; Riley and Fausch 1992). Model M_{bh} in program CAPTURE allows capture probability to vary (Otis et al. 1978; Rexstad and Burnham 1991). A goodness-of-fit test is used to determine whether or not capture probability is constant (Otis et al. 1978). At least three removal passes are required for goodness-of-fit testing, but at least four removal passes are required to allow capture probability to vary in the model. The power of this test is low at small population sizes (i.e., < 200 ; Riley and Fausch 1992) and was therefore not useful for analyzing Henrys Fork data. However, the removal data consisted of three passes and could therefore only be analyzed assuming a constant capture probability model. SLR and MCP models constructed from simulated data with a known constant capture probability did not significantly differ from models constructed for Henrys Fork data. This suggests that if capture probability did decrease on the second and third passes in the Henrys Fork, the decrease was not severe such that abundance was greatly underestimated.

Recommendations

I do not recommend the use of a SLR or MCP model to predict abundance for a bank unit or stream segment if that area is the only area of interest. The extra effort

required for the second and third pass greatly improves estimate precision. These models have the greatest utility for predicting total abundance from multiple samples. The SLR and MCP models can be used to reduce data collection effort for the estimation of total abundance in a river section or network of streams. The models can also be used to improve precision by reallocating a given amount of effort from three-pass sampling to single-pass sampling.

I recommend the use of the MCP model because no data transformations were needed. However, both the SLR and MCP models worked about equally well. A hybrid sampling protocol may be used that includes both three-pass and single-pass sampling. The three-pass samples could be used to check model adequacy for the present sampling situation (i.e., model validation) and to further calibrate the model, while the single-pass samples can be analyzed using a SLR or MCP model.

Summary

Three-pass removal data for juvenile rainbow trout (*Oncorhynchus mykiss*) along bank areas of the Henrys Fork of the Snake River, Idaho, were used to construct models to predict abundance from single-pass catch data. Simple linear regression (SLR) models and mean capture probability (MCP) models were evaluated by simulation for bank sampling units of different lengths (15, 30, or 60 m). The MCP model with log-odds prediction intervals performed best for predicting abundance within a specific bank unit, in terms of achieving the nominal coverage level, but precision was poor (log-odds intervals were about 7.5 times greater than three-pass removal intervals); I do not recommend using these models for this purpose. These models have the greatest utility

for predicting total abundance in a large area from multiple samples within it. The models can be used to reduce data collection effort, or reallocation of effort from three-pass removal sampling to single-pass sampling can be used to increase the precision of prediction intervals. Sampling with 150 removal passes as single passes rather than as 50 sets of three-pass samples resulted in a 48% increase in prediction interval precision for a simulated population of 10,000 fish. Increasing the area sampled by increasing the length of bank units provided a marginal increase in prediction interval precision. However, a large increase in precision was obtained by sampling more bank units of smaller length (while total length of bank sampled remained constant). Sampling 1,500 m of bank as 100 15-m bank units increased precision by about 28% versus sampling 50 30-m bank units, and by about 50% versus sampling 25 60-m bank units. Three-pass removal and SLR and MCP model predictions performed about equally well at a given sample size. I recommend the MCP model for ease of construction and use.

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Table 4.1.—Simple linear regression (SLR) models for Henrys Fork data and simulations of 15-m, 30-m, and 60-m bank units; CI = confidence interval.

SLR model		Intercept 95% CI	Slope 95% CI	r^2
Henrys Fork	$\hat{n} = -0.0384 + 1.1934 \cdot c_1$	[-0.0618, -0.0149]	[1.1917, 1.1952]	0.92
Simulation (15 m)	$\hat{n} = 0.0128 + 1.1451 \cdot c_1$	[-0.0015, 0.0271]	[1.1444, 1.1458]	0.96
Simulation (30 m)	$\hat{n} = 0.0689 + 1.1399 \cdot c_1$	[0.0504, 0.0873]	[1.1395, 1.1403]	0.97
Simulation (60 m)	$\hat{n} = 0.0571 + 1.1631 \cdot c_1$	[0.0058, 0.1085]	[1.1625, 1.1637]	0.97

Table 4.2.—Mean capture probability (MCP) models for Henrys Fork data and simulations of 15-m, 30-m, and 60-m bank units; CI = confidence interval.

MCP model		$\bar{p}$ (SE)	$\bar{p}$ log-odds 95% CI	N
Henrys Fork	$\hat{n} = \frac{c_1}{0.7334}$	0.7334 (0.1071)	[0.4845, 0.8895]	126
Simulation (15 m)	$\hat{n} = \frac{c_1}{0.762}$	0.762 (0.1161)	[0.4773, 0.9182]	116
Simulation (30 m)	$\hat{n} = \frac{c_1}{0.7546}$	0.7546 (0.1168)	[0.4717, 0.9137]	126
Simulation (60 m)	$\hat{n} = \frac{c_1}{0.7436}$	0.7436 (0.1205)	[0.4566, 0.9092]	129

Table 4.3.—Bias and interval statistics for three-pass estimates, simple linear regression (SLR) model predictions, and mean capture probability (MCP) model predictions of mean abundance per 15-m bank unit (1,000 replications). The true mean abundance per bank unit was 18.762. LB and UB = lower and upper bounds of 95% confidence or prediction intervals.

Sample Size	Mean bias	SE bias	Percent coverage	Mean LB	Mean UB	Mean interval length	SE interval length
Three-pass estimates (normal 95% confidence intervals)							
25	0.5	4.3	40.8	16.6	22.1	5.5	5.3
50	0.5	3.0	59.3	16.3	22.2	5.9	4.8
75	0.5	2.3	73.5	16.2	22.4	6.2	4.6
100	0.5	1.9	80.7	16.1	22.3	6.2	4.2
125	0.5	1.7	85.6	16.1	22.4	6.3	3.9
150	0.4	1.5	90.7	16.0	22.5	6.5	4.2
175	0.5	1.4	93.5	16.0	22.5	6.5	4.0
200	0.4	1.2	94.8	15.9	22.5	6.6	4.1
SLR model predictions (normal 95% prediction intervals)							
25	-0.5	4.1	90.3	12	26.0	14.0	2.1
50	-0.6	2.9	97.4	12	25.9	13.9	1.5
75	-0.6	2.3	99.3	12	26.0	14.0	1.2
100	-0.6	1.9	99.8	12	25.9	13.9	1.0
125	-0.6	1.7	99.9	12	25.9	13.9	0.9
150	-0.6	1.5	100	12	25.9	13.9	0.8
175	-0.6	1.3	100	12	25.9	13.9	0.7
200	-0.6	1.2	100	12	25.9	13.9	0.6

Table 4.3.—Continued.

Sample Size	Mean	SE	Percent	Mean	Mean	Mean	SE
	bias	bias	coverage	LB	UB	interval length	interval length
MCP model predictions (normal 95% prediction intervals)							
25	-0.6	4.1	71.9	13.5	22.8	9.3	1.1
50	-0.7	2.9	87.1	13.4	22.7	9.3	0.8
75	-0.6	2.3	94.9	13.5	22.8	9.3	0.6
100	-0.7	1.9	97.2	13.4	22.8	9.3	0.5
125	-0.6	1.7	98.2	13.4	22.8	9.4	0.4
150	-0.7	1.5	99.2	13.4	22.8	9.3	0.4
175	-0.7	1.3	99.7	13.4	22.8	9.4	0.3
200	-0.7	1.2	99.9	13.4	22.8	9.4	0.3

Table 4.4.—Interval statistics (normal 95% prediction intervals) for three-pass estimates, simple linear regression (SLR) model predictions, and mean capture probability (MCP) model predictions for population size = 10,000 (1,000 replications). Sample size = 50, 100, 150, and 200 for 15-m bank units, sample size = 50 and 100 for 30-m bank units, and sample size = 25 and 50 for 60-m bank units. LB = lower bound; UB = upper bound.

	Percent coverage	Mean LB	Mean UB	Mean interval length	SE interval length
Sample size = 50 (15-m bank units)					
Three-pass	94.1	7105	13383	6279	516
SLR model	93.2	6634	12714	6080	543
MCP model	93.1	6612	12665	6053	542
Sample size = 150 (15-m bank units)					
Three-pass	94.8	8610	11869	3259	136
SLR model	92.3	8094	11260	3166	143
MCP model	91.7	8075	11209	3134	142
Sample size = 100 (15-m bank units) (1,500 m of bank sampled)					
Three-pass	94.8	8132	12355	4223	222
SLR model	93.6	7636	11736	4099	238
MCP model	93.2	7615	11686	4071	237
Sample size = 50 (30-m bank units) (1,500 m of bank sampled)					
Three-pass	94.8	7329	13226	5897	448
SLR model	93.7	6830	12508	5678	474
MCP model	93.7	6839	12540	5701	480

Table 4.4.—Continued.

	Percent coverage	Mean LB	Mean UB	Mean interval length	SE interval length
Sample size = 25 (60-m bank units) (1,500 m of bank sampled)					
Three-pass	94.8	6121	14345	8224	866
SLR model	93.6	5871	14103	8231	988
MCP model	92.6	5785	13870	8085	977
Sample size = 200 (15-m bank units) (3,000 m of bank sampled)					
Three-pass	93.9	8917	11561	2645	94
SLR model	91.6	8391	10963	2572	98
MCP model	90.7	8374	10910	2536	98
Sample size = 100 (30-m bank units) (3,000 m of bank sampled)					
Three-pass	93.6	8436	12123	3687	178
SLR model	92.5	7902	11455	3553	185
MCP model	92.3	7926	11473	3547	187
Sample size = 50 (60-m bank units) (3,000 m of bank sampled)					
Three-pass	94.7	7631	12778	5147	326
SLR model	94.9	7384	12559	5175	373
MCP model	94.5	7290	12335	5045	368

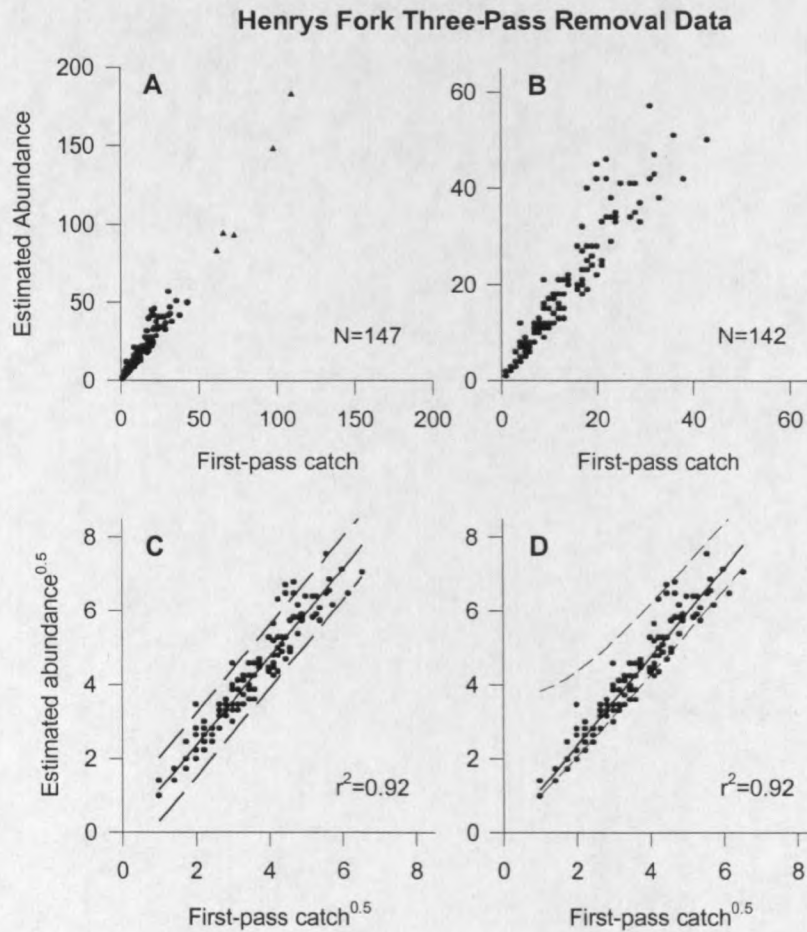


Figure 4.1.—Scatter plots of first-pass catch and estimated abundance from Henrys Fork data including (A) and excluding (B) five influential observations (indicated by triangles); and simple linear regression model of estimated abundance (square root transformation) as a function of first-pass catch (square root transformation) with normal (C) and log_e (D) 95% prediction intervals.

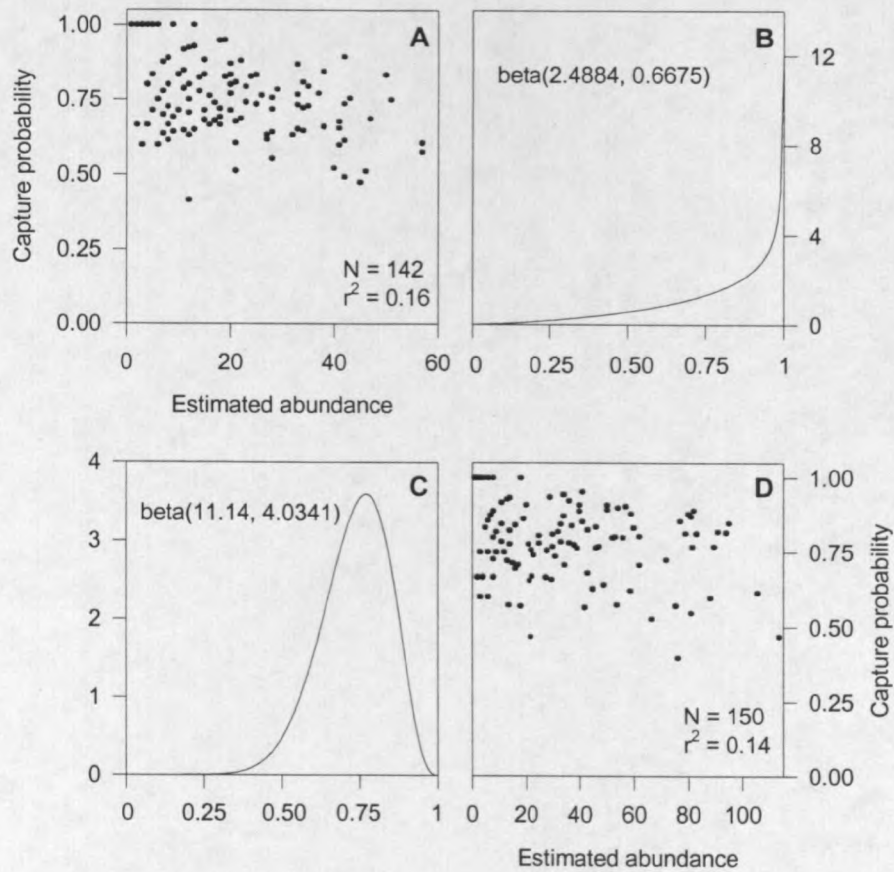


Figure 4.2.—(A) Scatter plot of abundance and capture probability estimates from Henrys Fork data; beta distribution fit to Henrys Fork capture probability estimates including (B) and excluding (C) 16 values of $\hat{p} = 1$; and (D) scatter plot of abundance and capture probability estimates from simulated data collected from 15-m bank units using p_{beta} from beta distribution excluding values of $\hat{p} = 1$.

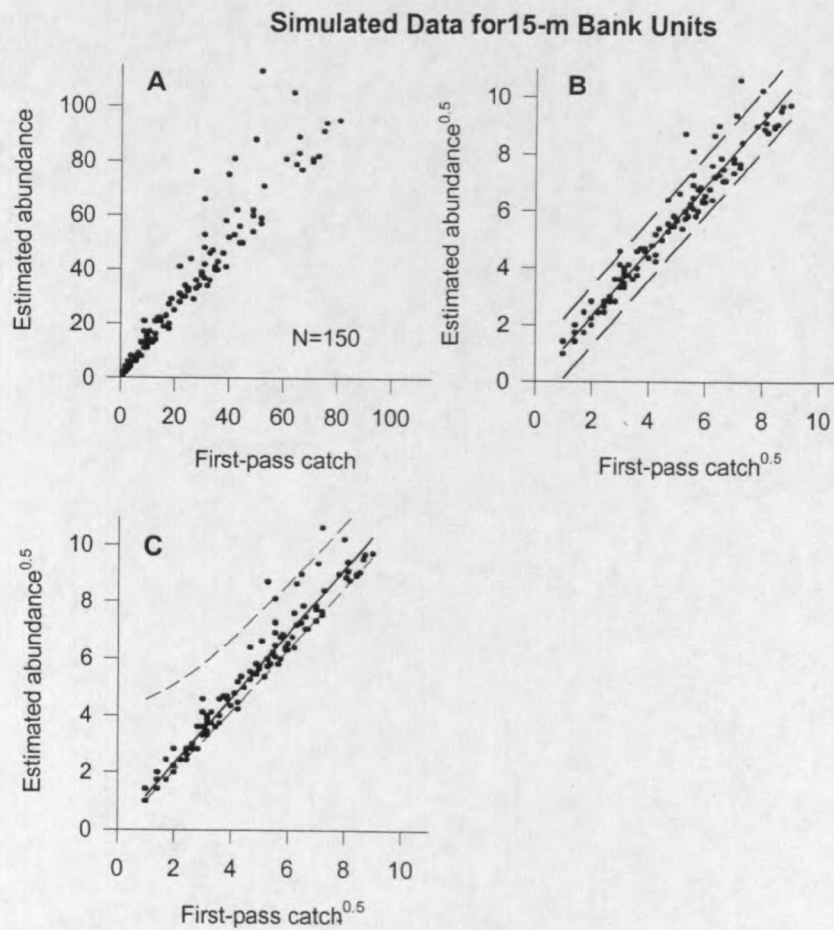


Figure 4.3.—Scatter plot of first-pass catch and estimated abundance from simulated data for 15-m bank units (A); and simple linear regression model of estimated abundance (square root transformation) as a function of first-pass catch (square root transformation) with normal (B) and log_e (C) 95% prediction intervals.

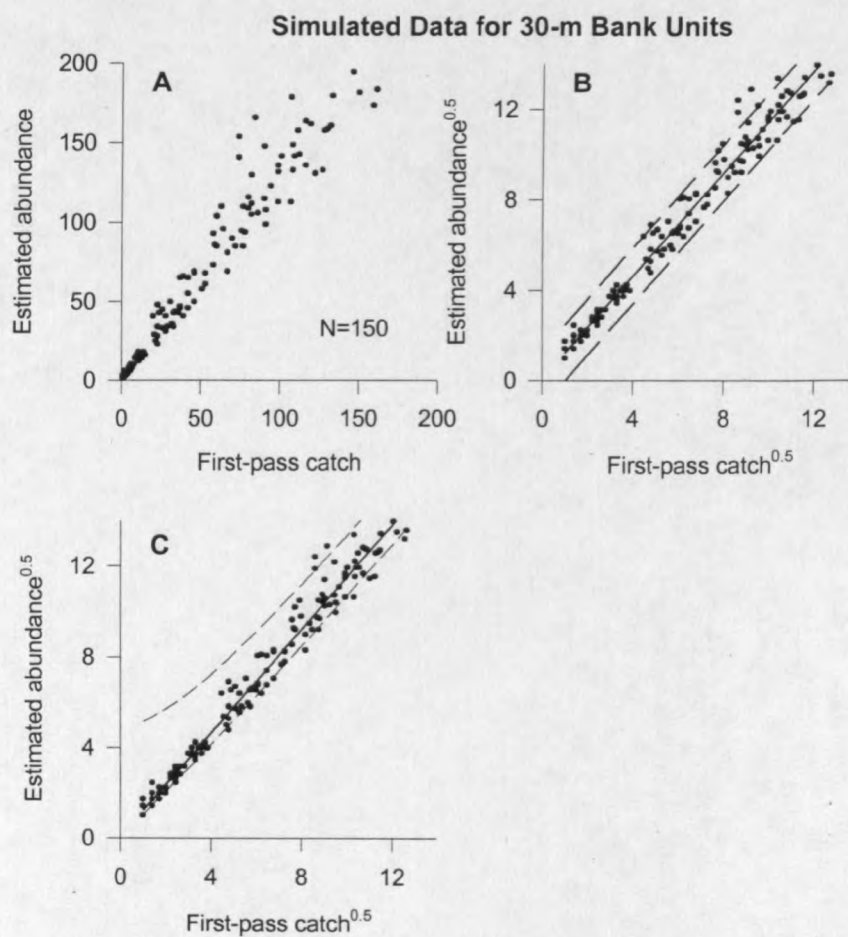


Figure 4.4.—Scatter plot of first-pass catch and estimated abundance from simulated data for 30-m bank units (A); and simple linear regression model of estimated abundance (square root transformation) as a function of first-pass catch (square root transformation) with normal (B) and $\log_e$ (C) 95% prediction intervals.

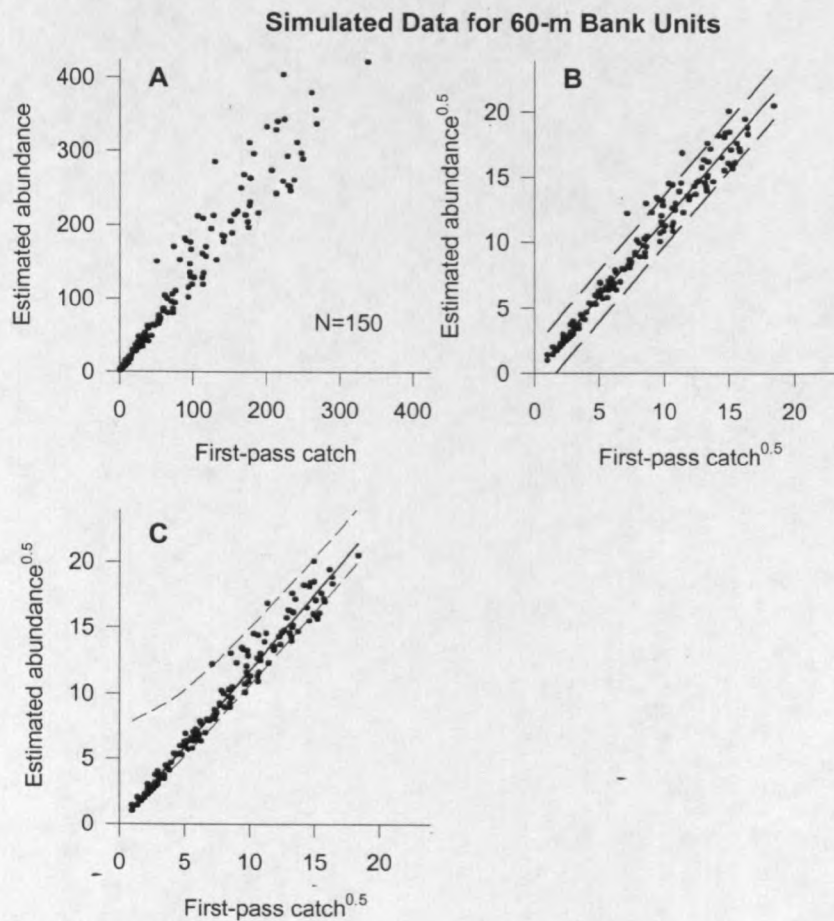


Figure 4.5.—Scatter plot of first-pass catch and estimated abundance from simulated data for 60-m bank units (A); and simple linear regression model of estimated abundance (square root transformation) as a function of first-pass catch (square root transformation) with normal (B) and log_e (C) 95% prediction intervals.

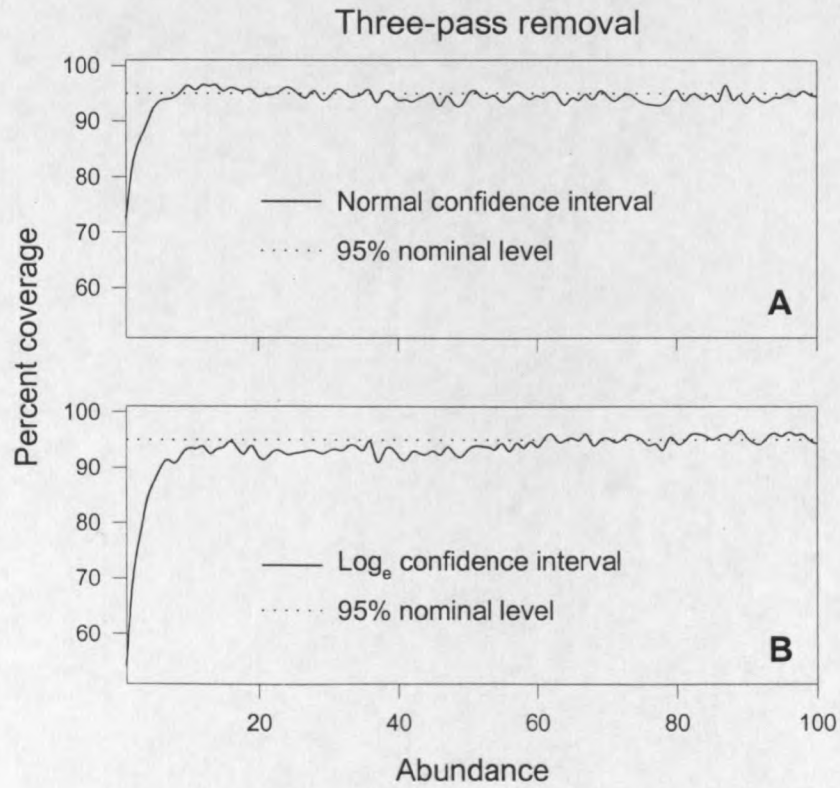


Figure 4.6.—Percent coverage of the true abundance (range, 1 to 100) for normal (A) and $\log_e$ (B) 95% confidence intervals for three-pass removal estimates of simulated data.

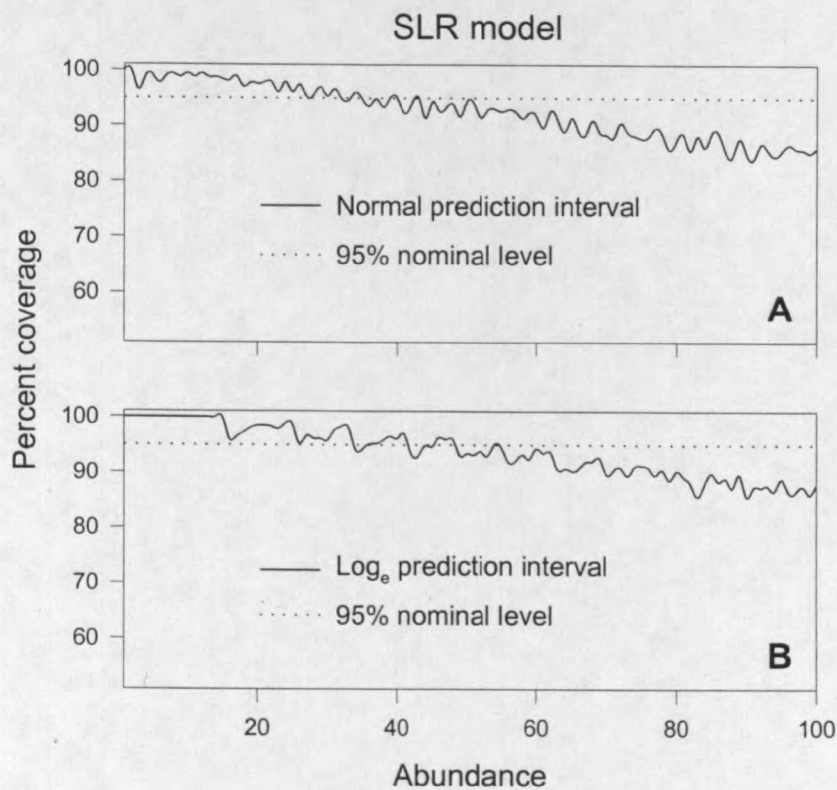


Figure 4.7.—Percent coverage of the true abundance (range, 1 to 100) for normal (A) and $\log_e$ (B) 95% prediction intervals for simple linear regression model predictions of simulated data.

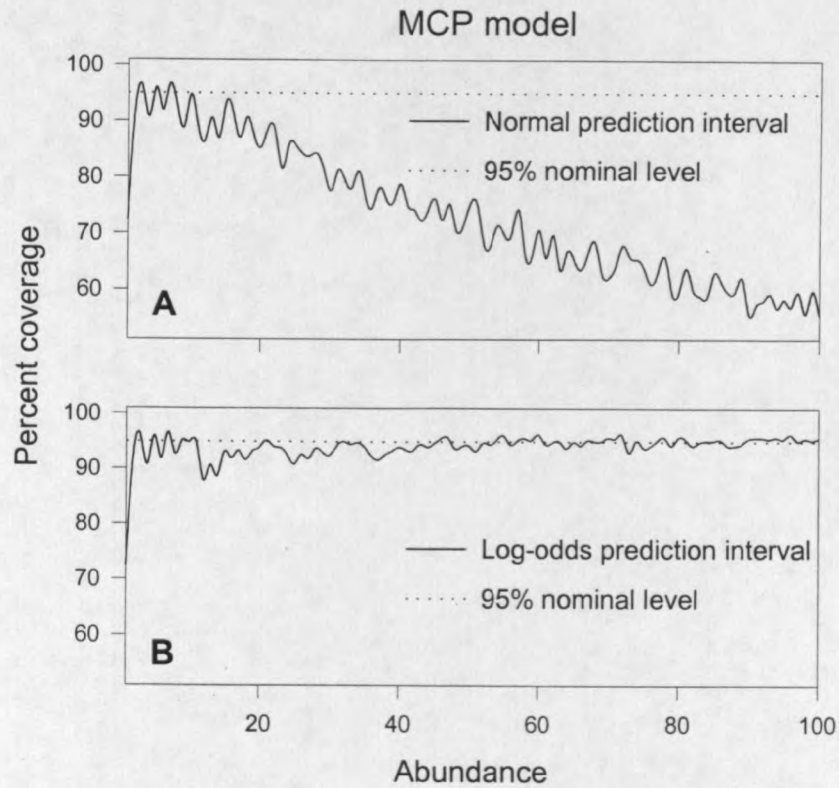


Figure 4.8.—Percent coverage of the true abundance (range, 1 to 100) for normal (A) and log-odds (B) 95% prediction intervals for mean capture probability model predictions of simulated data.

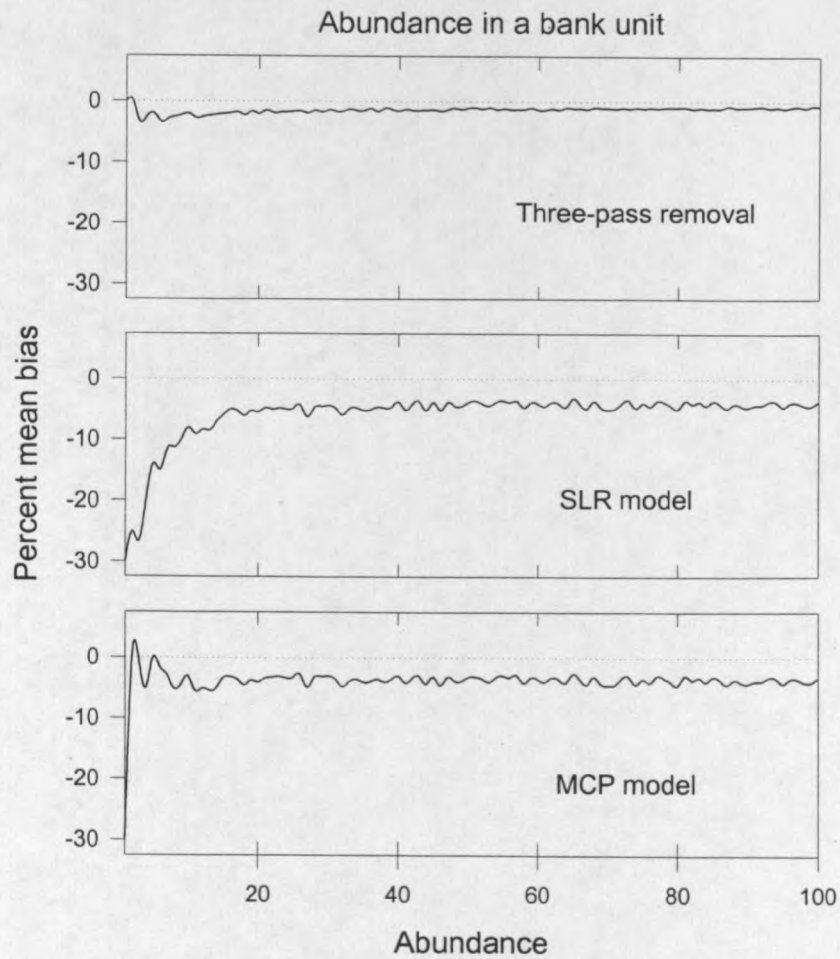


Figure 4.9.—Mean bias (expressed as a percentage of abundance) for three-pass removal estimates, simple linear regression (SLR) model predictions, and mean capture probability (MCP) model predictions for abundances ranging from 1 to 100.

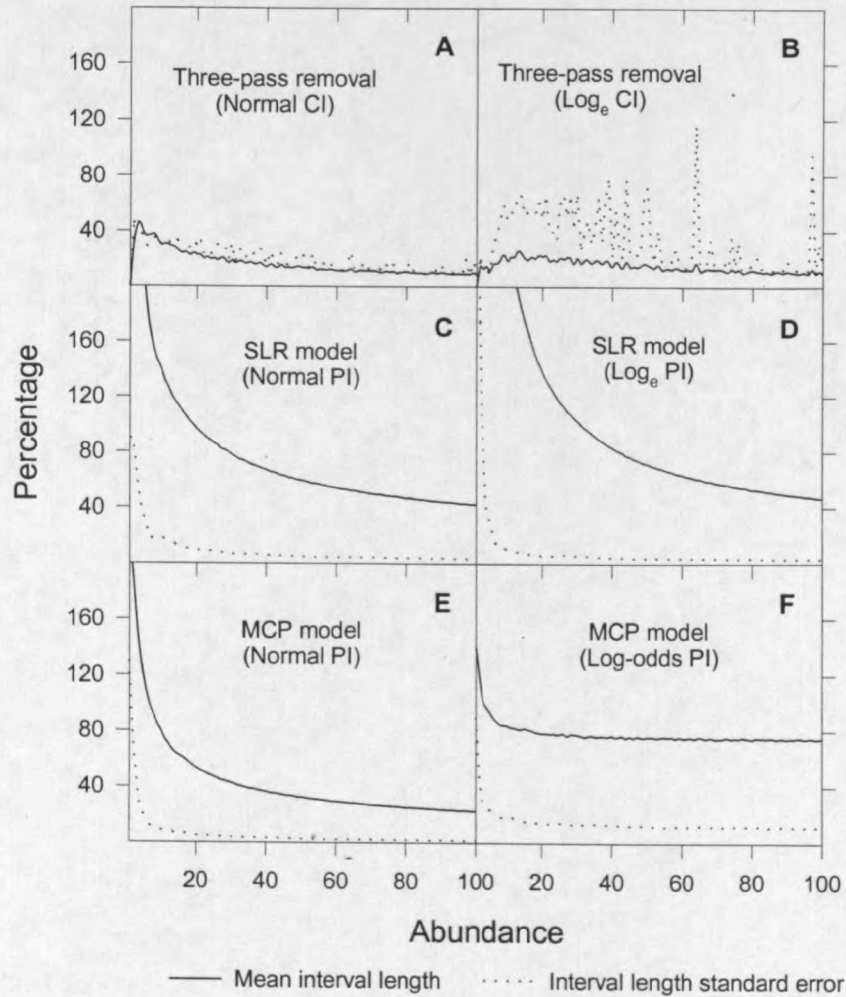


Figure 4.10.—Mean interval length and interval length standard error (each expressed as a percentage of abundance) for: (A) three-pass removal normal 95% confidence intervals (CI); (B) three-pass removal $\log_e$ 95% CI; (C) simple linear regression (SLR) model normal 95% prediction intervals (PI); (D) SLR model $\log_e$ 95% PI; (E) mean capture probability (MCP) model normal 95% PI; and (F) MCP model log-odds 95% PI.

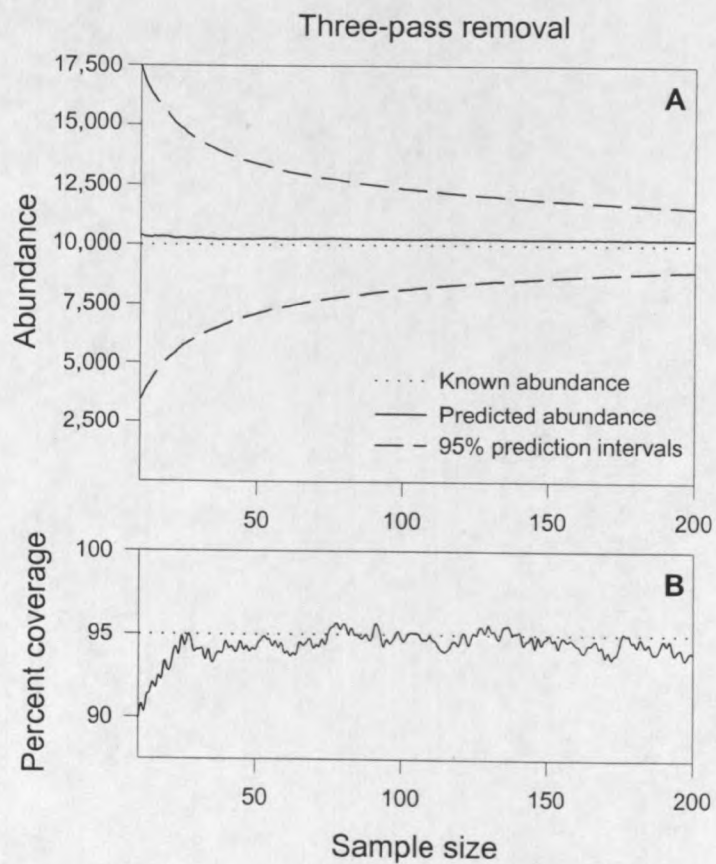


Figure 4.11.—Three-pass removal predicted abundance and 95% prediction intervals (A) and percent coverage of the true river-section abundance $N=10,000$ (B) for sample sizes ranging from 10 to 100.

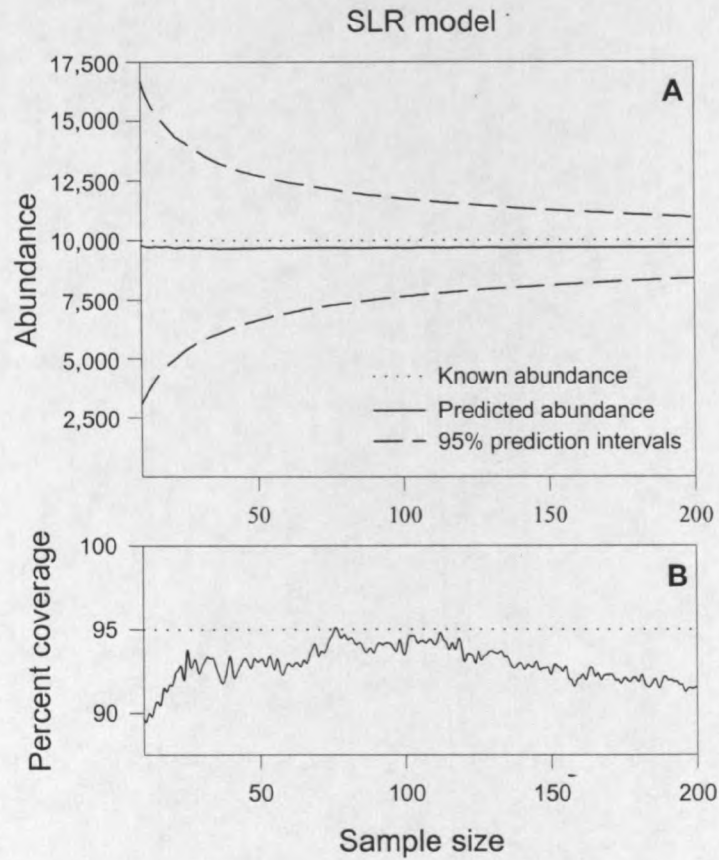


Figure 4.12.—Simple linear regression (SLR) model predicted abundance and 95% prediction intervals (A) and percent coverage of the true river-section abundance $N=10,000$ (B) for sample sizes ranging from 10 to 100.

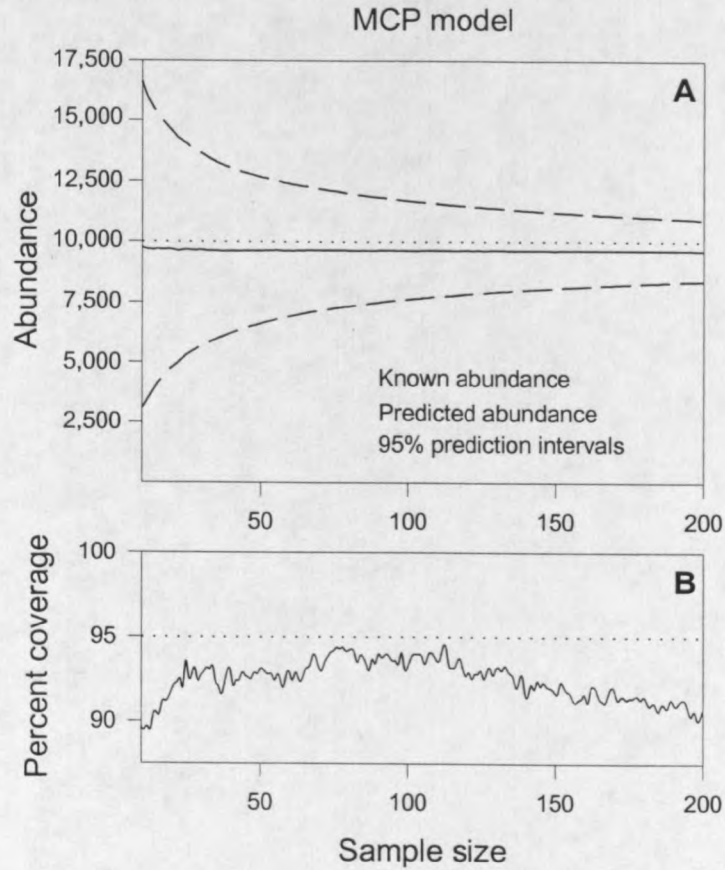


Figure 4.13.—Mean capture probability (MCP) model predicted abundance and 95% prediction intervals (A) and percent coverage of the true river-section abundance $N=10,000$ (B) for sample sizes ranging from 10 to 100.

CHAPTER 5

SEASONAL SURVIVAL, MOVEMENT, AND HABITAT USE OF AGE-0 RAINBOW TROUT IN THE HENRYS FORK OF THE SNAKE RIVER, IDAHO

Introduction

Abundance estimates of adult rainbow trout in the Henrys Fork of the Snake River, Idaho have indicated a fluctuating but overall decline in recruitment during the past two decades (Mark Gamblin, Idaho Department of Fish and Game, personal communication). Adult abundance estimates identified how many fish were recruited to the adult life stage, and a time series of these estimates indicated that a recruitment problem exists. However, adult abundance estimates cannot tell us why a particular recruitment pattern exists or at what life stage recruitment is limited. Recruitment is defined as the cumulative outcome or survival through a series of life stages (Trippel and Chambers 1997). The abundance of adult rainbow trout necessarily depends on the survival of rainbow trout through early life stages beginning with spawning and fertilization and extending through the juvenile life stage. The study of these early life history stages is critical to the understanding of year-class formation and changes in fish populations (Elliott 1994; Trippel and Chambers 1997).

Sampling methods used by the Idaho Department of Fish and Game and by Angradi and Contor (1988) to obtain data for abundance estimation have precluded making inferences on abundances of juvenile rainbow trout in the Henrys Fork. Rainbow trout less than 150 mm were consistently underrepresented in samples collected in

successive years by Angradi and Contor (1988). The failure to capture small trout is often a result of the sampling method; electrofishing is widely recognized as a size-selective sampling technique that favors capture of larger individuals (e.g., White et al. 1982; Bohlin et al. 1989; Jones and Stockwell 1995). Juvenile rainbow trout are also ecologically distinct from adults in their habitat requirements. Juvenile salmonids tend to occupy shallow, low velocity stream areas and may move to deeper habitat as they grow (Bohlin 1977; Gatz et al. 1987; Maki-Petays et al. 1997). Therefore, sampling must be directed specifically at juvenile rainbow trout if inferences concerning juvenile abundances are to be made.

Studies that have been directed at juvenile rainbow trout in the Henrys Fork have been limited in scope such that inferences on river-wide recruitment could not be made. We know that cobble-boulder concealment cover along banks is used by juvenile rainbow trout during winter (Contor 1989; Griffith and Smith 1995). Movement of juvenile rainbow trout from macrophyte cover to cobble-boulder cover along banks has been observed (Griffith and Smith 1995). The overwinter loss of macrophyte cover was positively correlated with a decrease in density of age-0 rainbow trout (Griffith and Smith 1995). Experimental studies indicated that winter survival of age-0 rainbow trout was higher in cages with cobble-boulder substrate than in cages without cover (Smith and Griffith 1994) and survival was higher with warmer 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). Size-dependent mortality (age-0 rainbow trout < 90-100 mm) occurred in cages with no cover or with colder water temperatures (Smith and Griffith 1994; Meyer and Griffith 1997). Angradi and Contor (1988)

estimated age-0 rainbow trout density by sampling along one bank in each of four river sections in summer. However, these estimates could not be extrapolated to both banks of the river because sampling was not representative of both banks. Studies of juvenile rainbow trout in the Henrys Fork should include multiple time periods and sampling areas representative of a large river reach such that recruitment can be quantified.

Estimates of temporal and spatial abundances of juvenile rainbow trout are essential to the evaluation of recruitment in the Henrys Fork. The estimation of survival and movement rates complements abundance estimation by aiding in the interpretation of temporal and spatial differences in abundances. Seasonal survival rates may be related to environmental changes in temperature and discharge, and spatial changes may be related to the movement of juvenile rainbow trout as habitat availability and habitat requirements change. The quantification of movement may also delineate the upper bound on the portion of a loss rate attributable to actual mortality. Therefore, a comprehensive study of juvenile rainbow trout to evaluate recruitment limitations must include the estimation of abundance, survival, movement, and habitat use across time and space.

Inferences concerning fish abundance, survival, movement, and habitat use are inherently difficult to make because individuals are not readily observable and information is only available on fish that are captured (Otis et al. 1978; Burnham et al. 1987; Gowan et al. 1994; Hilborn and Mangel 1997). Additional difficulties with juvenile fish are the typically large abundances and low capture probabilities that result in large variances and wide interval estimates (Cormack 1992). The yearly production of age-0 trout in the Henrys Fork may exceed 100,000. The size of the management area of interest, which is 25 km long with an average width of 90 m, poses additional sampling

problems concerning sampling efficiency (Kennedy and Strange 1981; Bohlin et al. 1989). Obviously, only a small percentage of such a population could ever be sampled given typical personnel and equipment constraints. However, sampling strategies and methods of analysis can be tailored to meet the demands of a recruitment study in a river such as the Henrys Fork.

The overall goal of this study was to develop an understanding of rainbow trout recruitment dynamics from spawning through the age-0 year class, in a 25-km management area of the Henrys Fork of the Snake River. I identified spawning areas and quantified spawning activity therein and I used electrofishing and mark-recapture and removal methodologies to quantify seasonal abundance, apparent survival, movement, and habitat use of age-0 rainbow trout. This information was used to produce a comprehensive analysis of age-0 rainbow trout recruitment in the Henrys Fork and to evaluate the ability of the fishery to sustain itself.

Study Area and Habitat Characteristics

The Henrys Fork is a medium-sized river that had a mean annual discharge of $24.3 \text{ m}^3/\text{s}$ in 1995-1997 at Island Park Dam (range, 6.9 to $78.4 \text{ m}^3/\text{s}$). The river elevation of the Henrys Fork at Island Park Dam is 1,897 m and the river drains a $1,246\text{-km}^2$ area. The Buffalo River joins the Henrys Fork about 0.6 km downstream of Island Park Dam (Figure 5.1). The Buffalo River is spring-fed and has a relatively constant discharge of about $6 \text{ m}^3/\text{s}$. A dam at the mouth of the Buffalo River prevented upstream migration of rainbow trout except during spring runoff prior to the installation of a fish ladder in October 1996.

I divided the Henrys Fork from the confluence with the Buffalo River to Riverside Campground into the following five sections for sampling age-0 rainbow trout: 1. Box Canyon (length $L = 4$ km, mean width $\bar{w} = 70$ m), 2. Last Chance ($L = 4$ km, $\bar{w} = 95$ m), 3. Harriman State Park ($L = 8$ km, $\bar{w} = 125$ m), 4. Harriman East ($L = 3$ km, $\bar{w} = 100$ m), and 5. Pinehaven-Riverside ($L = 3$ km, $\bar{w} = 85$ m) (Figure 5.1). Box Canyon was further divided into upper Box Canyon ($L = 1.5$ km) and lower Box Canyon ($L = 2.5$ km). 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. The Idaho Department of Fish and Game has traditionally used these sections to divide the river.

Box Canyon has a high gradient (0.45%) with cobble-boulder substrate and 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 (i.e., > 1 m deep), and large, uneven substrate. The channel depth is usually less than 1 m in lower Box Canyon. There is generally no ice formation in Box Canyon because winter water temperature is moderated by water released from the hypolimnion in Island Park Reservoir (2-4 °C) and water from the spring-fed Buffalo River (1-6 °C) (Figure 5.2).

Last Chance has an intermediate gradient (0.3%) with cobble substrate and 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 grazing by trumpeter swans *Cygnus buccinator*. There is generally no ice formation in Last Chance. The channel depth is usually less than 1 m throughout Last Chance.

Harriman State Park has a low gradient (0.1%) with a highly embedded sand-

gravel substrate and is characterized by a patchy distribution of dense macrophyte beds, but a general lack of cover in the channel and no 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, increased width (i.e., 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 (i.e., 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 and 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. There are some fallen trees and large rocks along the banks, but there is generally little bank habitat. The last 1 km of Pinehaven-Riverside flows through a canyon and has a high gradient, a deep channel (i.e., 1-3 m), and large boulders scattered throughout the channel and along the banks. Bank areas are generally

inundated with silt. Surface ice forms along bank areas in Pinehaven-Riverside during winter.

The short river section between Island Park Dam and the Buffalo River was included among the river sections searched for spawning redds. This section was divided into two sections for sampling and analysis: the section between Island Park Dam and the United States Geological Survey (USGS) gauging station ($L = 0.25$ km, $\bar{w} = 56$ m) and the section between the USGS gauging station and the Buffalo River ($L = 0.35$ km, $\bar{w} = 42$ m). These sections have an intermediate gradient (0.3%) with boulder substrate in the thalweg and gravel substrate in the adjacent shallow areas.

Methods

Spawning Redd Surveys

I used distance sampling techniques (Buckland et. al. 1993) to search sections of the Henrys Fork for spawning redds and the computer program DISTANCE (Laake et al. 1994) to estimate redd density therein. I searched for redds in river sections during spring (i.e., March and April) by wading or snorkeling along replicate transects perpendicular to the current and I recorded the perpendicular distance of each observed redd from the transect. The following river sections were surveyed: 1. Island Park Dam to the USGS gauging station (1995, 1996, and 1997; 10-15 transects per sampling date), 2. The USGS gauging station to the Buffalo River (1995; 10 transects), 3. Box Canyon (1995; 20 transects), 4. Last Chance (1995 and 1997; 20 transects), and 5. Harriman State Park (1997; 20 transects). I also searched for redds along alternating sides of the river

between transects to verify that transects were representative of river sections (i.e., that there were not many more or less redds between transects versus on or near transects). (See Chapter 2 for details on the distance sampling technique for redd surveys.)

Juvenile Trout Sampling Methodology

Sampling seasons were summer (August), autumn (October to mid-November), and spring (mid-May to mid-June). Five river sections were sampled in nine seasons from summer 1995 to spring 1998. I used a robust design to estimate seasonal abundances and apparent survival rates of age-0 rainbow trout for each river section (Pollock et al. 1990). 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. I used both removal and mark-recapture methodologies to estimate abundance. An open population model (i.e., the Jolly-Seber model) was used to estimate survival between seasons. Alternatively, survival was estimated by comparing abundances from one season to the next. Juvenile trout were marked with visible implants of fluorescent elastomer (Northwest Marine Technology, Inc.) for mark-recapture from season to season to estimate survival and to identify and quantify movement.

Marking

Juvenile trout were marked with visible implants of fluorescent elastomer (Northwest Marine Technology, Inc.) to identify capture seasons and capture sections. A

mark in the right post-ocular area was used in all river sections to indicate year of first capture for the year beginning in the summer sampling season. Colors to denote marking years were as follows: summer 1995 to spring 1996, red; summer 1996 to spring 1997, orange; and summer 1997 to spring 1998, green. An additional mark was used to denote the river section (using different colors) and season (using different marking locations) of capture. Colors to denote river sections were as follows: Box Canyon, blue; Last Chance, red; Harriman State Park, green; Harriman East, yellow; and Pinehaven-Riverside, orange. These were injected in the left post-ocular area in summer, the left pectoral fin in autumn, and the left pelvic fin in spring.

Within-season capture histories were indicated by a unique fin clip for each capture occasion. Fin clips were minimized (i.e., only the fin tip was clipped) in size to allow mark recognition within a season and regeneration thereafter.

Removal

A removal methodology was used to sample and estimate the abundance of age-0 rainbow trout along banks, particularly along banks with complex habitat and in river sections and seasons in which channel could not be waded. Trout were collected in bank sampling units using 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 extending out into the channel a minimum of 2 m, or further 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 using a systematic random procedure and sampled by three-pass or single-pass removal. Three-

pass removal data were analyzed using the Zippin maximum likelihood removal estimator (Zippin 1956; Otis et al. 1978; Rexstad and Burnham 1991) and single-pass removal data were analyzed using a mean capture probability model (see Chapter 4 for details). 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; 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 in summer and autumn and throughout Box Canyon in spring. All samples were collected by three-pass removal and an equal number of bank units were sampled on each side of the river unless otherwise noted. I sampled four 29.0 to 30.0-m bank units in summer 1995, ten 12.1 to 14.7-m bank units in summer 1996 (7 by single-pass removal), and eight 13.3 to 14.7-m bank units in summer 1997. I sampled seven 12.5 to 31.5-m bank units in autumn 1995 (west bank, 3; east bank, 4; 3 by single-pass removal), ten 11.0 to 14.8-m bank units in autumn 1996 (4 by single-pass removal), and ten 13.0 to 15.0-m bank units in autumn 1997. I sampled twenty 10.0 to 14.5-m bank units in spring 1996 (13 by single-pass removal), fifty 7.8 to 15.8-m bank units in spring 1997, and fifty 13.0 to 15.3-m bank units in spring 1998.

I also sampled along the banks in Last Chance and Pinehaven-Riverside in some years and seasons. I sampled twenty 12.6 to 15.5-m bank units in Last Chance in spring 1997. In Pinehaven-Riverside, I sampled ten 24.5 to 33.0-m bank units in summer 1995 and ten 17.0 to 27.0-m bank units in summer 1996 (all by single-pass removal). I sampled four 9.9 to 12.4-m bank units in autumn 1995. I sampled ten 12.0 to 15.0-m

bank units in spring 1996 (all by single-pass removal) and eight 12.4 to 14.6-m bank units in spring 1997.

Mark-Recapture

Mark-recapture sampling was used to obtain abundance estimates for sample areas in lower Box Canyon, Last Chance, and Harriman State Park in summer and autumn sampling seasons (high discharge necessitated the use of other sampling techniques in spring). 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. I 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 trout 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 using the Chao M_t estimator in program CAPTURE (Chao 1989; Rexstad and Burnham 1991). Sampling effort equaled the sum length of all transects on all capture occasions. (See Chapter 3 for details on the sampling procedure and estimator selection.)

Mark-recapture data were collected in Harriman East and Pinehaven-Riverside in all seasons by drifting with electrofishing gear (continuous DC, 175-250 V). I 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 a section, 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 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).

Separation of Age-0 and Age-1 Rainbow Trout

I separated age-0 rainbow trout for analysis by determining the age of a subset of sampled trout. Scales were collected from up to 10 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. Three scales from each trout were pressed onto cellulose acetate slides. I read each set of scales counting the number of annual rings and retained sets for further analysis if age readings were obtained for all three scales. Each trout was assigned the maximum age read from the set of three scales.

Logistic regression was used to partition trout into age classes based on length if the range of lengths for age-0 trout overlapped the range for age-1 trout. The length at which a logistic regression function (fitted to length and age data for a particular river section, season, and year) equaled 0.5 was used as the classification length. Any rainbow

trout (for that river section, season, and year) with total length less than the classification length was classified age 0. Logistic regression analyses were performed using the categorical data modeling procedure in SAS (PROC CATMOD; SAS Institute 1994).

Apparent Survival

I analyzed the mark-recapture data (i.e., from visible implants of fluorescent elastomer) using the Jolly-Seber model in program MARK (White and Burnham 1997) to estimate seasonal apparent survival (i.e., survival only within a sampled river section; survival of trout that moved outside of the study area was not estimated). Data from the five river sections were pooled for analysis. The simplest model had six parameters: apparent survival from summer to autumn, apparent survival from autumn to spring for each of three years, apparent survival from spring to older age classes, and a single capture probability for all years and seasons. Adding survival or capture probability parameters (up to nine parameters total) increased model complexity. Time intervals (months) between seasons were set to 1.0 between summer and autumn, 6.5 between autumn and spring, and 1.5 between spring and summer.

I also 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 estimated abundance at time $t+1$ by estimated abundance at time t . Apparent survival estimates greater than one indicated recruitment had occurred (i.e., via birth or immigration).

I obtained a more detailed description of apparent survival during winter in Last Chance by sampling once per month using a catch-per-unit-effort 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. I investigated whether or not catch per unit effort was linearly related to abundance and thus could be used as an indicator of change in abundance (i.e., apparent survival). I determined the correlation between catch per unit effort and estimated abundance for summer and autumn sample area data.

Movement

Seasonal movement (or lack thereof) was detected by recapturing juvenile trout marked with visible implants of elastomer. The same sample areas were re-sampled from season to season such that a high proportion of juvenile rainbow trout in these areas were marked, and restricted movement was recognized by the recapture of trout originally marked in these areas. 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.

A qualitative description of the seasonal movement of juvenile rainbow trout in the Henrys Fork was obtained by simply drawing arrows on a map from the capture location to the recapture location. Such an analysis indicated directional patterns of movement. A more rigorous quantitative analysis of seasonal movement was obtained by maximum likelihood estimation of movement probabilities.

I obtained maximum likelihood estimates of movement probabilities using a modification of the analysis proposed by Hilborn (1990). Movement probability estimates were used to estimate the total loss of age-0 trout attributable to movement to

another river section between summer, autumn, and spring. The analysis consisted of four steps:

1. A population dynamics and movement model was constructed to describe how the number of marked trout in each river section changed over time.

$$\hat{N}_{ijt+1} = (\hat{N}_{ijt} + T_{it})p_{ijt}$$

where $\hat{N}_{ijt+1}$ was the predicted number of trout marked in section i that were in section j at time $t+1$ ($i, j = 1$ to 5 and $t = 1$ to 2),

$\hat{N}_{ijt}$ was the predicted number of trout marked in section i that were in section j at time t and $\hat{N}_{ijt=1} = 0$,

T_{it} is the number of marked trout released in section i at time t .

and p_{ijt} is the probability of movement from section i at time t to section j at time $t+1$.

2. An observation model was constructed to describe how marks were recovered.

$$\hat{R}_{ijt} = \hat{N}_{ijt}(\hat{q}E)_{jt}$$

where $\hat{R}_{ijt}$ was the predicted number of trout marked in section i and recaptured in section j at time t ($t = 2$ to 3),

$\hat{N}_{ijt}$ was the predicted number of trout marked in section i that were in section j at time t ,

and $(\hat{q}E)_j$ was a product of the capture probability and sampling effort in section j at time t .

I estimated $(\hat{q}E)_j$ from the total number of age-0 trout captured divided by the total estimated abundance for the river section, which is equivalent to capture probability $\hat{q}$ times sampling effort E . If an abundance estimate was not available, I used an average capture probability $\bar{\hat{q}}$ (i.e., $(\hat{q}E)_j / E$ from other years or another season for a particular river section) and multiplied it by E for the section and season of interest.

3. A likelihood function was constructed to specify the likelihood of an observed number of recaptured trout in a river section (R) as a function of the predicted number of marked trout in that river section ($\hat{R}$). This function was defined under a set of parameters from the population dynamics and movement model and the observation model where we assume these models are true. The recaptures were assumed distributed according to a multinomial distribution and a Poisson distribution was used to approximate the multinomial. Hilborn (1990) stated that both the multinomial and the Poisson distributions are used in maximum likelihood estimation with mark-recapture data, but that the Poisson can approximate the multinomial because the probability of recapturing marked fish is small.

$$L(R | \hat{R}) = L(R | p, \hat{q}E, T) = \prod_{i=1}^5 \prod_{j=1}^5 \prod_{t=2}^3 \frac{e^{-\hat{R}_{ijt}} \hat{R}_{ijt}^{R_{ijt}}}{R_{ijt}!}.$$

4. I used the `fmins` optimization function in MATLAB® version 5 (MathWorks, Inc. 1998) to minimize the negative of the log-transformed likelihood function (i.e., obtain maximum likelihood estimates of p_{ijt}); the denominator $R_{ijt}!$ was ignored because it was a constant (Turchin 1998).

$$\log L(R | \hat{R}) = \sum_{i=1}^5 \sum_{j=1}^5 \sum_{t=2}^3 \left[-(\hat{R}_{ijt} + 1) + (R_{ijt} + 1) \cdot \log(\hat{R}_{ijt} + 1) \right].$$

Seasonal estimates of movement probabilities were obtained by pooling data across years and constraining parameters to equal zero if no movement was observed between two river sections. Estimates of p for fish marked and recaptured in the same river section were estimates of apparent survival. This modeling approach also provided an estimate of the loss rate from each river section if the p 's did not sum to 1, resulting from mortality or movement to areas not included in the model. The model I investigated had three parameters: 1. Apparent survival within a river section between summer and autumn, 2. Apparent survival within a river section between autumn and spring, and 3. Movement between river sections between summer, autumn, and spring.

I obtained a measure of confidence in the movement parameter estimates by investigating the numerical stability of the maximum likelihood estimates. If the log-likelihood were flat in the neighborhood of its maximum, then a confidence interval was relatively wide. Flatness (or lack thereof) of the log-likelihood near its maximum was detected by recalculating the log-likelihood over a range of values for two parameters while holding the third parameter constant (i.e., the third parameter equaled the MLE,

0.75 times the MLE, and 1.25 times the MLE). Small changes in the parameters resulting in small changes in the log-likelihood indicated a flat log-likelihood and wide confidence interval (Casella and Berger 1990; Hilborn 1990).

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 (i.e., about 187,500) received an adipose clip to allow recognition of 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

I quantified the use of river sections identified by habitat type (i.e., macrohabitat) by estimating the abundance of age-0 rainbow trout in each river section. I also identified the relative use of bank habitat versus channel habitat from 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 was recorded. Trout captured within a minimum of 2 m of either bank or any structure associated with the bank (e.g., woody debris) were classified as using bank habitat. All other trout were classified as using center channel habitat.

Winter habitat use was identified in Last Chance during winters 1996-1997 and 1997-1998 from samples of random transects. I compared abundances along the east and

west banks in Box Canyon after these winters (i.e., spring 1997 and 1998) by comparing density in sampled bank areas. These were the two spring sampling seasons for which 25 east and 25 west bank areas were sampled.

Results

Spawning Redd Surveys

Most spawning redds in the Henrys Fork were observed in the river section between Island Park Dam and the USGS gauging station. Redds occurred throughout the shallow gravel area adjacent to the thalweg. I observed 22 redds on 27 April 1995 ($\hat{N} = 28$, 95% confidence interval (CI) [12—67]) and 9 redds on 21 April 1996 ($\hat{N} = 16$, 95% CI [6—42]). Four weekly surveys between 30 March and 21 April 1996 indicated increasing spawning activity (i.e., redds) during this time period. Only one redd was observed in six weekly surveys from 11 March to 19 April 1997 in this river section. Increased discharge after the last survey date in each year precluded further searches for redds.

I observed one redd in the river section between the USGS gauging station and the Buffalo River on 27 April 1995 and one redd in Last Chance on 18 April 1995. Each redd was observed in a shallow gravel area adjacent to a bank. No additional redds were observed along the banks between transects in these sections. I did not observe any redds along transects or along the banks between transects in Box Canyon on 17 April 1995, in Last Chance on 20-21 April 1997, and in Harriman State Park on 21 April 1997.

A fish ladder installed in the Buffalo River in October 1996 allowed access to spawning areas in 1997 that were previously inaccessible to rainbow trout in the Henrys Fork prior to spring runoff. Redd surveys were not conducted in the Buffalo River.

Separation of Age-0 and Age-1 Rainbow Trout

There was no overlap in length ranges of age-0 and age-1 rainbow trout in 20 combinations of river sections and seasons for which scales were read to determine age (Table 5.1). No age-1 trout were identified in 10 of these combinations (i.e., 4 in 1995 samples, 5 in 1996 samples, and 1 in 1997 samples). A classification length to delineate age-0 and age-1 rainbow trout for which there was an overlap in length ranges was estimated for 14 combinations of river sections and seasons (Table 5.2). Eight classification lengths were estimated for 1997 samples, three for 1996 samples, and three for 1995 samples.

Apparent Survival

Comparisons of Abundance and Catch Per Unit Effort

Summer-to-Autumn. Comparisons of abundance estimates indicated a summer-to-autumn age-0 rainbow trout apparent survival rate in Box Canyon of 0.70 in 1995 (95% CI, [0.43—1.39]), 1.09 in 1996 (95% CI, [0.66—1.85]), and 0.70 in 1997 (95% CI, [0.46—1.13]). The apparent survival rate in Last Chance was 0.83 in 1995 (95% CI, [0.48-2.08]), 0.70 in 1996 (95% CI, 0.21—11.03]), and 0.75 in 1997 (95% CI, [0.50—1.31]). The apparent survival rate in Harriman State Park was 1.30 in 1996 (95% CI, [0.73—2.37]) and 1.10 in 1997 (95% CI, [0.77—1.67]).

I 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 because abundance estimates were not obtained for one or both seasons. Summer-to-autumn apparent survival could not be estimated by comparison of catch per unit effort because there was no correlation between catch per unit effort and estimated abundance in summer samples ($r^2=0.006$; Figure 5.3).

Autumn-to-Spring. Autumn-to-spring apparent survival estimates from abundance comparisons of age-0 rainbow trout were only obtained for Box Canyon. The apparent survival rate was 0.23 in 1995-1996 (95% CI, [0.19—0.34]), 0.18 in 1996-1997 (95% CI, [0.12—0.29]), and 0.21 in 1997-1998 (95% CI, [0.14—0.32]).

Too few trout were captured and none were recaptured in Pinehaven-Riverside in autumn and in Last Chance, Harriman State Park, and Harriman East in spring. Therefore, I could not estimate autumn-to-spring apparent survival by comparison of abundance estimates. However, there was a positive linear relation between catch-per-unit-effort and estimated abundance in autumn ($r^2=0.54$; Figure 5.3) which suggested that a comparison of catch per unit effort between seasons (rather than comparisons of estimated abundance) could be used to estimate apparent survival. A comparison of catch per unit effort between November and April from samples of 10 random transects in Last Chance indicated an apparent survival rate of 0.11 in 1996-1997 and 0.03 in 1997-1998. A comparison of catch per unit effort between autumn and spring samples in Harriman State Park indicated an apparent survival rate of 0.003 in 1995-1996, 0.001 in 1996-1997, and 0.004 in 1997-1998. The apparent survival rate in Harriman East was

0.005 in 1995-1996, 0 in 1996-1997, and 0.014 in 1997-1998. The apparent survival rate in Pinehaven-Riverside was 0.24 in 1995-1996, 1.10 in 1996-1997, and 1.35 in 1997-1998.

The greatest loss of age-0 trout occurred during winter. Most age-0 trout that survived their first winter were found in Box Canyon and Pinehaven-Riverside the following spring. There was an almost complete loss of age-0 trout from Harriman State Park and Harriman East. There was some survival in Last Chance, but the loss from this river section was great considering the abundances present at the start of each winter.

Mark-Recapture Estimates of Apparent Survival

The analysis of mark-recapture data using Jolly-Seber models in program MARK did not yield maximum likelihood estimates of apparent survival that were consistent with abundance estimates or catch per unit effort. Apparent survival estimates from program MARK were often greater for autumn to spring (e.g., 0.76) than for summer to autumn (e.g., 0.24).

Capture probability estimates from program MARK for among-season mark-recapture data were consistent with capture probability estimates from program CAPTURE for within-season mark-recapture data. Program MARK estimated a capture probability of about 0.06 for age-0 and age-1 trout (i.e., a single parameter capture probability model) and about 0.09 for age-0 trout and 0.01 for age 1 trout (i.e., a two parameter capture probability model). The mean capture probability for data sets analyzed in program CAPTURE was about 0.04 (see Chapter 3 for details). These capture probabilities yielded insufficient data for valid mark-recapture survival analysis.

Movement

Qualitative Descriptions of Movement Patterns

I 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 5.3). Most 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.

There was little summer-to-autumn movement of age-0 rainbow trout in Box Canyon and Last Chance, the two river sections with the greatest abundance of age-0 trout. I recaptured in autumn 53 age-0 trout marked in summer in Box Canyon and 77 in Last Chance. An equal amount of summer-to-autumn downstream and upstream movement was detected. Two age-0 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 trout marked in Harriman State Park was recaptured upstream in Last Chance and two marked in Last Chance were recaptured upstream in Box Canyon.

There was little autumn-to-spring movement of age-0 rainbow trout in Box Canyon. I recaptured in spring 44 age-0 trout marked in autumn in Box Canyon. One age-0 trout marked in Pinehaven-Riverside in autumn was recaptured there in spring. No trout marked prior to winter in Last Chance, Harriman State Park, and Harriman East were recaptured after winter in the same river section. Pre-winter-to-post-winter downstream movement was detected from all river sections to Pinehaven-Riverside

(Figure 5.4). Three age-0 trout marked in Box Canyon, three in Last Chance, two in Harriman State Park, and one in Harriman East were recaptured after winter in Pinehaven-Riverside. Pre-winter-to-post-winter upstream movement was also detected (Figure 5.4). Two age-0 trout marked in Last Chance were recaptured after winter in Box Canyon.

Movement among river sections was not detected for most trout marked at age 0 (i.e., summer, autumn, or spring) and recaptured at age 1 (i.e., the following summer, autumn, or spring). Seventeen rainbow trout marked at age 0 in Box Canyon, two in Last Chance, and twelve in Pinehaven-Riverside were recaptured at age 1 in the same river sections. Both trout recaptured in Last Chance were marked in that river section during the spring after their first winter. Four trout were recaptured at age 1 in river sections downstream from the section in which they were marked at age 0. Two trout moved from Box Canyon to Last Chance and one trout from Box Canyon and one from Last Chance moved to Pinehaven-Riverside. One of the trout that moved from Box Canyon to Last Chance moved between spring and summer; the other moved between autumn and summer.

Limited movement among river sections was also detected within a season. One age-0 rainbow trout marked in Last Chance in autumn was recaptured upstream in Box Canyon during the same autumn. One age-0 trout marked in Last Chance in spring was recaptured downstream in Pinehaven-Riverside during the same spring.

Most movement of age-0 rainbow trout was from summer growth habitat to overwinter habitat and occurred between autumn and spring: 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 stay the duration of winter, but they were detected moving out of these sections. The movement data indicated that 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.

Maximum Likelihood Estimates of Movement Probabilities

The estimated probability of summer-to-autumn and autumn-to-spring movement of age-0 rainbow trout among river sections was 0.0092 (Table 5.4). Summer-to-autumn movement included movement from Box Canyon to Harriman East, from Last Chance to Box Canyon and Pinehaven-Riverside, and from Harriman State Park to Last Chance. Autumn-to-spring movement included movement from Last Chance to Box Canyon and from all river sections to Pinehaven-Riverside.

The estimated probability of apparent survival from summer to autumn (i.e., no movement) was 1.0099 (Table 5.4). Apparent survival was estimated for Box Canyon, Last Chance, Harriman State Park, and Pinehaven-Riverside. The estimated probability of apparent survival from autumn to spring (i.e., no movement) was 0.0776 for Box Canyon and 0.0092 for Pinehaven-Riverside (i.e., the same parameter used to estimate movement).

The sum of summer-to-autumn apparent survival and movement probabilities for a river section subtracted from 1 ranged from -0.0099 to -0.0283 (Table 5.4). The sum of autumn-to-spring apparent survival and movement probabilities for a river section subtracted from 1 ranged from 0.9132 to 0.9908 (Table 5.4). Values less than zero

indicated net recruitment; values greater than zero indicated net loss (i.e., mortality or movement to river sections outside of the study area).

The predicted numbers of recaptures of marked trout by river section were generally within ± 1 of observed values (Table 5.5). However, predicted and observed recapture values differed by about 20 for Box Canyon ($\hat{R}_{112} = 74$ and $R_{112} = 54$) and Last Chance ($\hat{R}_{112} = 56$ and $R_{112} = 77$) in autumn.

Small changes in the movement probability parameters yielded small changes in the log-likelihood for the equation in step 4 of the movement analysis (Figure 5.5). Log-likelihood regions for parameter 1 (i.e., apparent survival between summer and autumn) were flat for parameter values ranging from 0.4 to 1.5. Log-likelihood regions for parameter 2 (i.e., apparent survival between autumn and spring in Box Canyon) were flat for parameter values ranging from 0.05 to 0.30. Log-likelihood regions for parameter 3 (i.e., summer-to-autumn and autumn-to-spring movement) were flat for parameter values ranging from 0 to 0.10. Log-likelihood profiles were generally flat in the neighborhood of the maximum likelihood estimate for each parameter, indicating a lack of estimate precision.

The movement and apparent survival estimates were within the range expected based on abundance estimates. The estimated probability of apparent survival from summer to autumn (i.e., not moving) was 1.0099 in Box Canyon, Last Chance, Harriman State Park, and Pinehaven-Riverside. This estimate suggested there was no significant mortality during this time period. There was also no significant difference in abundance between summer and autumn for these river sections. The estimated probability of

apparent survival from autumn to spring was 0.0776 in Box Canyon. This estimate was less than apparent survival estimates obtained by comparing abundances (0.18-0.23), but the likelihood profile was flat for parameter estimates ranging from 0.05 to 0.30, suggesting no significant difference between these estimates.

The loss of age-0 rainbow trout from river sections could not be attributed solely to mortality. The estimated probability of movement between river sections was 0.0092. The probability of movement can be multiplied by an abundance estimate to estimate the number of trout moving from one river section to another. For example, multiplying 0.0092 times the total abundance for Box Canyon, Last Chance, Harriman State Park, and Harriman East in autumn 1997 indicates that 1,841 age-0 trout moved to Pinehaven-Riverside between autumn and spring. This number is about 45% of the spring 1998 abundance estimate for Pinehaven-Riverside. This estimate of movement to Pinehaven-Riverside was consistent with the apparent survival estimate obtained by comparing catch per unit effort, which was 1.35 and indicated recruitment had occurred.

Immigration of Hatchery Rainbow Trout

There was no indication that age-0 rainbow trout stocked in Island Park Reservoir were significantly contributing to recruitment in the Henrys Fork. Only one age-0 rainbow trout marked with an adipose clip was identified after inspecting over 30,000 age-0 trout from summer 1995 to spring 1998.

Habitat Use

Summer and Autumn

Most age-0 rainbow trout were located in Box Canyon and Last Chance prior to their first winter (i.e., summer and autumn samples). Box Canyon and Last Chance are the river sections closest to the major spawning area near Island Park Dam and to the Buffalo River. There were about 2.5 times as many age-0 rainbow trout in Last Chance as there were in Box Canyon in each year and season. There were about 50,000 to 75,000 age-0 trout in Box Canyon and about 110,000 to 220,000 in Last Chance in summers 1995-1997; there were about 35,000 to 80,000 in Box Canyon and about 90,000 to 150,000 in Last Chance in autumns 1995-1997 (Figure 5.6; Appendix Table A.7).

The density of age-0 rainbow trout was about 1.5 times greater in Last Chance than in lower Box Canyon. There was one age-0 rainbow trout per 2.8-4.2 m² in lower Box Canyon and one per 1.7-3.4 m² in Last Chance in summers 1995-1997. There was one age-0 rainbow trout per 2.9-6.7 m² in lower Box Canyon and one per 2.4-4.2 m² in Last Chance in autumns 1995-1997.

The mean number of age-0 rainbow trout captured per transect in Box Canyon indicated that more age-0 trout used bank habitat versus center channel habitat in summer and autumn (Figures 5.7 and 5.8). In Last Chance, more age-0 trout used center channel habitat (i.e., macrophytes) versus bank habitat. There were more age-0 trout in bank habitat in Box Canyon versus Last Chance and there were more age-0 trout in center channel habitat in Last Chance versus Box Canyon. These differences were significant at the $\alpha=0.05$ level as judged by confidence intervals.

There was an overlap in the size of age-0 rainbow trout using bank habitat and center channel habitat in summer and autumn 1996 and 1997 as indicated by size distributions by river section; however, there was a tendency towards smaller trout using bank habitat (Figures 5.9 and 5.10).

There were about 10,000 to 12,000 age-0 rainbow trout in a 1-km reach in Harriman State Park in summers 1996 and 1997 (no estimate was obtained for summer 1995) and about 13,000 in autumns 1995-1997 (Figure 5.6; Appendix Table A.7). The density of age-0 rainbow trout in Harriman State Park was less than the density in Box Canyon and Last Chance. There was one age-0 rainbow trout per 7.7 m^2 in summer 1996 and per 6.3 m^2 in summer 1997. There was one trout per 5.9 m^2 in autumns 1995-1997. The mean number of trout captured per transect indicated that most age-0 trout in Harriman State Park were using center channel habitat (Figures 5.7 and 5.8). The number of trout using bank habitat in autumn was not significantly different from zero.

Few age-0 rainbow trout were captured and none were recaptured in Harriman East in summer. Therefore, I concluded that abundances in Harriman East were negligible and this river section was essentially not used by age-0 trout in summer. Habitat in Harriman East was generally not suitable for age-0 rainbow trout. This river section was deep (1-2 m) and devoid of cover. Age-0 trout did move downstream to Harriman East in autumn but were likely transient. (One age-0 trout marked in Harriman East in autumn was recaptured in Pinehaven-Riverside in spring.) There were about 3,000 to 15,000 age-0 trout in Harriman East in autumn and they were captured throughout the center channel. The density of age-0 trout in Harriman East in autumn

was much less than in Box Canyon and Last Chance. There was one age-0 rainbow trout per 20-100 m².

Most rainbow trout captured in Pinehaven-Riverside in summer and autumn were age 1 rather than age 0 (Table 5.1). Abundance estimates were not obtained for this river section in summer and autumn with the exception of summer 1996 for which I obtained an estimate of 742 age-0 rainbow trout. There were usually few captures and no recaptures of age-0 trout and sampling effort was limited in autumn because of the onset of winter conditions limiting river access. There were generally few trout captured in bank areas. There were 247 age-0 rainbow trout along the banks of the upper 2 km of Pinehaven-Riverside in summer 1995 (95% CI, [29—465]), 507 in summer 1996 (95% CI, [185—830]), and 784 in autumn 1995 (95% CI, [-299—1,867]). There was on average 1 age-0 rainbow trout per 16.2 m of bank in summer 1995, 1 trout per 7.9 m of bank in summer 1996, and 1 trout per 5.1 m of bank in autumn 1995. (For comparison, there was on average 1 trout per 0.7-1.7 m of bank in summers 1995-1997 in Box Canyon and 1 trout per 0.3-0.7 m of bank in autumns 1995-1997.)

There was no shortage of age-0 rainbow trout rearing or summer growth habitat in the Henrys Fork. Age-0 trout were found throughout Box Canyon, Last Chance, and Harriman State Park in summer and autumn, primarily in complex bank habitat (e.g., rocks, woody debris) and macrophytes in the center channel. Trout dispersed to these areas at the fry stage (i.e., 25-35 mm TL), first occupying low velocity areas along the banks. Movement from bank areas to center channel habitat likely occurred as trout fry grew during summer and exceeded the carrying capacity (based on trout size) of bank areas.

Winter

There was relatively consistent use of bank habitat in Last Chance throughout the winter and declining use of center channel habitat (Figure 5.11). 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 (i.e., autumn samples). The use of center channel habitat decreased by about 50% in January, but there were still significantly more trout using the center channel versus bank habitat ($\alpha=0.05$). There was no significant difference in the use of center channel habitat versus bank habitat in February and March. The numbers of trout per transect increased in April and the number of trout in the center channel versus bank habitat was significantly greater in April 1998.

Spring

Most age-0 rainbow trout were located in Box Canyon and Pinehaven-Riverside after their first winter. These are the two river sections with complex bank habitat (Box Canyon in particular), higher gradients, and larger substrates. There were about 8,000 to 15,000 age-0 rainbow trout along the banks in Box Canyon in springs 1996-1998 and about 3,500 to 4,100 in Pinehaven-Riverside in springs 1997 and 1998 (no estimate was obtained for spring 1996; Figure 5.6; Appendix Table A.7). Age-0 trout remained in complex bank areas, where such habitat was available, throughout their first year.

The density of age-0 rainbow trout per m in Box Canyon was significantly greater along the west bank (2.83, SE = 0.36) than along the east bank (1.14, SE = 0.16) in spring 1997 ($P = 0.0002$). The density was similar between banks in spring 1998 (west = 1.29,

SE = 0.16; east = 1.12, SE = 0.27; $P = 0.58$). I also observed 25 to 35-mm age-0 rainbow trout (new cohort) in Box Canyon bank samples, predominantly along the east bank. I did not attempt to quantify new-cohort age-0 rainbow trout.

There was a slight shift or increase in the size distributions of age-0 rainbow trout using bank habitat in spring versus autumn (Figure 5.12). However, the age-0 trout along the banks in spring were generally smaller than the age-0 trout in the center channel in autumn. About 50% of the age-0 trout sampled in spring were less than 100 mm TL.

Most age-0 rainbow trout captured in Pinehaven-Riverside were in the center channel. I never captured more than two rainbow trout in a single-pass removal sample for a bank area in Pinehaven-Riverside in spring 1996 and I never captured more than one in a three-pass removal sample in spring 1997. There were 118 age-0 rainbow trout along the banks of the upper 2 km of Pinehaven-Riverside in spring 1996 (95% CI, [-8—244]) and 432 in spring 1997 (95% CI, [160—706]). There was on average 1 age-0 rainbow trout per 33.9 m of bank in Pinehaven-Riverside in spring 1996 and 1 trout per 9.3 m of bank in spring 1997. For comparison, there was on average about 1 trout per 1 m of bank in Box Canyon in spring 1996 and 1 trout per 0.5 m of bank in spring 1997. Pinehaven-Riverside had suitable habitat for age-0 trout, but its remote location relative to the spawning and summer growth areas probably limited the number of age-0 trout found there. The siltation of bank areas in Pinehaven-Riverside also limited the number of age-0 trout that could overwinter in that river section.

I sampled along the banks in Box Canyon in each spring when discharge was at the highest levels recorded during a year, and I sampled Pinehaven-Riverside about two weeks later when discharge had decreased. In spring 1997 I sampled again along the

banks in Box Canyon in mid-June when spring runoff had subsided (i.e., conditions similar to those encountered when sampling Pinehaven-Riverside). I did not capture any age-0 rainbow trout from the previous year's cohort but did capture many 25 to 45-mm trout from the new cohort that recently emerged. The age-0 trout that had occupied the bank habitat through their first year up to and during spring runoff had now moved away from the banks.

I could not sample by electrofishing along bank-to-bank transects in Last Chance in spring because of unsafe wading conditions during spring runoff. Some age-0 rainbow trout were captured in the center channel by drifting and electrofishing, indicating that this habitat was used (Appendix Table A.7). Monthly sampling of random transects in Last Chance prior to spring indicated that center channel habitat use declined during winter (i.e., through March) and increased at the onset of spring (i.e., April). Only three age-0 trout (1996 cohort) were captured in three-pass removal samples along the banks in Last Chance in June 1997. However, there were many 21 to 54-mm 1997-cohort age-0 trout in removal samples. I estimated that there were 69,058 recently emerged age-0 trout along the banks in Last Chance in spring 1997 (95% CI, [51,763—86,353]) and 70% of the trout were along the west bank.

Few age-0 rainbow trout were captured and none were recaptured in Harriman State Park and Harriman East in spring. No more than eight age-0 rainbow trout were ever captured in 2-3 days sampling in Harriman State Park or Harriman East. I concluded that abundances were negligible in these river sections and that age-0 trout throughout winter into spring did not use these sections throughout winter into spring. Harriman State Park and Harriman East were devoid of instream cover (i.e.,

macrophytes) each spring.

Discussion

Natural production of rainbow trout occurred in the Henrys Fork in each year of this study and yearly production ranged from 150,000 to 250,000 in the 25-km management area downstream from Island Park Dam. There was no evidence that recruitment in the river was dependent on trout stocking in Island Park Reservoir. There was suitable habitat throughout the channel and in the five river sections to support these abundances of age-0 trout through summer and autumn. However, most river sections did not support age-0 trout through their first winter. The highest overwinter survival occurred in Box Canyon, a river section characterized by complex bank habitat, high gradient, and large substrate. The loss of age-0 trout in winter in Last Chance was from center channel habitat. There was relatively consistent use of available bank habitat in Last Chance during winter and movement was detected from river sections with simple bank habitat to river sections with complex bank habitat.

Spawning

I observed an increasing trend in spawning activity in the section between Island Park Dam and the USGS gauging station in spring 1996, but not in spring 1997. The installation of the Buffalo River fish ladder in October 1996 provided access to spawning areas in the Buffalo River in spring 1997. The Buffalo River was previously inaccessible to rainbow trout in the Henrys Fork prior to spring runoff. Spawning rainbow trout that may have formerly used the area near Island Park Dam could have spawned in the

Buffalo River instead. Prior to the spring 1997 runoff, 224 rainbow trout greater than 400 mm TL migrated upstream through the fish ladder (Rob Van Kirk, Henrys Fork Foundation, personal communication). The water temperature at the Buffalo River spillway was 5.5 °C warmer (8.5 °C) than at Island Park Dam (3.0 °C) on 11 March 1997. Rainbow trout may be stimulated to spawn at water temperatures of about 3-6 °C, but typically spawn at higher water temperatures of about 6-9 °C (Behnke 1992). Early spawners stimulated by rising water temperature would be more likely to enter the Buffalo River to spawn than to use the area near Island Park Dam.

Spawning may have been limited in other sections of the Henrys Fork by unsuitable substrate. There are few areas of gravel substrate in Box Canyon and in Last Chance suitable for spawning. There are large areas of gravel substrate in Harriman State Park, but these areas are highly embedded and unsuitable for spawning.

Spawning likely occurred in the Henrys Fork during and after the time of increased discharge, when water temperatures were warmer. Spawning could not be observed by wading or snorkeling at those times. The presence of age-0 (new cohort) rainbow trout, about 25-35 mm TL, in samples collected from mid-May to mid-August was indirect evidence of spawning across a large temporal scale. Spawning may have continued into July. Most age-0 rainbow trout observed in Box Canyon in mid-May were along the east bank and could be attributed to downstream dispersal from the Buffalo River, which enters the Henrys Fork on the east side (Figure 5.1). However, in June 1997 70% of the age-0 rainbow trout captured along the banks in Last Chance were along the west bank and could be attributed to spawning activity in the Henrys Fork.

Apparent Survival

The precision of apparent survival estimates based on comparisons of abundance was dependent on the precision of the abundance estimates. All intervals for summer-to-autumn apparent survival estimates were relatively large and included 1.0; an apparent survival estimate of 1.0 indicates no mortality and an estimate greater than 1.0 indicates recruitment also occurred. The period between summer and autumn was not a time of significant mortality and recruitment may have continued to occur (e.g., the growth of recently emerged age-0 rainbow trout).

The first-winter apparent survival rates for rainbow trout in the Henrys Fork were low and varied little from year to year. The minimum apparent survival for a river section ranged from 0.1 to 0.4% (Harriman State Park) and the maximum apparent survival ranged from 18 to 23% (Box Canyon). Other studies found more variation in first-winter salmonid survival. Steelhead (anadromous rainbow trout *Oncorhynchus mykiss*) fry-to-smolt survival ranged from 3.3 to 21.9% in the Keogh River, Vancouver Island, British Columbia (Ward and Slaney 1993). Steelhead presmolt winter survival ranged from 13 to 90% in the Little Manistee River, Michigan (Seelbach 1993). Juvenile coho salmon *Oncorhynchus kisutch* survival was 25.4% and 46.2% for two winters in Big Beef Creek, Washington (Quinn and Peterson 1996). Brown trout *Salmo trutta* first winter survival ranged from 15 to 84% in Convict Creek, California (Needham et al. 1945). Brook trout *Salvelinus fontinalis* first-winter survival ranged from 35 to 73% in Lawrence Creek, Wisconsin (Hunt 1969). Survival in these rivers was more variable because winter conditions were more variable. Winter temperatures in the Henrys Fork

were less variable because the water originated from hypolimnetic releases from Island Park Reservoir and the spring-fed Buffalo River. Therefore, large year-to-year variations in survival would not be expected because of winter severity.

There did not appear to be significant size-dependent winter mortality in Box Canyon. There was considerable overlap in the size distributions of age-0 trout in bank areas of Box Canyon in autumn and spring and no indication of higher mortality for small trout. Smith and Griffith (1994) observed in cages in the Henrys Fork 100% mortality of trout less than 100 mm TL in October. Meyer and Griffith (1997) observed a temperature effect on survival of age-0 trout in cages in the Henrys Fork. They did not find a significant difference in survival of trout less than and greater than 90 mm TL at warm sites (3.1-4.3 °C); all mortality at cold sites (1.5-4.3 °C) occurred in trout less than 90 mm TL. However, I found in spring 1997 and 1998 samples in Box Canyon about 50% of age-0 rainbow trout were less than 100 mm TL. The median size did increase by 8 mm in winter 1996-1997 and by 3 mm in winter 1997-1998. This increase may have resulted from limited size-dependent mortality or movement of larger age-0 trout from the center channel to bank areas during winter or during spring runoff. Movement to more suitable habitat could have counteracted the temperature effect on survival.

I did not use comparison of catch per unit effort to estimate apparent survival between summer and autumn because there was no correlation between catch per unit effort and abundance for summer samples. Trout were more active in summer because of warmer water temperatures (12-18 °C) and capture probabilities were therefore more likely to vary with changes in weather (e.g., cloud cover) and time of day. Catch per unit effort was not a reliable indicator of abundance in summer.

Catch per unit effort was positively correlated with abundances in autumn samples. Trout were less active in the cooler water temperatures from October to May ($< 10^{\circ}\text{C}$) and capture probabilities were therefore less likely to vary with changes in weather and time of day. Therefore, catch per unit effort was sometimes used as a surrogate for abundance to estimate apparent survival between autumn and spring.

Catch-per-unit-effort sampling on a monthly basis through winter indicated that the loss from Last Chance occurred in the latter half of each winter. The catch per unit effort decreased by about 52-56% between December and January and by another 77-94% between January and March. This is contrary to the experimental results of Smith and Griffith (1994) and Meyer and Griffith (1997) who found most age-0 trout mortality in cages to occur in early winter (i.e., October-November).

I was unable to obtain valid estimates of apparent survival by analyzing mark-recapture data with Jolly-Seber type models in program MARK. The estimates were not consistent with abundance and catch-per-unit-effort data and with apparent survival estimates from the analysis of movement data (i.e., the probability that trout did not move). For example, Jolly-Seber apparent survival estimates were greater for autumn to spring than for summer to autumn; all other analyses indicated that mortality was greatest during winter. Jolly-Seber type models use ratios of estimates of the number of marked trout in a population in successive time periods to estimate survival (Pollock 1991). The number of parameters to estimate is large. Many recaptures are required for estimates to be precise (Pollock et al. 1990). Constraints, such as specifying constant apparent survival from summer to autumn in each year, can be placed on Jolly-Seber models to reduce the number of parameters to estimate and thereby improve estimate precision.

Models considered for analysis incorporated such constraints, but did not yield valid apparent survival estimates.

Another reason why the Jolly-Seber type models did not yield valid apparent survival estimates may have been the study design and sampling priorities. For example, sample areas in Box Canyon were sampled on four to five dates each autumn and trout were marked with fin clips for within-season abundance estimation and visible implants of fluorescent elastomer (VIE) for among-season apparent survival and movement estimation. However, occasionally there were time or personnel constraints that limited the number of trout that could be marked with VIE, resulting in season-to-season variation in the number of marked trout in sample areas. When time permitted, trout were collected in random locations in Box Canyon to add additional marked trout to the population. What this approach to marking trout did was in some seasons to concentrate marked trout in sample areas and in other seasons to have a more widespread distribution of marked trout in the river section. The number of marked trout captured in subsequent seasons may have been more closely related to the distribution of marked trout rather than the apparent survival of marked trout. This may be the reason for the large difference in the observed versus predicted number of recaptured trout that did not move in Box Canyon and Last Chance (Table 5.5).

Movement

Movement is an integral variable in defining the use of time and space by fishes (Wootton 1991). Movement is common in resident stream salmonids and may result from seasonal changes in the stream environment, the presence of conspecifics, or

behaviors including fry dispersal and ontogenetic shifts in habitat use or diet (see review in Gowan et al. 1994). Temporal and spatial changes in the abundance of juvenile salmonids can often be attributable to movement, as well as mortality or recruitment. Therefore, the 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 short sample areas in Box Canyon, Last Chance, and Harriman State Park, and sampling throughout Harriman East and Pinehaven-Riverside, I was able to detect the movement of juvenile rainbow trout. Other studies have not been able to detect long range movement because sampling was confined to one area (see review in Gowan et al. 1994). If a high proportion of fish in a single area was marked, resampling in that area would show restricted movement if marked fish were recaptured. This was evident in Box Canyon, Last Chance, and Harriman State Park sample areas. However, by sampling in many areas, long range movements of juvenile rainbow trout were detected by recaptures in sections other than those in which they were marked.

There was the chance of not detecting movement by failing to recapture any trout when movement was known to have occurred based on catch data. For example, the juvenile rainbow trout catch-per-day in Harriman East was often 0 in spring and summer, but greater than 150 in autumn in all years data was collected. Two juvenile trout marked in Box Canyon in summer were recaptured in Harriman East in autumn 1995. No trout were recaptured in Harriman East in 1996 or 1997. Does this mean that movement did not occur in 1996 or 1997? No. The catch data indicated that movement did occur, but

the mark-recapture technique failed to detect it. Mark-recapture data was therefore pooled by year for analysis.

Maximum likelihood estimators developed by Hilborn (1990) to quantify movement in a marine fishery have not been widely applied to quantify movement in rivers (Gowan et al. 1994). I showed that these estimators could be modified to analyze mark-recapture data in rivers. However, the movement and apparent survival estimates, obtained using these estimators for age-0 trout in the Henrys Fork, were not precise. Estimates of abundance for the five river sections suggested there were in excess of 150,000 age-0 rainbow trout at certain times of the year. Capture and recapture rates tend to be very small when populations are large. I recaptured only 245 of 11,881 age-0 trout marked in previous seasons. Quantitative analysis of such mark-recapture data will necessarily result in large confidence intervals (Cormack 1992).

The sum of apparent survival and movement probabilities for a particular river section was the estimated apparent survival for trout originating in that river section and remaining within the 25-km management area (i.e., the five river sections). This estimate subtracted from 1.0 was an estimate of loss that could be attributed to mortality or movement downstream of Pinehaven-Riverside (Table 5.4). Age-0 trout can move to a section of river that extends downstream of Pinehaven-Riverside for 25 km to a 35-m waterfall barrier. The movement of trout downstream of Pinehaven-Riverside is considered mortality from a management perspective of the 25-km reach downstream of Island Park Dam.

The large abundances and small capture probabilities probably limit the utility of maximum likelihood estimators for quantifying movement of early life stages of fish.

We only have information on fish captured two or more times when using mark-recapture to make inference on movement. I only recaptured about 2% of marked trout in another season or river section from which the trout was marked. Inference is improved when a greater proportion of fish in a population is captured. This method of analysis may be more appropriate for adult salmonids rather than juvenile salmonids.

Habitat Use

The highest densities 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. Maki-Petays et al. (1997) observed similar habitat use for brown trout in a third-order river in northern Finland. Age-0 brown trout used areas in the river with large amounts of aquatic vegetation in summer and autumn.

Winter habitat was limiting in the Henrys Fork. Habitat is the most important factor regulating river salmonid populations in winter (Cunjak 1996). I primarily found age-0 trout in spring using complex bank habitat in Box Canyon and to a lesser extent Pinehaven-Riverside. Movement was detected between autumn and spring from river sections with simple bank habitat (i.e., Last Chance, Harriman State Park, and Harriman East) to river sections with complex bank habitat (i.e., Box Canyon and Pinehaven-Riverside). The greatest winter survival was in Box Canyon.

There was little difference in the density of age-0 rainbow trout along the east bank in Box Canyon between spring 1997 and spring 1998. However, the density along the west bank was more than two times greater in spring 1997 than in spring 1998. This

difference may have been related to differences in water temperature during winter. The water on the west side of the river originated from the hypolimnion of Island Park Reservoir and the water temperature was relatively stable through winter (2-4 °C) (Figure 5.2). The water on the east side of the river originated from the spring-fed Buffalo River and the water temperature was relatively variable (1-6 °C). Smith and Griffith (1994) and Meyer and Griffith (1997) observed greater survival of age-0 rainbow trout in cages in the Henrys Fork in warmer versus colder winter temperatures. Although the maximum winter water temperature was higher along the east bank versus the west bank, the minimum winter water temperature was lower. The colder minimum water temperature along the east bank may have resulted in greater winter mortality. Swimming ability and critical holding velocity are lower at colder water temperatures, thereby increasing age-0 trout susceptibility to predation by endothermic predators (Cunjak 1996). The greater variability and higher maximum water temperature along the east bank also may have been more demanding on age-0 trout physiology. Sudden increases in winter water temperature result in increased metabolic demand and therefore increased consumption (Cunjak 1996).

Winter sampling in Last Chance showed the failure of macrophytes in the center channel to provide winter habitat for age-0 rainbow trout. The loss of age-0 trout from Last Chance was from the center channel and the available bank habitat was consistently used through each winter. These results were consistent with Griffith and Smith (1995) who also found that age-0 rainbow trout did not use macrophyte cover in Last Chance throughout their first winter.

Conclusions

The abundance of juvenile rainbow trout in streams and rivers can be limited by a lack of suitable spawning habitat, summer growth habitat, or overwinter habitat (Waters 1995). Although the amount of spawning activity observed in the Henrys Fork was limited, especially in 1997, 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 growth habitat was not a limiting factor. However, interstitial spaces necessary for overwinter habitat are largely confined to Box Canyon, especially along the banks. Consequently, most overwinter survival has been in Box Canyon and most trout observed in other sections in autumn have not been found in those sections in the following spring.

Summary

I identified spawning areas and quantified spawning activity therein and I used electrofishing and mark-recapture and removal methodologies to quantify seasonal abundance, apparent survival, movement, and habitat use of age-0 rainbow trout in a 25-km management reach of the Henrys Fork. Spawning was not a limiting factor for rainbow trout recruitment. Natural production of rainbow trout occurred in each year of this study and yearly production ranged from 150,000 to 250,000. There was no evidence that recruitment in the river was dependent on trout stocking in Island Park Reservoir. Mark-recapture data were insufficient to obtain apparent survival estimates using program MARK; rather, I estimated apparent survival by comparing seasonal

changes in abundance or catch per unit effort. I did not observe a significant loss of age-0 trout between summer and autumn; the greatest loss occurred during winter. The highest overwinter survival occurred in Box Canyon (18-23%), a river section characterized by complex bank habitat, high gradient, and large substrate. The loss of age-0 trout in winter in Last Chance was from center channel habitat. There was relatively consistent use of available bank habitat in Last Chance during winter and movement was detected from river sections with simple bank habitat to river sections with complex bank habitat. Maximum likelihood estimates of movement (or lack thereof) were 0.0092 for summer-to-autumn and autumn-to-spring movement, 1.0099 for summer-to-autumn apparent survival, and 0.0776 for autumn-to-spring apparent survival in Box Canyon. Log-likelihood contours were generally flat in the neighborhood of the maximum likelihood estimate, indicating that estimates lacked precision. There was suitable habitat throughout the channel and in the five river sections to support the large abundances of age-0 trout through summer and autumn. However, most river sections did not support age-0 trout through their first winter, indicating that winter habitat was a limiting factor in rainbow trout recruitment in the Henrys Fork.

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Table 5.1.—Number and length range of age-0 and age-1 rainbow trout identified by reading scales for each river section from summer 1995 to autumn 1997.

Sampling Season	River Section	Number of age- 0 trout	Number of age-1 trout	Age- 0 length range (mm)	Age-1 length range (mm)
1995					
Summer	Box Canyon	76	1	44-120	160
	Last Chance	69	0	50-133	--
	Harriman State Park	40	0	68-155	--
	Harriman East	10	0	73-141	--
	Pinehaven-Riverside ^a	37	55	41-181	148-262
Autumn	Box Canyon ^a	129	8	49-195	169-217
	Last Chance ^a	119	3	52-199	188-220
	Harriman State Park	38	0	75-196	--
	Harriman East	19	6	160-183	191-199
	Pinehaven-Riverside	1	4	181	189-214
1996					
Spring	Box Canyon	138	0	56-198	--
	Pinehaven-Riverside	12	0	98-224	--
Summer	Box Canyon	76	25	60-139	155-221
	Last Chance	107	7	61-139	171-216
	Harriman State Park	38	0	52-103	--
	Harriman East	1	0	134	--
	Pinehaven-Riverside ^a	58	62	65-179	165-253

Table 5.1.—Continued.

Sampling Season	River Section	Number of age- 0 trout	Number of age-1 trout	Age- 0 length range (mm)	Age-1 length range (mm)
Autumn	Box Canyon ^a	111	5	62-183	180-216
	Last Chance	83	7	65-171	196-217
	Harriman State Park	25	0	70-169	--
	Harriman East ^a	66	3	112-197	195-227
	Pinehaven-Riverside	18	8	109-158	184-305
1997					
Spring	Box Canyon	122	5	59-173	213-274
	Pinehaven-Riverside ^a	56	16	122-239	213-242
Summer	Box Canyon ^a	51	64	90-170	160-253
	Last Chance ^a	59	73	90-159	151-248
	Harriman State Park	19	1	60-102	193
	Pinehaven-Riverside ^a	7	105	76-154	150-254
Autumn	Box Canyon ^a	123	22	74-199	174-258
	Last Chance ^a	85	5	93-193	170-217
	Harriman State Park	118	0	72-181	--
	Harriman East ^a	106	24	86-210	186-276
	Pinehaven-Riverside ^a	53	21	91-180	173-311

^a Logistic regression used to estimate length for classifying rainbow trout as age 0 or age 1.

Table 5.2.—Number of age-0 and age-1 rainbow trout identified by reading scales and estimated total length (mm) separating these age classes (i.e., classification length). Classification length was estimated using logistic regression (β_0 = intercept; β_1 = slope). $P(\text{age } 0 \mid \text{age } 0)$ = probability of classifying a trout as age 0 given that the trout is age 0 ($P(\text{age } 1 \mid \text{age } 1)$ = probability of classifying a trout as age 1 given that the trout is age 1) using the logistic regression equation and classification length.

		Number of	Number of	Parameter					Classification	
River section		age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
1995										
Summer	Pinehaven- Riverside	37	55	β_0	-11.2102	(3.4247)	0.0011	0.76	0.96	158 mm
				β_1	0.0700	(0.0198)	0.0004			
Autumn	Box Canyon	129	8	β_0	-22.7532	(7.1184)	0.0014	0.98	0.88	182 mm
				β_1	0.1242	(0.0400)	0.0019			
	Last Chance	119	3	β_0	-34.7767	(17.2950)	0.0443	1	0.67	200 mm
				β_1	0.0443	(0.0906)	0.0551			

Table 5.2.—Continued.

		Number of	Number of	Parameter						Classification
River section		age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
1996										
Summer	Pinchaven-	58	62	β_0	-49.8659	(16.2538)	0.0022	0.93	0.95	171 mm
	Riverside			β_1	0.2907	(0.0951)	0.0022			
Autumn	Box Canyon	111	5	β_0	-72.8275	(52.1161)	0.1623	0.99	0.80	183 mm
				β_1	0.3983	(0.2878)	0.1664			
	Harriman	66	3	β_0	-63.8827	(67.3279)	0.3427	1	0.67	198 mm
	East			β_1	0.3229	(0.3451)	0.3494			

Table 5.2.—Continued.

		Number of	Number of	Parameter					Classification	
	River section	age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
1997										
Spring	Pinehaven- Riverside	56	16	β_0	-39.1991	(12.1794)	0.0013	0.95	0.81	220 mm
				β_1	0.1778	(0.0554)	0.0013			
Summer	Box Canyon	51	64	β_0	-50.3360	(16.6355)	0.0025	0.94	0.95	165 mm
				β_1	0.3049	(0.1006)	0.0024			
	Last Chance	59	73	β_0	-54.1926	(18.2134)	0.0029	0.93	0.97	156 mm
				β_1	0.3480	(0.1157)	0.0026			
	Pinehaven- Riverside	7	105	β_0	-35.9417	(33.9126)	0.2892	0.86	1	145 mm
				β_1	0.2465	(0.2195)	0.2614			

Table 5.2.—Continued.

		Number of	Number of	Parameter					Classification	
	River section	age-0 trout	age-1 trout		estimate	(SE)	<i>P</i>	<i>P</i> (age 0 age 0)	<i>P</i> (age 1 age 1)	length
Autumn	Box Canyon	123	22	β_0	-26.4600	(7.0017)	0.0002	0.97	0.82	183 mm
				β_1	0.1435	(0.0384)	0.0002			
	Last Chance	85	5	β_0	-23.6526	(8.8096)	0.0073	0.99	0.60	180 mm
				β_1	0.1304	(0.0518)	0.0118			
	Harriman	106	24	β_0	-30.1318	(9.5412)	0.0016	0.97	0.96	196 mm
				β_1	0.1528	(0.0481)	0.0015			
	East									
Pinehaven-	53	21	β_0	-46.4266	(29.0789)	0.1104	0.98	1	173 mm	
			β_1	0.2673	(0.1663)	0.1080				
Riverside										

Table 5.3.—Movement, or lack thereof, of juvenile rainbow trout between seasons (i.e., summer, autumn, and spring) and between sections within a season (separated by a comma). Age-0 trout were marked in nine seasons from spring 1995 to autumn 1997 and were recaptured at age 0 or age 1 in ten seasons from spring 1995 to spring 1998. Recaps is the number of recaptured trout, the first number is the section in which the trout were marked, and the second number is the section in which the trout were recaptured. Sections are as follows: 1. Box Canyon, 2. Last Chance, 3. Harriman State Park, 4. Harriman East, and 5. Pinehaven-Riverside. A vertical dashed line indicates the overwinter period.

Recaps	Summer	Autumn	Spring	Summer	Autumn	Spring
	Box Canyon (1)					
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

Table 5.3.-Continued.

Recaps	Summer	Autumn	Spring	Summer	Autumn	Spring
Last Chance (2)						
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 (3)						
10	3	3				
1	3	2				
2		3	5			
Harriman East (4)						
1		4	5			

Table 5.3.-Continued.

Recaps	Summer	Autumn	Spring	Summer	Autumn	Spring
	Pinehaven-Riverside (5)					
5	5	5				
1		5	5			
1		5		5		
9			5	5		
1			5		5	
1			5			5

Table 5.4.—Number of marked age-0 rainbow trout released, estimated movement probabilities, and estimated capture probability times measured effort, by river section for summer (1995-1997 pooled), autumn (1995-1997 pooled), and spring (1996-1998 pooled). River sections are BC = Box Canyon, LC = Last Chance, HS = Harriman State Park, HE = Harriman East, PR = Pinehaven-Riverside, OT = other (i.e., movement out of the five river sections or mortality; negative numbers indicate recruitment). A 0 indicates that no trout were recaptured and no movement probability estimate was made. Subscripts with the same number indicate a single parameter estimate.

		BC	LC	HS	HE	PR	
Autumn $\hat{q}E$		0.060	0.033	0.045	0.142	0.050	
Summer							
Number of marks released	Marking sections	Probability of movement to recapture sections (autumn)					
		BC	LC	HS	HE	PR	OT
1,228	BC	1.0099 ₍₁₎	0	0	0.0092 ₍₃₎	0	-0.0191
1,686	LC	0.0092 ₍₃₎	1.0099 ₍₁₎	0	0	0.0092 ₍₃₎	-0.0283
204	HS	0	0.0092 ₍₃₎	1.0099 ₍₁₎	0	0	-0.0191
58	HE	0	0	0	0	0	0
123	PR	0	0	0	0	1.0099 ₍₁₎	-0.0099

Table 5.4.—Continued.

		BC	LC	HS	HE	PR	
Spring $\hat{q}E$		0.181	0.006	0.045	0.045	0.143	
Autumn							
Number of marks released	Marking sections	Probability of movement to recapture sections (Spring)					
		BC	LC	HS	HE	PR	OT
2,106	BC	0.0776 ₍₂₎	0	0	0	0.0092 ₍₃₎	0.9132
1,720	LC	0.0092 ₍₃₎	0	0	0	0.0092 ₍₃₎	0.9816
749	HS	0	0	0	0	0.0092 ₍₃₎	0.9908
917	HE	0	0	0	0	0.0092 ₍₃₎	0.9908
191	PR	0	0	0	0	0.0092 ₍₃₎	0.9908

Table 5.5.—Observed (top) and predicted (3-parameter model, bottom) recaptures by river section for autumn (1995-1997 pooled) and spring (1996-1998 pooled). River sections are BC = Box Canyon, LC = Last Chance, HS = Harriman State Park, HE = Harriman East, and PR = Pinehaven-Riverside. A 0 indicates that no trout were recaptured and no prediction was made.

Marking sections (summer)	Recapture sections (Autumn)				
	BC	LC	HS	HE	PR
BC	54	0	0	2	0
	74.4094			1.6043	
LC	2	77	0	0	1
	0.9307	56.1888			0.7756
HS	0	1	10	0	0
		0.0619	9.2709		
HE	0	0	0	0	0
PR	0	0	0	0	5
					6.2109

Table 5.5.—Continued.

Marking sections (autumn)	Recapture sections (spring)				
	BC	LC	HS	HE	PR
BC	47	0	0	0	2
	46.9988				2.7707
LC	2	0	0	0	2
	2.8900				2.2832
HS	0	0	0	0	2
					0.9854
HE	0	0	0	0	1
					1.2064
PR	0	0	0	0	1
					0.4147

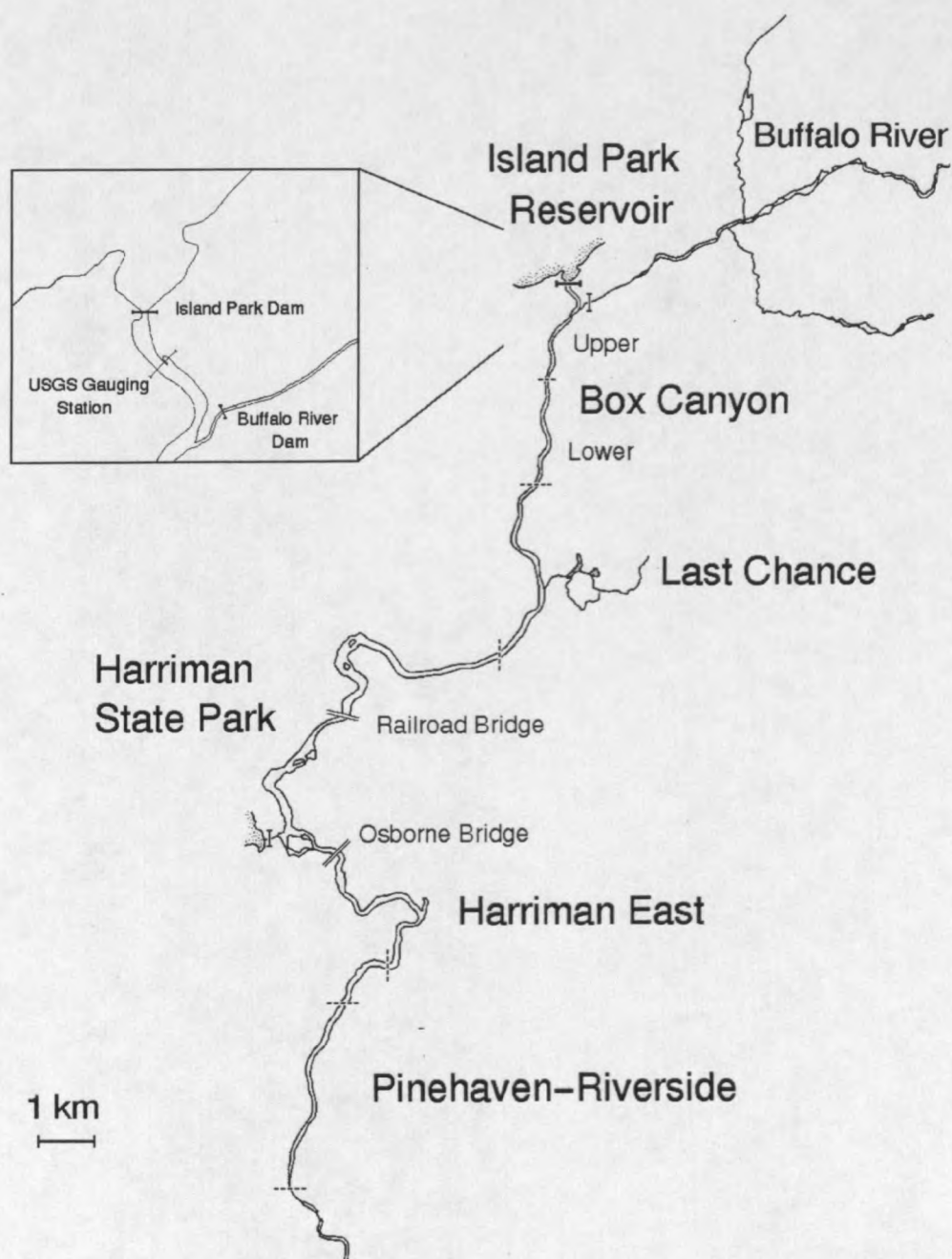


Figure 5.1.—River sections of the Henrys Fork downstream of Island Park Reservoir: Box Canyon, Last Chance, Harriman State Park, Harriman East, and Pinehaven-Riverside.

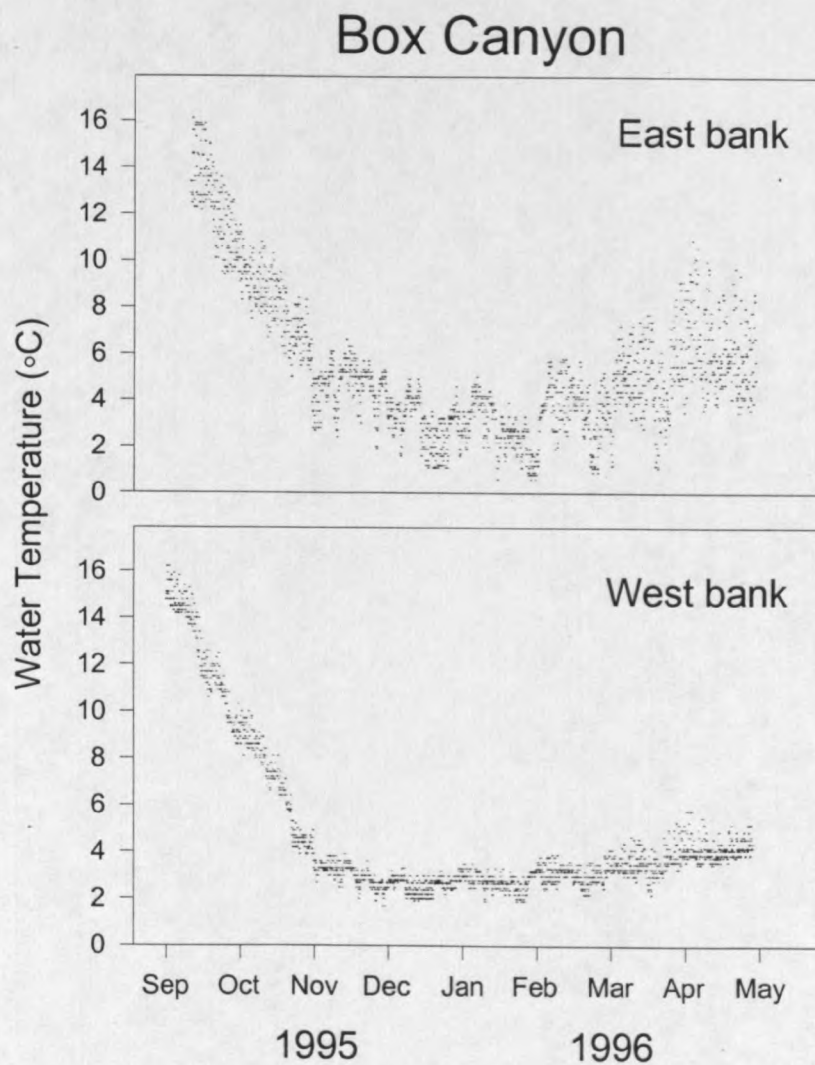


Figure 5.2.—Water temperature ($^{\circ}\text{C}$) along the east and west banks in Box Canyon from 11 September 1995 to 5 May 1996. Temperature was recorded every 3 hours. Tick marks indicate the 15th day of each month.

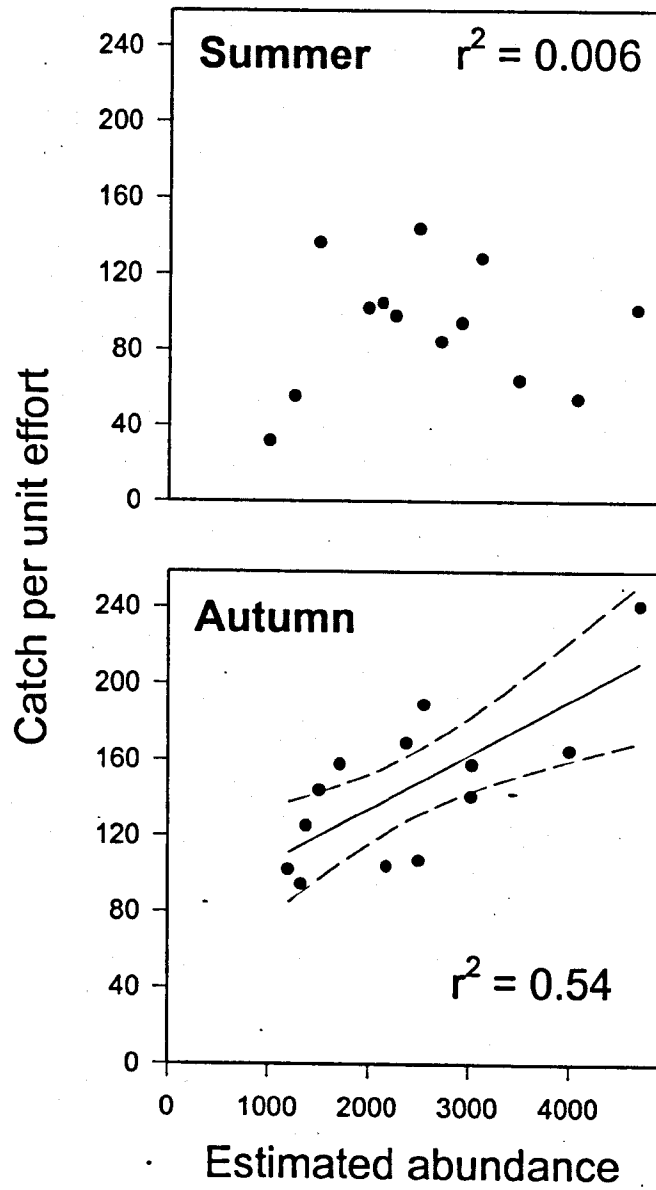


Figure 5.3.—Relation between catch per unit effort and estimated abundance for sample areas in Box Canyon, Last Chance, and Harriman State Park in summer ($N=13$) and autumn ($N=13$).

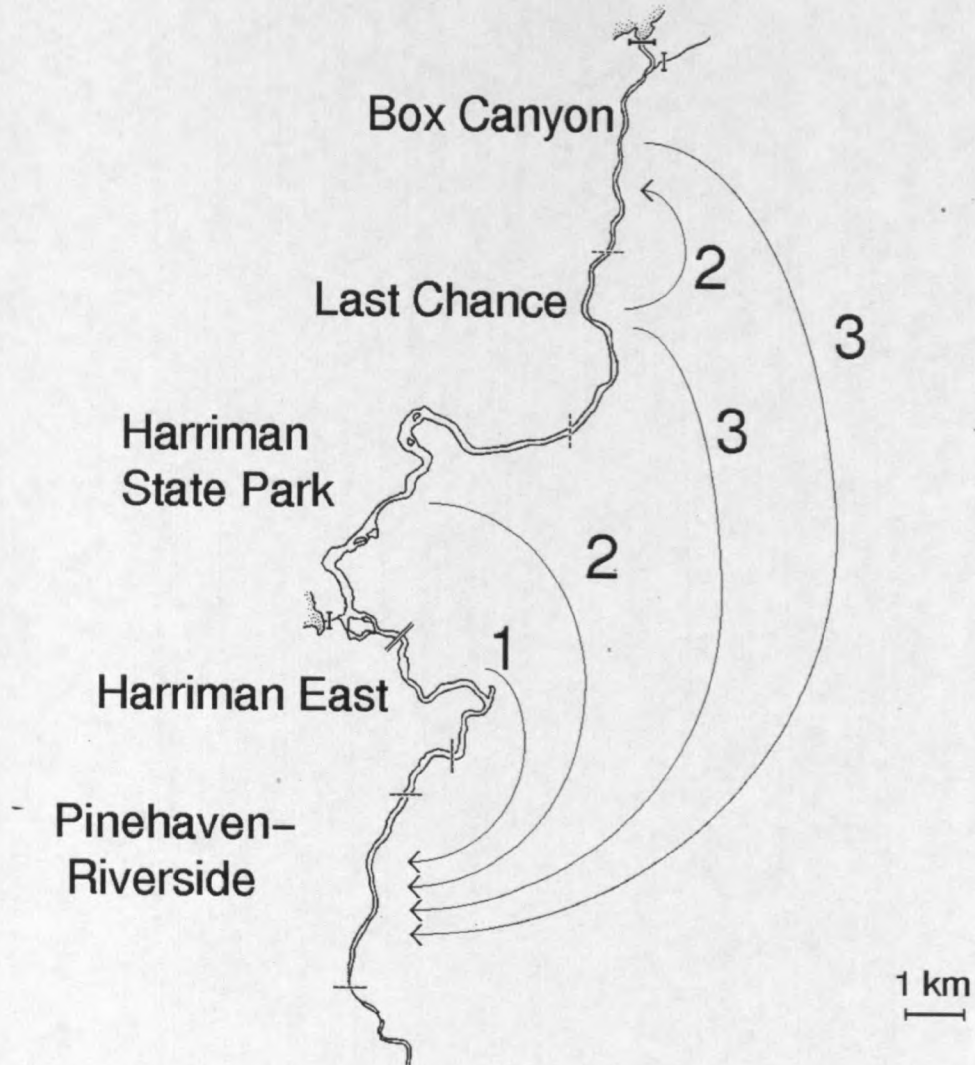


Figure 5.4.—Pre-winter-to-post-winter movement of age-0 rainbow trout.

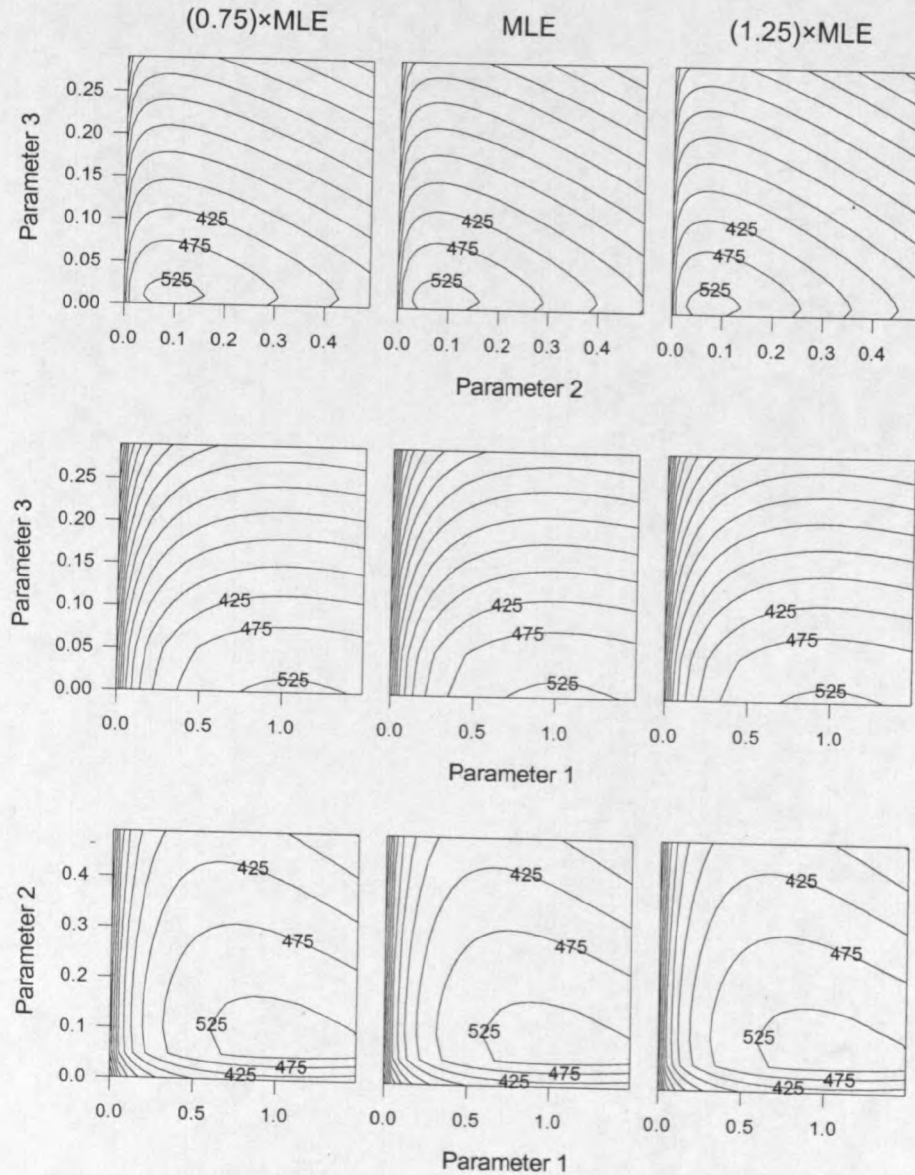


Figure 5.5.—Likelihood contours for two movement model parameters with the third parameter held constant. Parameter 1 = apparent survival from summer to autumn (i.e., no movement). Parameter 2 = apparent survival from autumn to spring. Parameter 3 = movement between river sections from summer to autumn and from autumn to spring. Parameters were held constant at the maximum likelihood estimate (MLE), at 75% of the MLE, and at 125% of the MLE. The three highest contours are labeled.

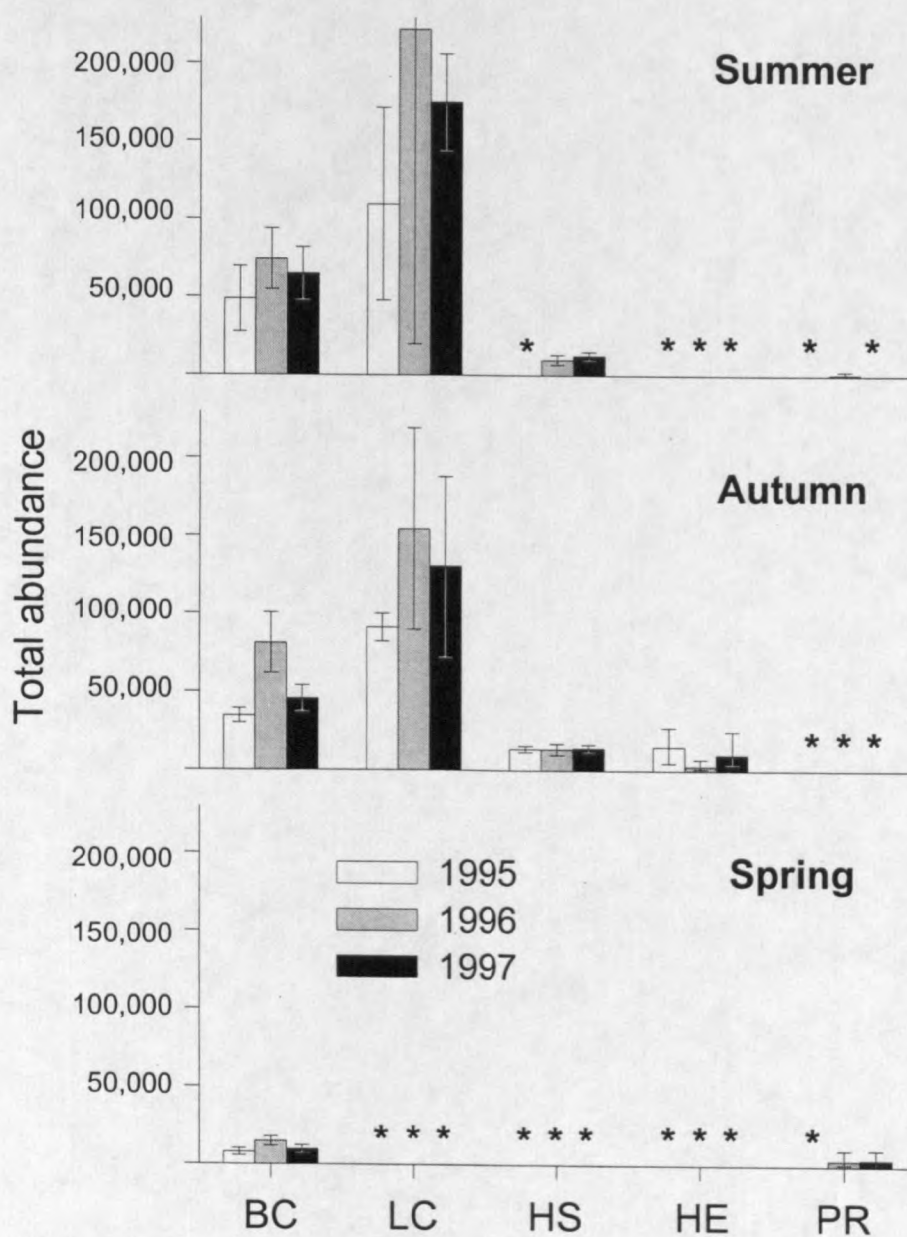


Figure 5.6.—Total abundance and 95% confidence intervals of age-0 rainbow trout in Box Canyon (BC), Last Chance (LC), Harriman State Park (HS), Harriman East (HE), and Pinehaven-Riverside (PR) in summer and autumn 1995-1997 and spring 1996-1998. * = no estimate available.

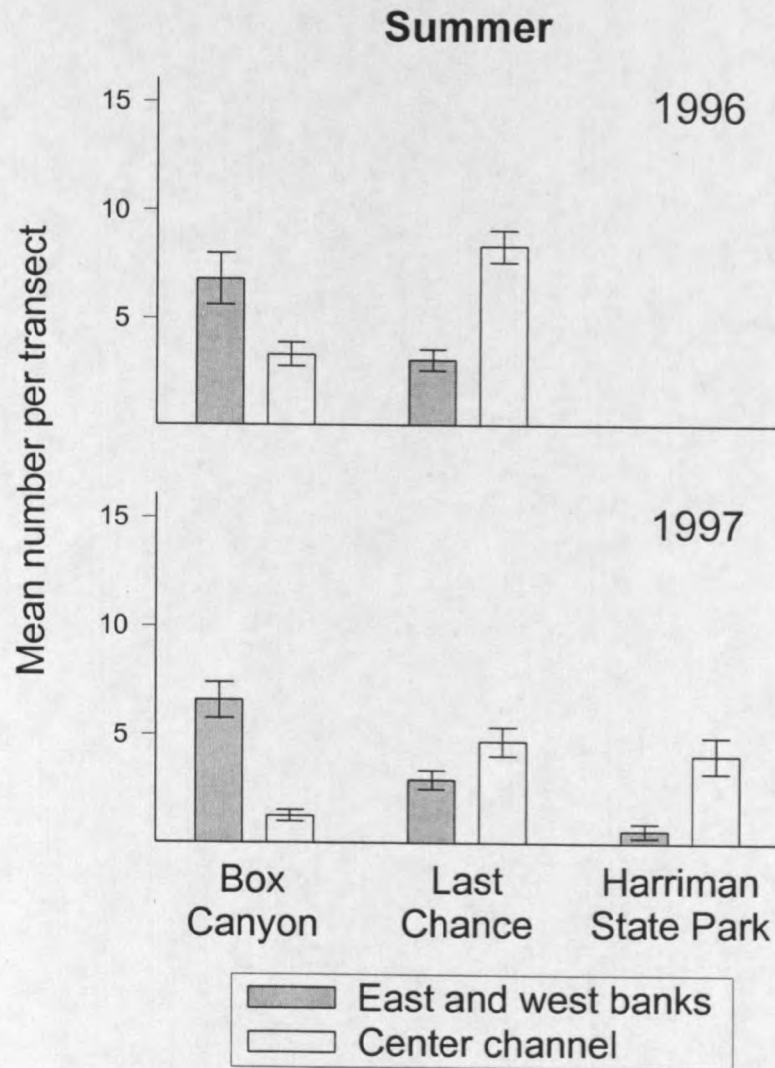


Figure 5.7.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals for bank areas and center channel habitat in Box Canyon, Last Chance, and Harriman State Park, summers 1996 and 1997. No habitat use data were available for Harriman State Park in summer 1996.

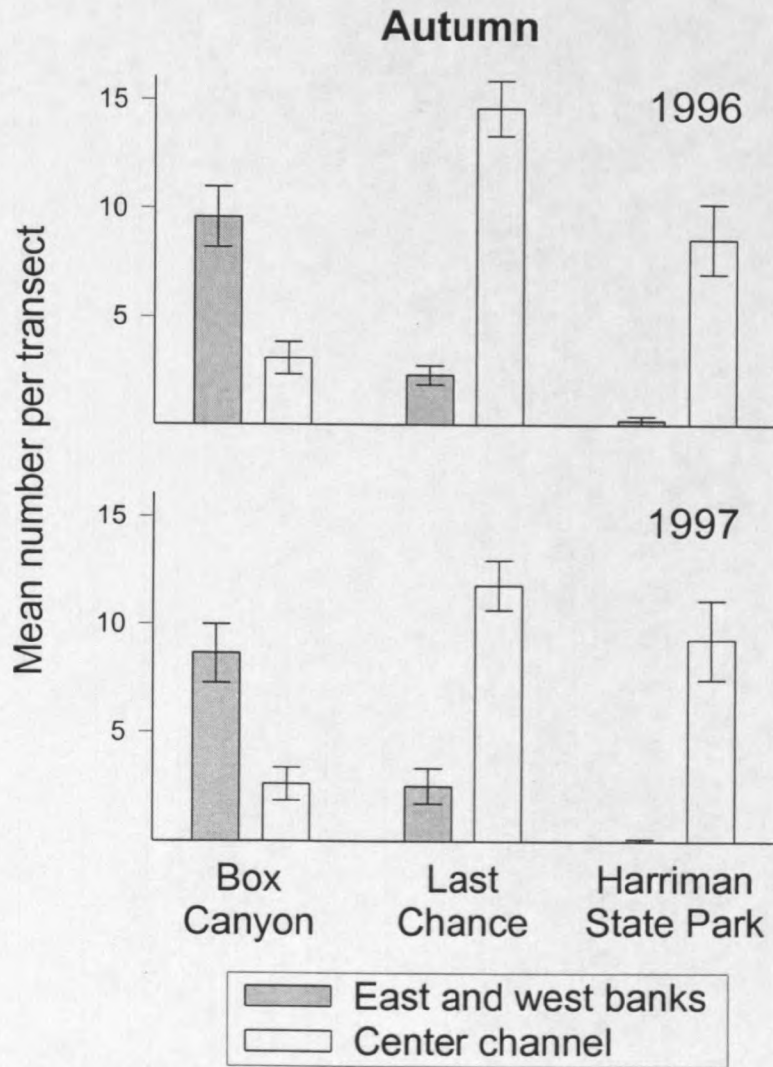


Figure 5.8.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals for bank areas and center channel habitat in Box Canyon, Last Chance, and Harriman State Park, autumns 1996 and 1997.

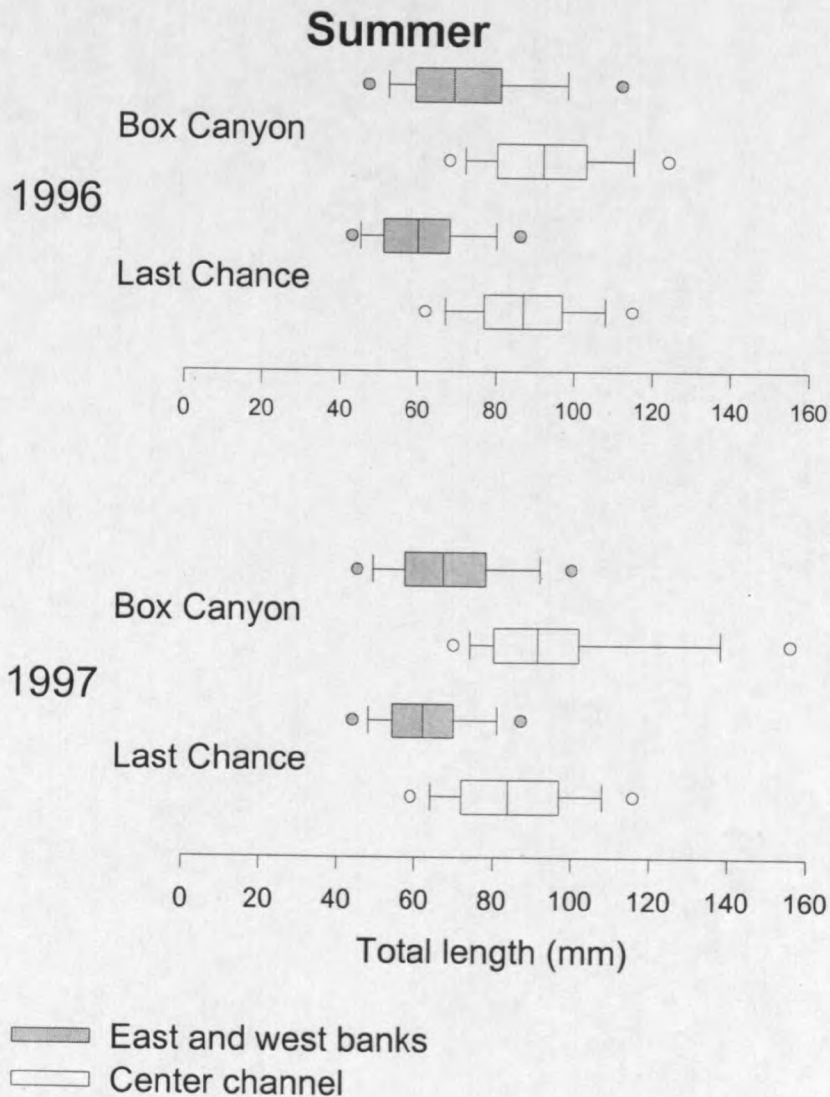


Figure 5.9.—Box plots showing the size distribution of age-0 rainbow trout in bank areas and center channel habitat in Box Canyon and Last Chance, summers 1996 and 1997. The ends of the box mark the 25th and 75th percentiles, the line inside the box marks the 50th percentile (i.e., median), the capped bars mark the 10th and 90th percentiles, and the circles mark the 5th and 95th percentiles.

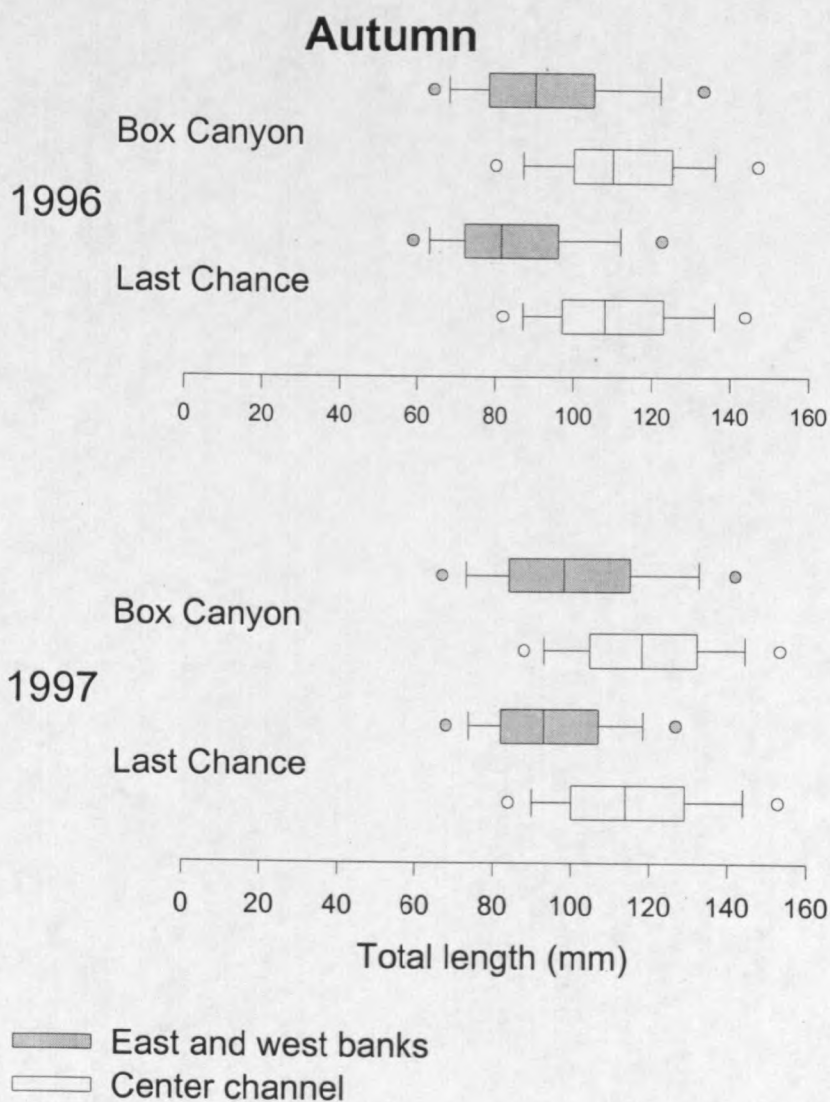


Figure 5.10.—Box plots showing the size distribution of age-0 rainbow trout in bank areas and center channel habitat in Box Canyon and Last Chance, autumns 1996 and 1997. The ends of the box mark the 25th and 75th percentiles, the line inside the box marks the 50th percentile (i.e., median), the capped bars mark the 10th and 90th percentiles, and the circles mark the 5th and 95th percentiles.

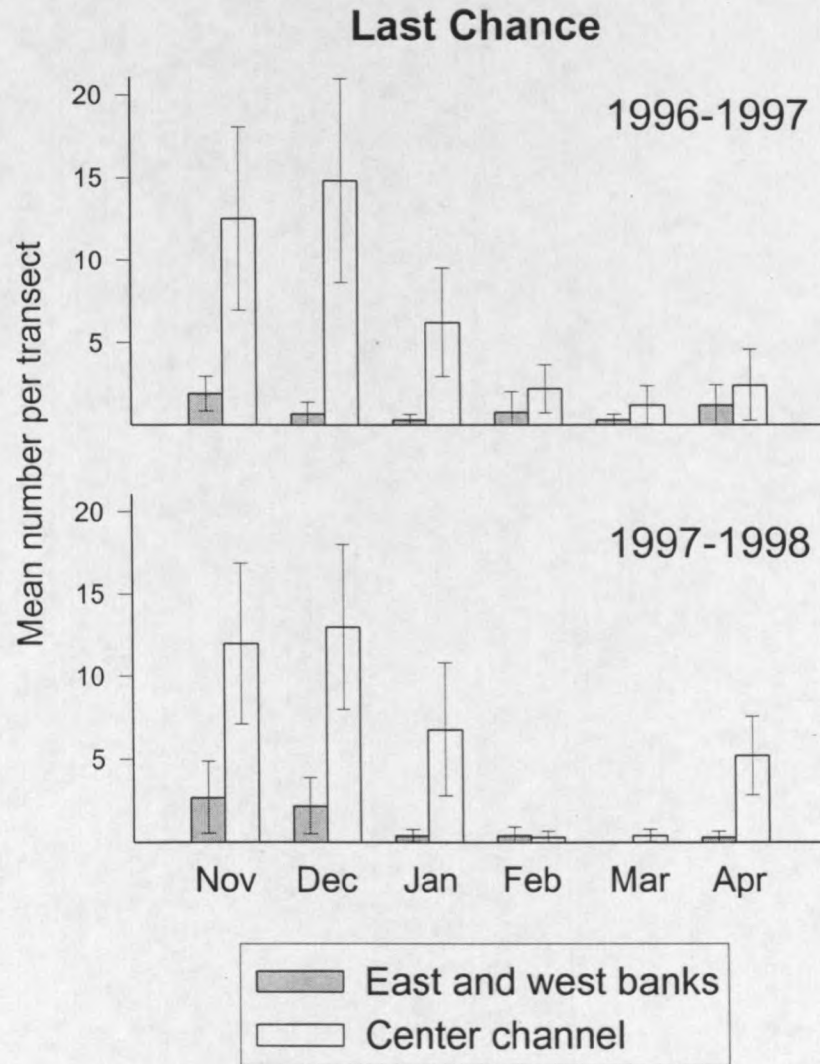


Figure 5.11.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals for bank areas and center channel habitat in Last Chance from November to April 1996-1997 and 1997-1998.

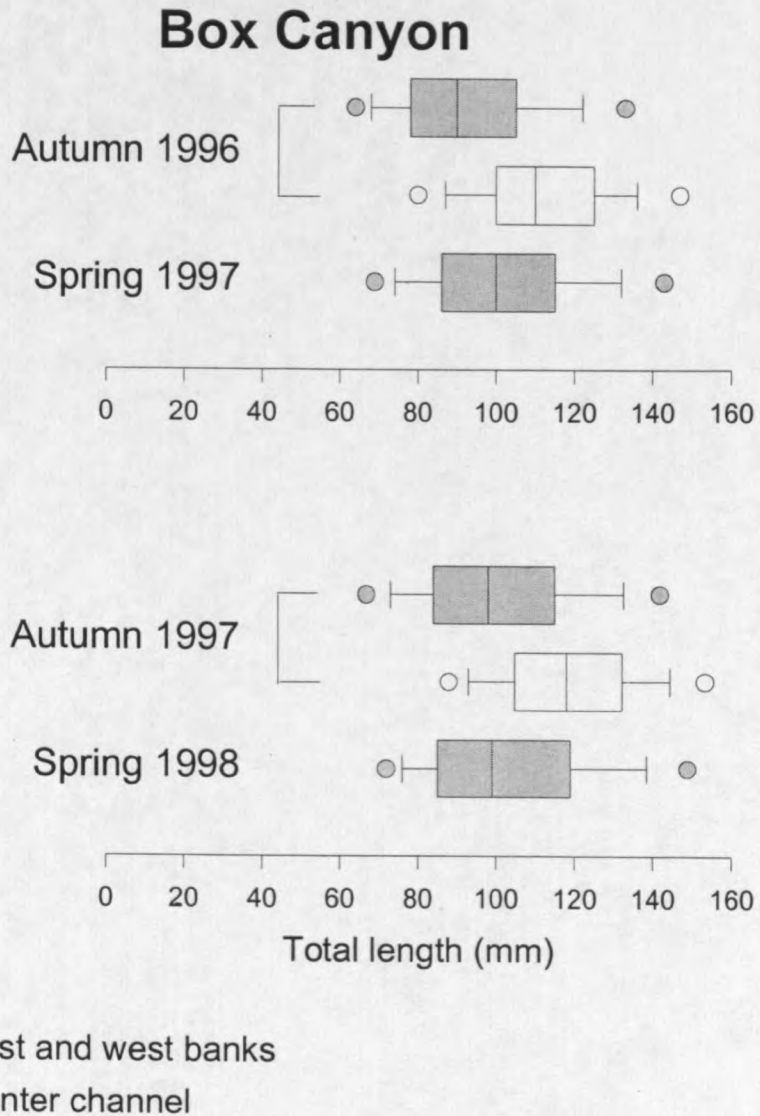


Figure 5.12. —Box plots showing the size distribution of age-0 rainbow trout in bank areas and center channel habitat in Box Canyon in autumn 1996 and 1997 and in bank areas in spring 1997 and 1998. The ends of the box mark the 25th and 75th percentiles, the line inside the box marks the 50th percentile (i.e., median), the capped bars mark the 10th and 90th percentiles, and the circles mark the 5th and 95th percentiles.

CHAPTER 6

WINTER DISCHARGE AND THE DYNAMICS OF AGE-0 RAINBOW TROUT IN THE HENRYS FORK OF THE SNAKE RIVER, IDAHO

Introduction

A 25-km reach of the Henrys Fork of the Snake River, Idaho has been managed as a wild rainbow trout fishery since 1978. The wild trout management area lies immediately downstream of Island Park Reservoir and discharge is regulated through Island Park Dam. Prior to 1978 the Idaho Department of Fish and Game stocked this reach of the Henrys Fork with fingerling and catchable rainbow trout. Trout abundances have generally declined since 1978, but with large, unexplained annual fluctuations. Trout abundances have ranged from a high of about 18,000 catchable rainbow trout in a 4-km river section to a low of about 3,000 (Mark Gamblin, Idaho Department of Fish and Game, personal communication). A considerable amount of interest exists among anglers, angler advocacy groups, and fisheries managers and biologists in understanding why recruitment in the Henrys Fork is so poor and what can be done about it, while retaining the river's status as a wild trout fishery.

I conducted extensive sampling for juvenile rainbow trout in the Henrys Fork from 1995 to 1998 to quantify production and the recruitment process, to identify factors limiting the rainbow trout population, and to propose management actions to improve natural recruitment. I found that spawning was not a limiting factor; yearly production ranged from about 150,000 to 250,000 age-0 rainbow trout at the end of the summer growth season. However, few age-0 trout survived their first winter in the Henrys Fork.

Average first-winter apparent survival ranged from less than 1% in river sections without suitable winter habitat to 21% in a river section with suitable winter habitat.

Winter is a dynamic period in northern latitude and high elevation rivers (Cunjak 1996; Cunjak et al. 1998). Riverine salmonids have to contend with extreme conditions that may change rapidly. Such conditions are defined by water temperature, discharge, and ice formation and break-up. Rapidly declining water temperature in early winter may lead to a metabolic deficit in acclimating salmonids, thereby lowering body condition and increasing the likelihood of early winter mortality (Cunjak 1988). Susceptibility of juvenile salmonids to predation by endothermic predators (e.g., mergansers *Mergus merganser* and river otters *Lutra canadensis*) increases at low temperatures because of impaired swimming ability and lower critical holding velocity (Cunjak 1996). Discharge in unregulated streams and rivers is usually lowest during late winter (Frenette et al. 1984), thereby limiting available habitat. Both surface and subsurface ice formation occlude river-margin habitat (Cunjak et al. 1998). Ice break-up can scour the substrate, possibly injuring concealed salmonids (Cunjak et al. 1998).

Much research has been done on winter habitat requirements of juvenile salmonids in streams and rivers (e.g., Heifetz et al. 1986; Heggenes et al. 1993; Maki-Petays et al. 1997). However, winter studies of juvenile rainbow trout in the Henrys Fork have been limited in scope such that inferences on river-wide recruitment could not be made. Winter survival of age-0 rainbow trout in the Henrys Fork was higher in cages with cobble-boulder substrate than in cages without cover; about 95% of the mortality occurred in early winter (Smith and Griffith 1994). Survival was also higher in cages located in warmer water (3.1-4.3 °C) versus colder water (1.5-4.3 °C) (Meyer and

Griffith 1997). Smaller age-0 rainbow trout (i.e., < 100 mm total length) in cages with no cover or with colder water temperatures experienced higher mortality than trout in cages with cover or warmer water temperatures (Smith and Griffith 1994; Meyer and Griffith 1997). Age-0 rainbow trout have also been observed using cobble-boulder concealment cover along banks in the Henrys Fork during winter (Contor 1989; Griffith and Smith 1995) and have been observed moving laterally from macrophyte cover in the center channel to cover along the banks (Griffith and Smith 1995). However, low discharge from Island Park Dam (i.e., $\leq 3.8 \text{ m}^3/\text{s}$) was observed leaving bank habitat dry and unavailable during winter 1992-1993, possibly limiting survival (Griffith and Smith 1995).

I conducted a river-wide study from 1995 to 1998 to obtain basic information on the winter ecology of age-0 rainbow trout in the Henrys Fork. Data were collected on the winter apparent survival, movement, and habitat use of age-0 trout. Discharge, a variable that defines winter habitat conditions and a variable of potential importance in a regulated river such as the Henrys Fork, was compared to the number of age-0 rainbow trout surviving winter to determine whether or not they were related.

Study Area

The Henrys Fork of the Snake River at Island Park Dam is at $44^{\circ}24'59''$ latitude and $111^{\circ}23'41''$ longitude and 1,897 m elevation and has a drainage area of $1,246 \text{ km}^2$. The mean annual discharge through Island Park Dam from October 1994 through April 1999 was $23 \text{ m}^3/\text{s}$ (range, $5.9\text{-}78.4 \text{ m}^3/\text{s}$). The Buffalo River joins the east side of the

Henrys Fork about 0.25 km downstream of Island Park Dam. The Buffalo River is a spring-fed river that has a relatively constant discharge of about $6 \text{ m}^3/\text{s}$.

The 25-km reach downstream of Island Park Reservoir was divided into five river sections based on habitat type. This study is primarily concerned with Box Canyon and Last Chance, the two river sections found to be the most important for age-0 rainbow trout production.

Box Canyon begins at the confluence of the Henrys Fork and the Buffalo River and is 4 km long with a mean width of 70 m (Figure 6.1). Box Canyon is a high gradient area (0.45%) with a cobble-boulder substrate. This river section has complex bank habitat consisting of rocks and woody debris; there are few macrophytes across the channel. Box Canyon was divided into two sections for the purpose of estimating abundance: upper Box Canyon (1.5 km) and lower Box Canyon (2.5 km). In upper Box Canyon there are areas of rapids, depths exceeding 1 m, and large uneven substrate. Lower Box Canyon is wider and the depth is usually less than 1 m. There is generally no ice formation in Box Canyon. Water from Island Park Reservoir is taken from the hypolimnion and the Buffalo River is spring-fed. Water temperatures recorded during the winter 1.5 km downstream from the confluence of the Henrys Fork and the Buffalo River were 2-4 °C along the west bank and 1-6 °C along the east bank.

Last Chance is downstream adjacent to Box Canyon and is 4 km long with a mean width of 95 m (Figure 6.1). Last Chance is a moderate gradient area (0.3%) with a cobble substrate. The channel depth is usually less than 1 m and there are extensive macrophyte beds across the channel throughout the river section. Bank habitat in Last Chance is simple, lacking the rocks and woody debris prevalent upstream in Box Canyon.

Macrophyte beds decrease through winter (but are not eliminated) because of senescence and grazing by trumpeter swans *Cygnus buccinator*. There was no ice formation in Last Chance during this study.

Methods

Apparent Survival

Winter apparent survival of age-0 rainbow trout was estimated by comparing autumn and spring estimates of abundance. Estimates of abundance in autumn were estimates of the number of age-0 rainbow trout entering winter. Estimates of abundance in spring were estimates of the number of age-0 rainbow trout that survived winter.

Both mark-recapture and removal techniques were used to estimate abundance. I used mark-recapture to estimate abundance in two sample areas in lower Box Canyon and two sample areas in Last Chance in autumns (i.e., October) 1995-1997. High discharge during spring precluded wading across the channel in sample areas. I sampled Last Chance in springs (i.e., May) 1996-1998 by drifting with electrofishing gear (continuous DC, 250 V). I used removal sampling to estimate the abundance of age-0 rainbow trout along the banks in upper Box Canyon in autumn and along the banks throughout Box Canyon in spring. The mean estimates for sample areas or for bank units in each river section were extrapolated to areas not sampled to obtain estimates of total abundance.

Mark-recapture sample areas were 100 m long and extended from bank to bank. Sample areas were selected using a stratified-random procedure and were separated by at

least 1 km to reduce the likelihood that trout marked in one area would move to another within a season. I used the same sample areas each autumn. I collected juvenile rainbow trout by wading with boat mounted electrofishing gear (continuous DC, 250 V) from one bank to the other along eight transects perpendicular to the flow. Each sample area was sampled either four or five days in a season, generally every other day. Trout were marked with partial fin clips and a different fin clip was used on each day. Sample areas were considered closed (i.e., no significant losses or additions during the sampling period) and the mark-recapture data were analyzed using the Chao M_t estimator in program CAPTURE (Chao 1989; Rexstad and Burnham 1991). Confidence intervals (95%) for estimates of total abundance included within-sample area, among-sample area, and extrapolation error. (See Chapter 3 for details on the sampling procedure and data analysis for sample areas.)

Bank units about 10-15 m long were either sampled by three-pass or single-pass removal by wading with a hand-held electrode (continuous DC, 250 V). Three-pass removal data were analyzed using the Zippin maximum likelihood removal estimator (Zippin 1956; Otis et al. 1978; Rexstad and Burnham 1991). Single-pass removal data were analyzed using a mean capture probability model calibrated for the Henrys Fork (see Chapter 4 for details). Confidence intervals (95%) for estimates of total abundance included within-bank unit, among-bank unit, and extrapolation error. I sampled 7 bank units in Box Canyon in autumn 1995, 10 in autumn 1996, and 10 in autumn 1997. I sampled 20 bank units in Box Canyon in spring 1996 and 50 in spring 1997 and 1998. The number of bank units sampled was divided equally between the east and west banks, except for autumn 1995 when I sampled four bank units along the east bank and three

along the west bank. Single-pass removal sampling was used for 3 bank units in autumn 1995, 4 in autumn 1996, and 13 in spring 1996. I also sampled twenty bank units (each about 15 m long) using three-pass removal in Last Chance in spring 1997.

Winter apparent survival in Last Chance was also estimated by comparing monthly catch-per-unit-effort data collected through the winter. Ten random bank-to-bank transects were sampled by electrofishing (continuous DC, 250 V) once a month from November through April in winters 1994-1995, 1996-1997, and 1997-1998. This sampling was used to identify when during winter the loss of age-0 trout occurred.

Movement

Age-0 rainbow trout were marked with visible implants of fluorescent elastomer to detect movement (or lack thereof) between river sections during winter. The color of the mark identified the river section in which the trout was first captured (blue = Box Canyon and red = Last Chance). Age-0 trout were marked prior to winter in both summer (i.e., August) and autumn and were recaptured after winter.

Habitat Use

I quantified habitat use of age-0 rainbow trout in Box Canyon and Last Chance in autumn and in Last Chance through winter by noting the location of trout captured along bank-to-bank transects in sample areas. Any trout captured within of 2 m of either bank or any structure associated with a bank (e.g., a fallen tree) was considered using bank

habitat. All other trout were considered using center channel habitat (e.g., macrophytes). I also quantified monthly habitat use in Last Chance during winter using the catch-per-unit-effort data collected by sampling random transects.

Discharge

Discharge data for the Henrys Fork were obtained for each winter from the United States Geological Survey gauging station near Island Park Dam (Station 13042500). I used simple linear regression analysis to investigate the relation between discharge and spring estimates of abundance.

Results

Apparent Survival, Movement, and Habitat Use

There were consistently greater abundances of age-0 rainbow trout in Last Chance versus Box Canyon in autumn (Figure 6.2). The estimated total abundance of age-0 trout in Box Canyon was 34,353 in autumn 1995 (95% confidence interval (CI), [29,781—38,924]), 81,165 in autumn 1996 (95% CI, [61,858—100,471]), and 45,723 in autumn 1997 (95% CI, [37,335—54,110]). The estimated total abundance of age-0 trout in Last Chance was 91,320 in autumn 1995 (95% CI, [82,520—100,120]), 154,580 in autumn 1996 (95% CI, [90,020—219,140]), and 130,800 in autumn 1997 (95% CI, [72,180—188,220]). The differences between Box Canyon and Last Chance were significant at the $\alpha=0.05$ level in 1995 and 1997 as judged by confidence intervals. There were also

significantly more age-0 trout in Box Canyon in 1996 versus 1995 and 1997; there was no detectable difference among years in Last Chance ($\alpha=0.05$).

There were great overwinter losses of age-0 rainbow trout in both Box Canyon (Figure 6.3) and Last Chance (Figure 6.4). I used the term loss to include both mortality and emigration. The estimated total abundance of age-0 trout that survived winter in Box Canyon were 7,903 in spring 1996 (95% CI, [5,608—10,197]), 14,788 in spring 1997 (95% CI, [11,835—17,740]), and 9,730 in spring 1998 (95% CI, 7,372—12,082]). The percentage of age-0 trout that survived each winter in Box Canyon was about 23% in 1996, 18% in 1997 and 21% in 1998. Spring abundance estimates for Last Chance were not obtained because of sampling difficulties during high discharge. Few trout were captured in the center channel and no trout were recaptured. Three age-0 trout were captured in 20 bank units. However, winter catch-per-unit-effort sampling indicated a consistent pattern of loss in each winter (Figure 6.4). The loss rate of age-0 trout from Last Chance was about 89% in 1997 and 97% in 1998 (no estimate was obtained for 1996).

Although the pattern of loss for age-0 rainbow trout from Last Chance was consistent from year to year, there was a difference in the timing of the loss (Figure 6.4). The loss was initiated between November and December in winter 1994-1995, a minimum was reached in February and March, and an increase occurred in April. The loss was initiated one month later, between December and January, in winters 1996-1997 and 1997-1998. A minimum was again reached in February and March and an increase occurred in April. The differences in loss patterns were related to winter discharge (Figure 6.5). Discharge was relatively low during winter 1994-1995 (mean, 7.2 m³/s;

Table 6.1). Discharge was high, however, in winters 1996-1997 and 1997-1998 (mean, 16.4-19.9 m³/s; Table 6.1). The loss of age-0 rainbow trout from Last Chance occurred earlier during the low discharge winter and later during the high discharge winters.

Age-0 rainbow trout were primarily using bank habitat in Box Canyon and center channel habitat in Last Chance prior to winter (Figure 6.6A,B). There were more age-0 trout using bank habitat in Box Canyon versus Last Chance and there were more age-0 trout using center channel habitat in Last Chance versus Box Canyon. All differences were significant at the $\alpha=0.05$ level as judged by confidence intervals. Habitat use within a river section was similar from year to year.

The loss of age-0 rainbow trout from Last Chance occurred from the center channel in each winter (Figure 6.7A-C). There was relatively consistent use of available bank habitat through each winter.

Some of the winter loss of age-0 rainbow trout from Box Canyon and Last Chance was attributed to movement. I recaptured 53 age-0 trout after winter of 6,740 age-0 trout marked before winter. Two age-0 trout marked in Box Canyon and two marked in Last Chance were recapture downstream in Pinehaven-Riverside, a river section 14 km from Last Chance that has habitat characteristics similar to Box Canyon. Two age-0 trout marked in Last Chance were recaptured upstream in Box Canyon. No trout marked in Last Chance prior to winter were ever recaptured in Last Chance after winter. However, 47 age-0 trout marked in Box Canyon prior to winter were recaptured there after winter.

Survival and Discharge

I observed a large fluctuation in the number of age-0 rainbow trout that survived each winter in Box Canyon (Figure 6.8B) and large variation in winter discharge within and among years (Figure 6.8A). The mean abundance estimate in spring 1997 was about 87% greater than in spring 1996 and about 52% greater than in spring 1998. The difference between spring 1996 and 1997 was significant at the $\alpha=0.05$ level as judged by confidence intervals. The differences in the number of age-0 trout surviving winter in Box Canyon were related to discharge in the latter half of winter ($r^2 = 0.9997$; Figures 6.8 and 6.9). Discharge was relatively constant through winter 1995-1996 (mean, $16.4 \text{ m}^3/\text{s}$; Table 6.1). Discharge in winter 1996-1997 was about $15.1 \text{ m}^3/\text{s}$ during the first half of winter and about $22.8 \text{ m}^3/\text{s}$ during the latter half of winter. Discharge in winter 1997-1998 was just the opposite: about $21.1 \text{ m}^3/\text{s}$ during the first half and about $18.7 \text{ m}^3/\text{s}$ during the latter half. Discharge during the first half of winter was not related to the number of age-0 rainbow trout surviving in Box Canyon ($r^2 = 0.11$).

Recall that age-0 trout were not lost from Last Chance during the first half of winter (Figure 6.4), but during the latter half of winter regardless of discharge (Figure 6.5). Higher discharge during the latter half of winter flooded more bank habitat at a time when age-0 trout were leaving center channel habitat in search of bank habitat. Therefore, higher discharge at a critical time for survival (i.e., the latter half of winter) likely increased the number age-0 trout surviving winter in Box Canyon, a river section with complex bank habitat.

The increased number of age-0 rainbow trout surviving in Box Canyon during winter 1996-1997 was evident in sampling of age-1 trout in summer 1997. The cumulative number of age-1 trout captured (standardized by transect) increased about four-fold compared to summer 1996 (Figure 6.10).

Experimental Validation of the Flow-Survival Relation

I conducted a river-wide experiment in winter 1998-1999 to validate the flow-survival relation identified in this study during 1995-1998. Discharge from Island Park Dam was maintained at about 20-21 m³/s from 22 January 1999 through the end of winter, a level greater than that of two of the previous three winters. I hypothesized that the spring abundance estimate for Box Canyon would be correspondingly greater than that of two of the previous three winters. The number of age-0 rainbow trout entering winter was estimated in Box Canyon in October 1998 by using mark-recapture in two sample areas and three-pass removal sampling in 10 bank units as described earlier. The overwinter loss of age-0 trout in Last Chance was monitored using the catch-per-unit-effort methodology once per month as described earlier. The number of age-0 trout that survived the winter in Box Canyon was estimated in May 1999 by three-pass removal sampling in 50 bank units as described earlier.

The estimated total abundance of age-0 trout in Box Canyon in autumn 1998 was 26,460 (95% CI, [18,654—34,266]). This estimate was significantly less than estimates for autumn 1996 and 1997 but not 1995 ($\alpha=0.05$; Figure 6.2). The spring estimate of total abundance indicated that about 11,109 age-0 trout survived the winter in Box

Canyon (95% CI, [8,986—13,233]; Figure 6.3). Therefore, about 42% of age-0 trout in Box Canyon in autumn survived through winter in Box Canyon.

The loss of age-0 rainbow trout from Last Chance primarily occurred between December and January, a minimum was reached in February and March, and an increase occurred in April (Figure 6.4). Discharge was relatively high throughout winter (mean, 20.1 m³/s; Table 6.1; Figure 6.5). The pattern of loss from Last Chance was consistent with other high discharge winters.

Age-0 rainbow trout again primarily used bank habitat in Box Canyon in autumn 1998, similar to previous years ($\alpha=0.05$; Figure 6.6C). Age-0 trout in Last Chance used center channel habitat at the start of winter in 1998 (Figure 6.7D). The loss of age-0 trout from Last Chance occurred from the center channel and there was relatively consistent use of available bank habitat throughout winter.

The mean discharge during the latter half of winter 1998-1999 was 2.3 m³/s less than during the latter half of winter 1996-1997 and 1.8 m³/s greater than during the latter half of winter 1997-1998 (Table 6.1). The number of age-0 rainbow trout surviving in Box Canyon in winter 1998-1999 was about 25% less than the number surviving winter 1996-1997 but about 14% greater than the number surviving winter 1997-1998.

Experimental results from winter 1998-199 supported the flow-survival relation identified from the three previous winters ($r^2 = 0.9783$; Figure 6.9).

Discussion

I identified and validated a flow-survival relation for age-0 rainbow trout in the Box Canyon river section of the Henrys Fork. The number of age-0 trout that survived

their first winter in Box Canyon was related to higher discharge during the latter half of winter; there was no relation between discharge during the first half of winter and the number of age-0 trout surviving winter in Box Canyon. The success of the 1996 age class, which experienced higher discharge during the latter half of winter 1996-1997, was detectable at age 1 by a greater catch per unit effort the following summer, relative to age-1 trout in other summers.

Winter survival of age-0 trout in the Henrys Fork was related to the interaction of complex bank habitat and discharge. As discharge increases, the water level in Box Canyon rises and floods rocks and woody debris along the banks, creating additional bank habitat. Complex bank habitat that provides interstitial space for shelter is critical to the winter survival of age-0 river salmonids (Bjornn 1971; Hillman et al. 1987; Heggenes et al. 1993; Griffith and Smith 1993; Cunjak 1996; Maki-Petays et al. 1997; Cunjak et al. 1998).

There was relatively consistent use of available bank habitat in Last Chance. However, higher discharge was not expected to increase the availability of bank habitat in Last Chance because of the simple bank habitat. The banks in Last Chance did not have the abundance of rocks and woody debris found upstream in Box Canyon. Higher discharge also would not raise the water level to the same degree as in Box Canyon because the river was on average about 25 m wider in Last Chance.

The loss rate of age-0 rainbow trout was greater in Last Chance than in Box Canyon. Prior to winter, most age-0 trout in Last Chance were located in macrophyte cover in the center channel. Macrophytes were used through the first half of winter, but failed to provide suitable habitat for age-0 trout through the latter half of winter, as

indicated by the loss of trout from the center channel. Macrophytes declined during winter because of senescence and grazing by trumpeter swans. However, some dense macrophyte beds did persist, and no trout were captured in them during late winter. Macrophytes were not as prevalent in Box Canyon as in Last Chance and few trout used center channel habitat in Box Canyon. Therefore, the loss rate from Box Canyon was expected to be less than from Last Chance.

Winter loss rates from Last Chance obtained by comparing catch per unit effort of age-0 rainbow trout at the beginning (November) and end (March) of winter may not be indicative of the actual number of age-0 trout that survived winter in that river section. Sampling ten random transects was sufficient to indicate the severity of the loss of age-0 trout from Last Chance during winter. However, estimates of a loss or apparent survival rate were highly sensitive to the number of age-0 trout captured in November and March. A small change in the number of age-0 trout captured could effect a relatively large change in an apparent survival rate estimate. This was likely a result of sampling only ten transects.

This study showed that apparent survival rates in and of themselves were not very informative about the number of age-0 rainbow trout surviving winter. The lowest apparent survival rate for Box Canyon occurred in winter 1996-1997 (0.18), but the largest number of age-0 trout surviving winter occurred during the same time period (14,788). The apparent survival rate was only informative in conjunction with the number of age-0 trout entering the winter period (81,165).

The large number of age-0 rainbow trout surviving winter 1996-1997 and the large number of age-0 trout entering that winter raises the question of the importance of

production. If more age-0 trout survived winter when more were produced, then perhaps discharge was not an important variable. However, production in 1998 was lower than in any other year of this study and the number of age-0 trout surviving winter 1998-1999 was the second largest. This suggests that habitat availability (i.e., higher discharge during the latter half of winter) and not production was the driving factor in first winter survival.

The loss of age-0 rainbow trout could not be attributed only to mortality. Movement of age-0 trout among habitat types was detected. Griffith and Smith (1995) observed marked age-0 trout moving from macrophytes in the center channel to the banks within Last Chance. I detected the movement of marked age-0 trout from river sections with simple bank habitat to river sections with complex bank habitat (both upstream and downstream).

An increase in the number of age-0 rainbow trout captured in ten random transects in Last Chance occurred in April each year (Figure 6.4). This increase occurred among trout using center channel habitat and suggested that age-0 trout were moving back into Last Chance at the end of winter, probably from Box Canyon. These trout were probably not concealed in the substrate earlier in the winter because the substrate in Last Chance is highly embedded. The movement of age-0 trout back to center channel habitat in April suggests that higher discharge is no longer critical at that time.

The movement of age-0 rainbow trout between habitat types is critical when considering the effect of higher discharge on habitat. The catch-per-unit-effort data from Last Chance indicated that the loss of age-0 rainbow trout, which likely included movement, occurred in mid-winter. It is at this time that increasing the level of discharge

will enhance overall survival. As center channel macrophyte habitat becomes unsuitable for winter survival and trout begin to move to bank habitat, increasing discharge will provide more bank habitat in Box Canyon and some trout from other river sections will move upstream to find it.

Other studies have also identified flow-survival relations for salmonids. A positive relation between the mean discharge in February and the survival of age-0 Atlantic salmon *Salmo salar* was observed in three New Brunswick rivers and one Newfoundland river (Gibson and Meyers 1988). A positive relation was also found between winter discharge and age-0 Atlantic salmon survival in Catamaran Brook, New Brunswick (Cunjak et al. 1998). Unlike the streams in these studies, the Henrys Fork is a regulated river. Discharge can be controlled and used as a management tool to improve natural recruitment of rainbow trout in the Henrys Fork.

I showed that only higher levels of discharge during the latter half of winter were related to the number of age-0 rainbow trout surviving to age 1. Any increase in discharge should coincide with the initiation of the loss of age-0 trout. The timing of the loss of age-0 trout was related to discharge in the first half of winter. When discharge was relatively low in winter 1994-1995 (mean, $7.2 \text{ m}^3/\text{s}$) the loss was initiated between November and December. When discharge was relatively high during the first half of the next four winters (means, $15.1\text{-}21.1 \text{ m}^3/\text{s}$) the loss was initiated one month later.

I recommend a high level of discharge (i.e., $> 20 \text{ m}^3/\text{s}$) during the latter half of winter to improve the recruitment of age-0 rainbow trout in the Henrys Fork. The water stored in Island Park Reservoir is currently managed for multiple uses including power production and irrigation. In past winters excess water has been released from the

reservoir in early winter in anticipation of a large snow pack. This study showed that if that water is released later in winter, more habitat along the banks in Box Canyon can be created at a critical time for age-0 trout survival. I also recommend continued monitoring of age-0 trout abundance in Box Canyon in spring to further validate the flow-survival relation, whether discharge is high or low.

Summary

Age-0 rainbow trout were sampled from 1995 to 1998 to obtain river-wide information on winter apparent survival, movement, and habitat use. Many age-0 rainbow trout were being produced in the Henrys Fork each year, but recruitment to the fishery was limited by poor survival during their first winter. I identified a flow-survival relation for age-0 trout in a river section with complex bank habitat. The number of age-0 trout that survived their first winter in Box Canyon was related to higher discharge during the latter half of winter. The higher discharge during the latter half of winter created more available habitat in the section with complex bank habitat and coincided with the loss of age-0 trout from non-bank areas. Movement of age-0 trout was detected from river sections with simple bank habitat to sections with complex bank habitat. I conducted a river-wide experiment in winter 1998-1999 whereby discharge during the latter half of winter was maintained at a relatively high level in an attempt to repeat the successful recruitment previously observed under a similar discharge scenario. The mean discharge in the latter half of winter 1998-1999 was less than during the same time period of winter 1996-1997, but greater than during two other years. Likewise, the number of age-0 trout surviving winter 1998-1999 in Box Canyon was less than the number

surviving winter 1996-1997, but greater than the number surviving the two other years. Therefore, the winter 1998-1999 discharge and survival data supported the flow-survival relation.

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Table 6.1.—Discharge (mean, standard deviation, and minimum and maximum) from Island Park Dam during winter.

Year	Mean (m ³ /s)	(SD)	Minimum	Maximum
1 November-31 March				
1994-1995	7.2	(0.5)	6.0	8.0
1995-1996	16.4	(1.2)	14.2	18.4
1996-1997	19.0	(4.6)	13.6	28.2
1997-1998	19.9	(2.7)	15.8	26.6
1998-1999	20.1	(1.7)	16.8	23.5
1 November-14 January				
1995-1996	15.6	(0.7)	14.7	17.1
1996-1997	15.1	(1.4)	13.6	17.8
1997-1998	21.1	(3.1)	18.4	26.6
1998-1999	19.6	(2.0)	16.8	23.5
15 January-31 March				
1995-1996	17.1	(1.2)	14.2	18.4
1996-1997	22.8	(3.3)	17.7	28.2
1997-1998	18.7	(1.4)	15.8	21.6
1998-1999	20.5	(1.1)	17.2	21.7

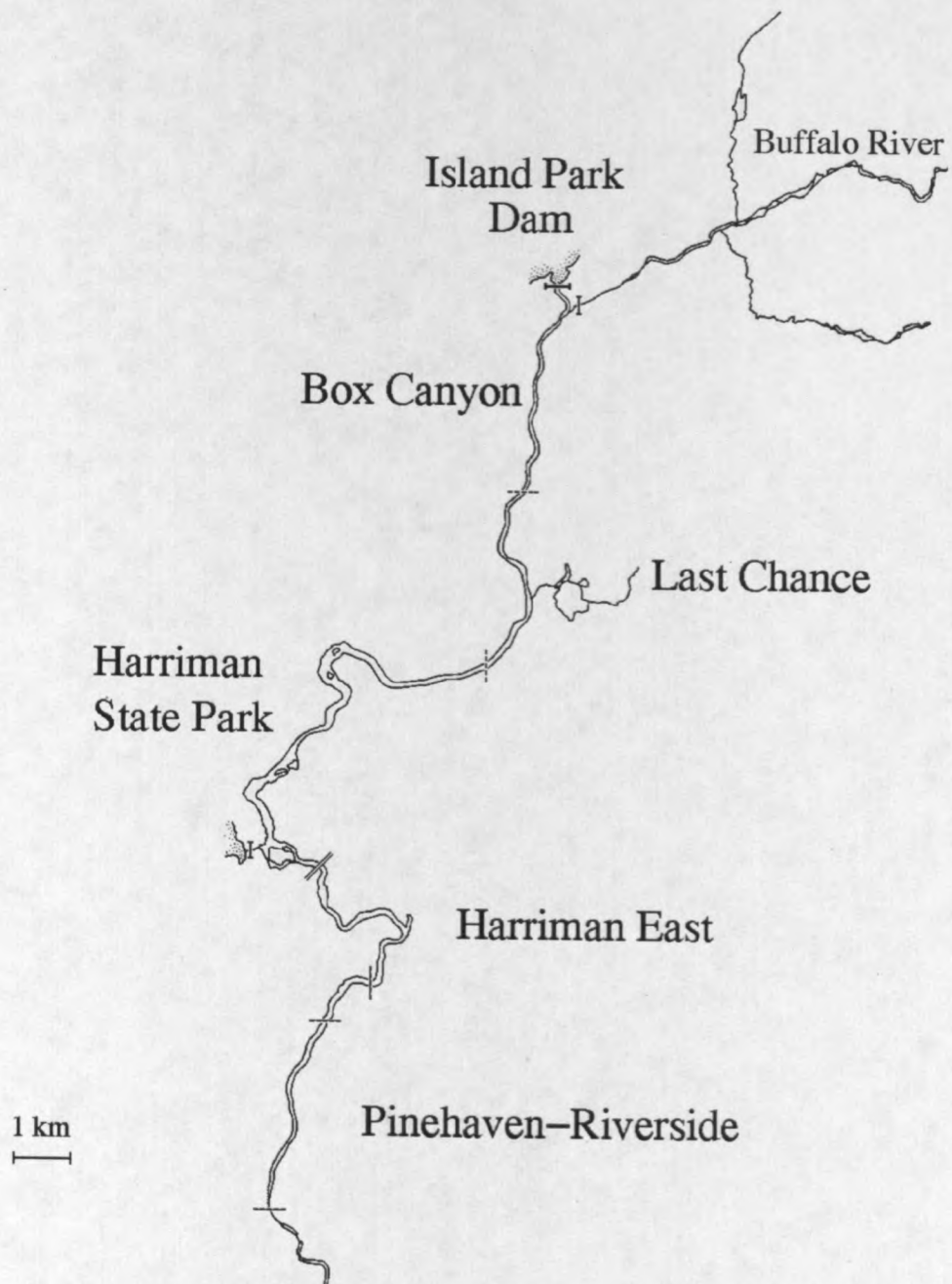


Figure 6.1.— River sections of the Henrys Fork downstream of Island Park Reservoir: Box Canyon, Last Chance, and Pinehaven-Riverside.

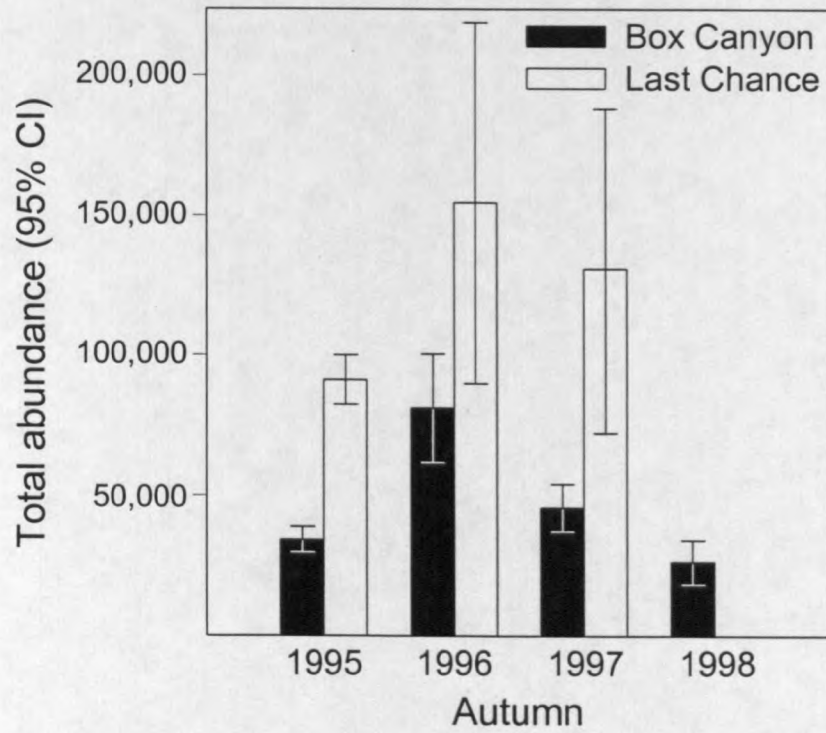


Figure 6.2.—Total abundance and 95% confidence intervals (CI) of age-0 rainbow trout in Box Canyon and Last Chance in autumns 1995-1997 (and Box Canyon autumn 1998).

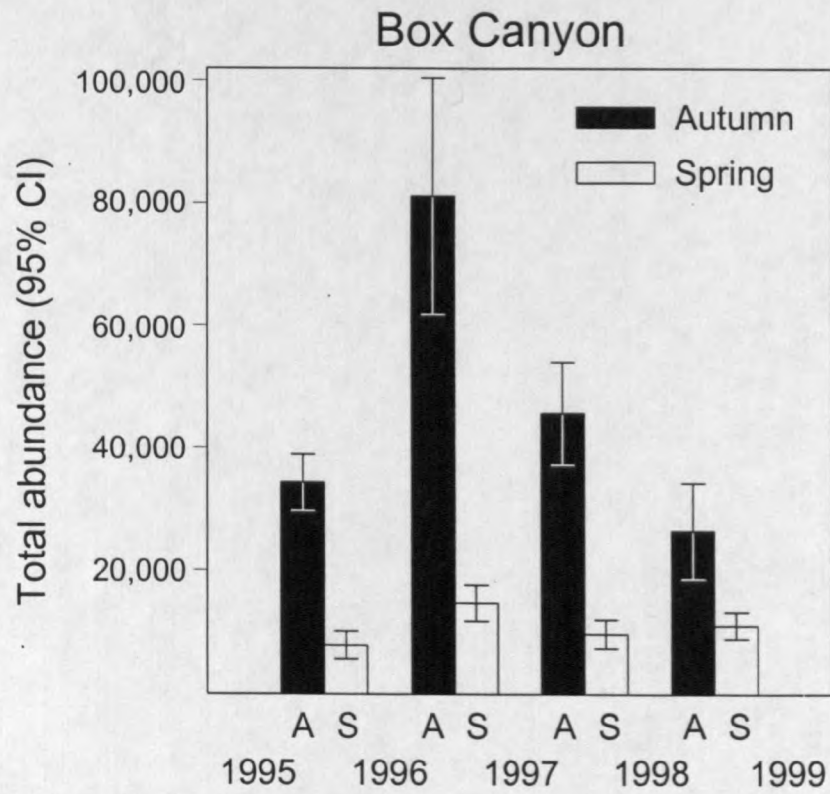


Figure 6.3.—Total abundance and 95% confidence intervals (CI) of age-0 rainbow trout in Box Canyon in autumns 1995-1998 and springs 1996-1999.

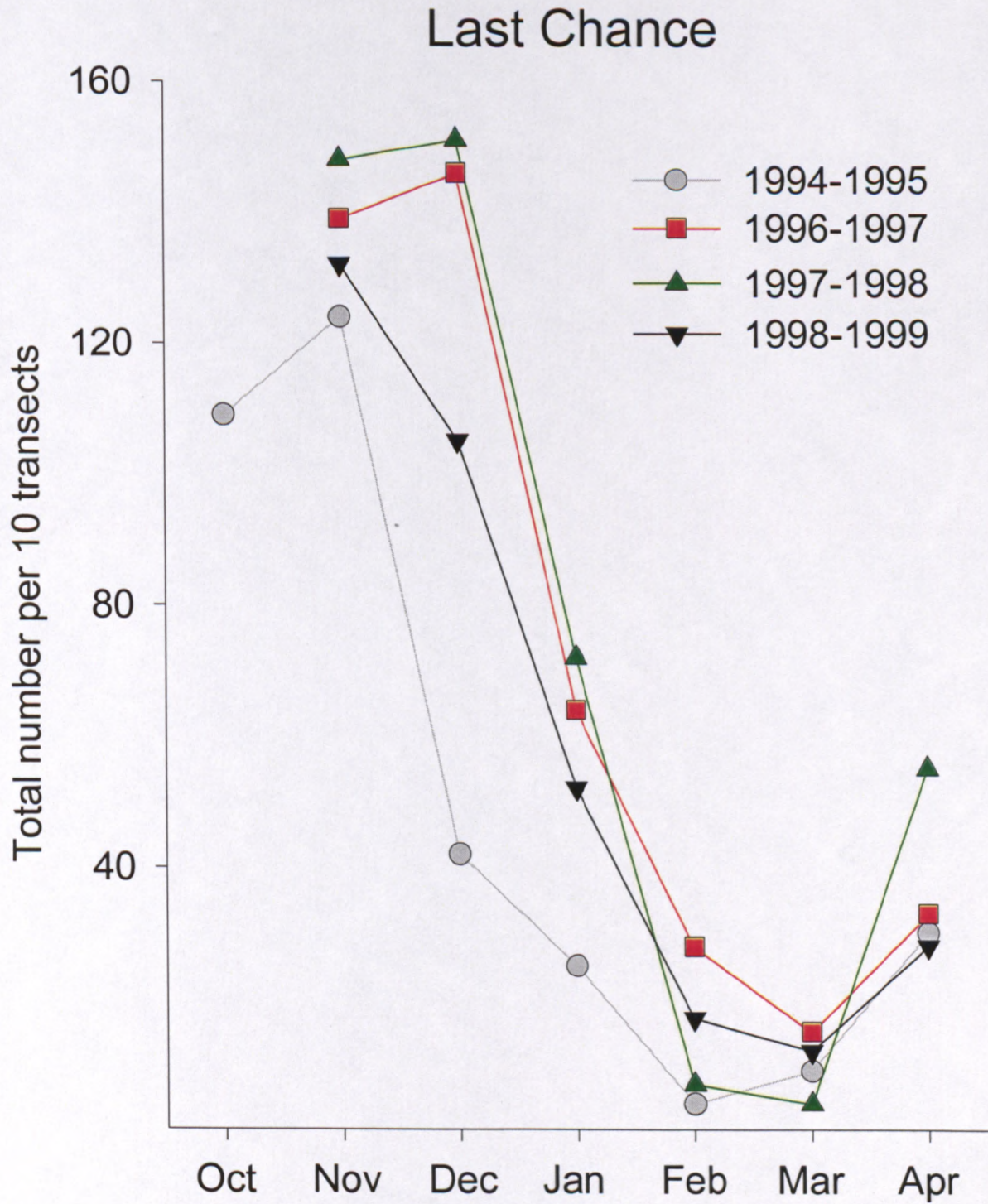


Figure 6.4.—Total number of age-0 rainbow trout captured along 10 transects in Last Chance from October or November through April in four winters.

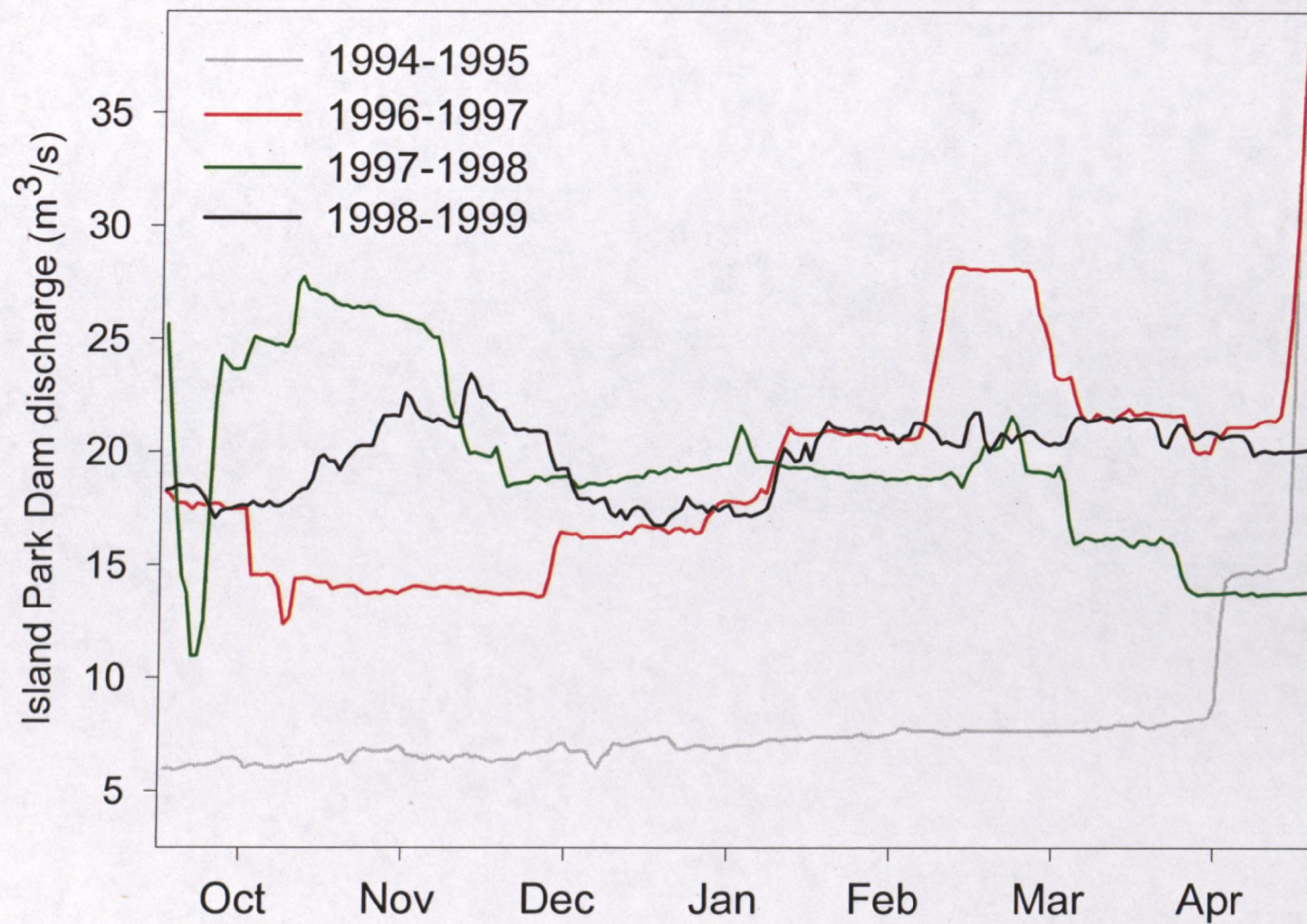


Figure 6.5.—Discharge (m^3/s) from Island Park Dam from October through April in four winters. Tick marks indicate the 15th day of each month.

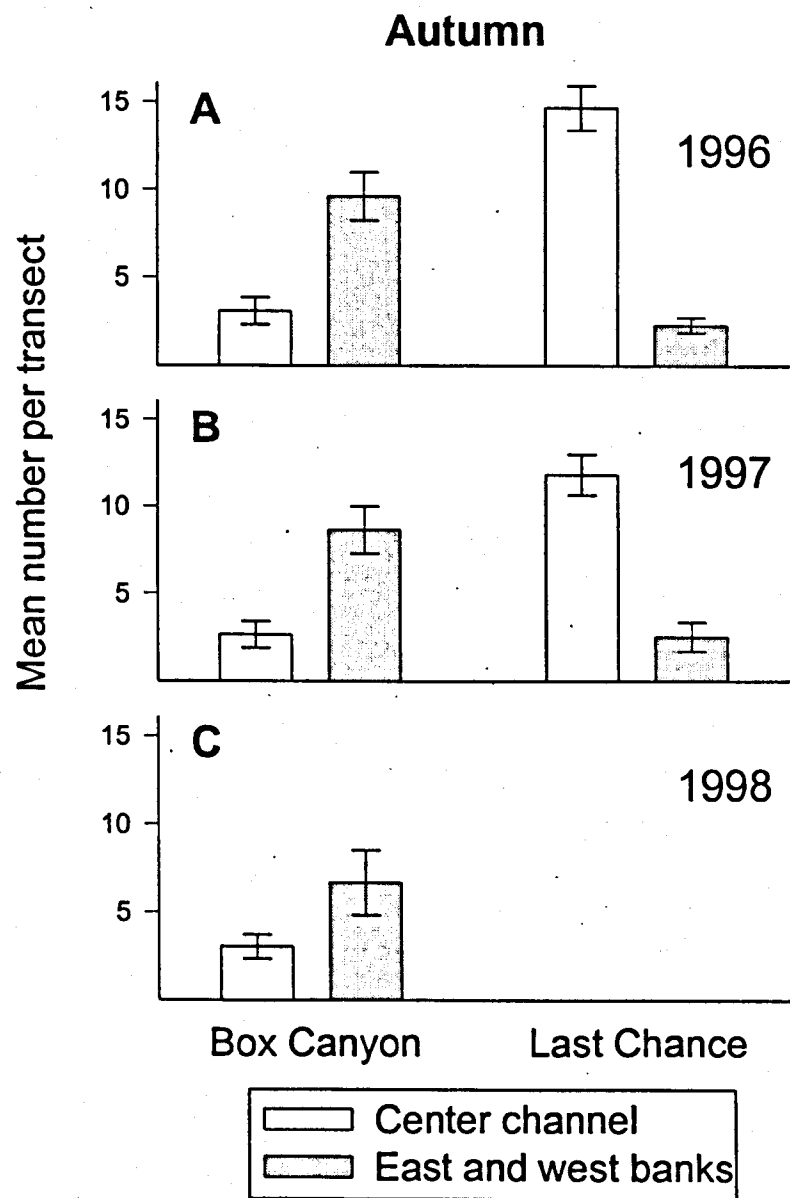


Figure 6.6.—Mean number of age-0 rainbow trout per transect and 95% confidence intervals (CI) for the center channel and the east and west banks in Box Canyon and Last Chance in autumn: (A) 1996 (Box Canyon, $N=80$; Last Chance, $N=104$), (B) 1997 (Box Canyon, $N=80$; Last Chance, $N=72$), and (C) 1998 (Box Canyon, $N=80$).

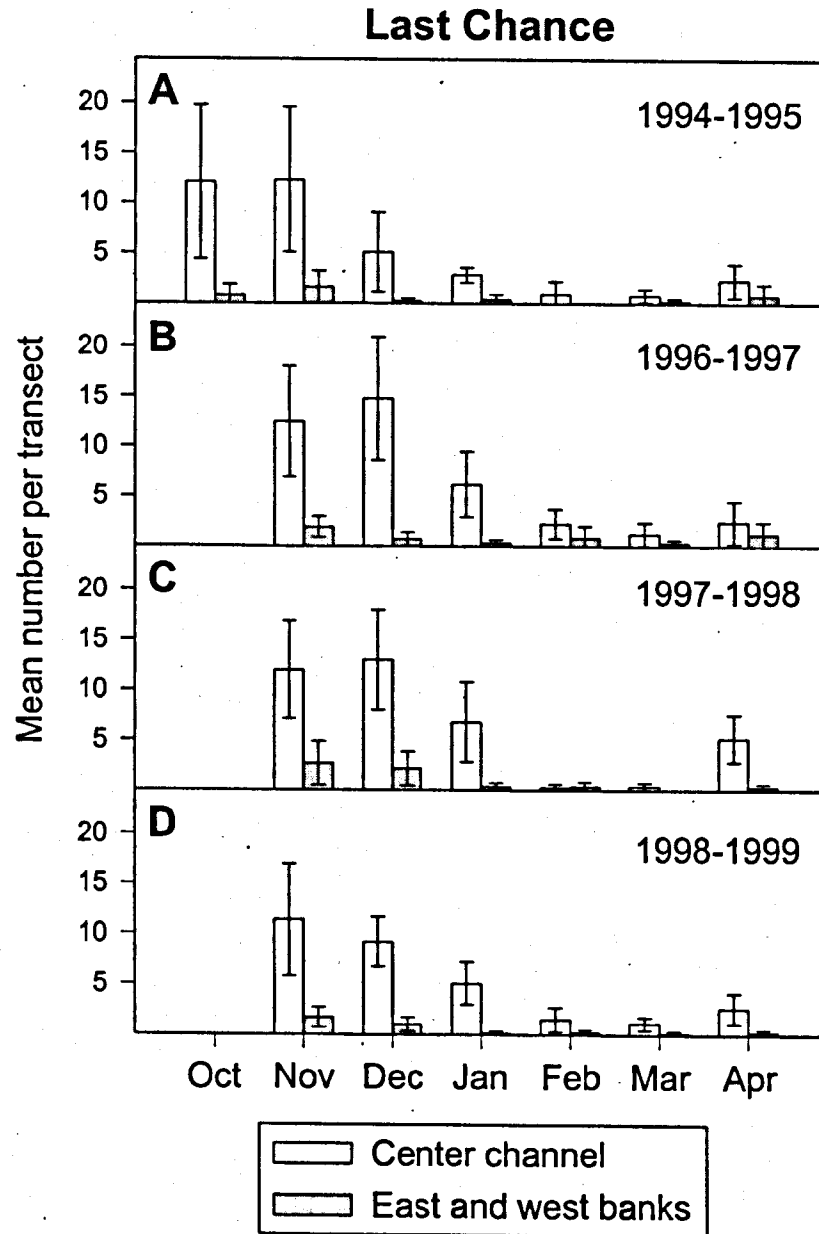


Figure 6.7.—Mean number of age-0 rainbow trout per transect ($N=10$) and 95% confidence intervals for the center channel and the east and west banks in Last Chance for winters (A) 1994-1995, (B) 1996-1997, (C) 1997-1998, and (D) 1998-1999.

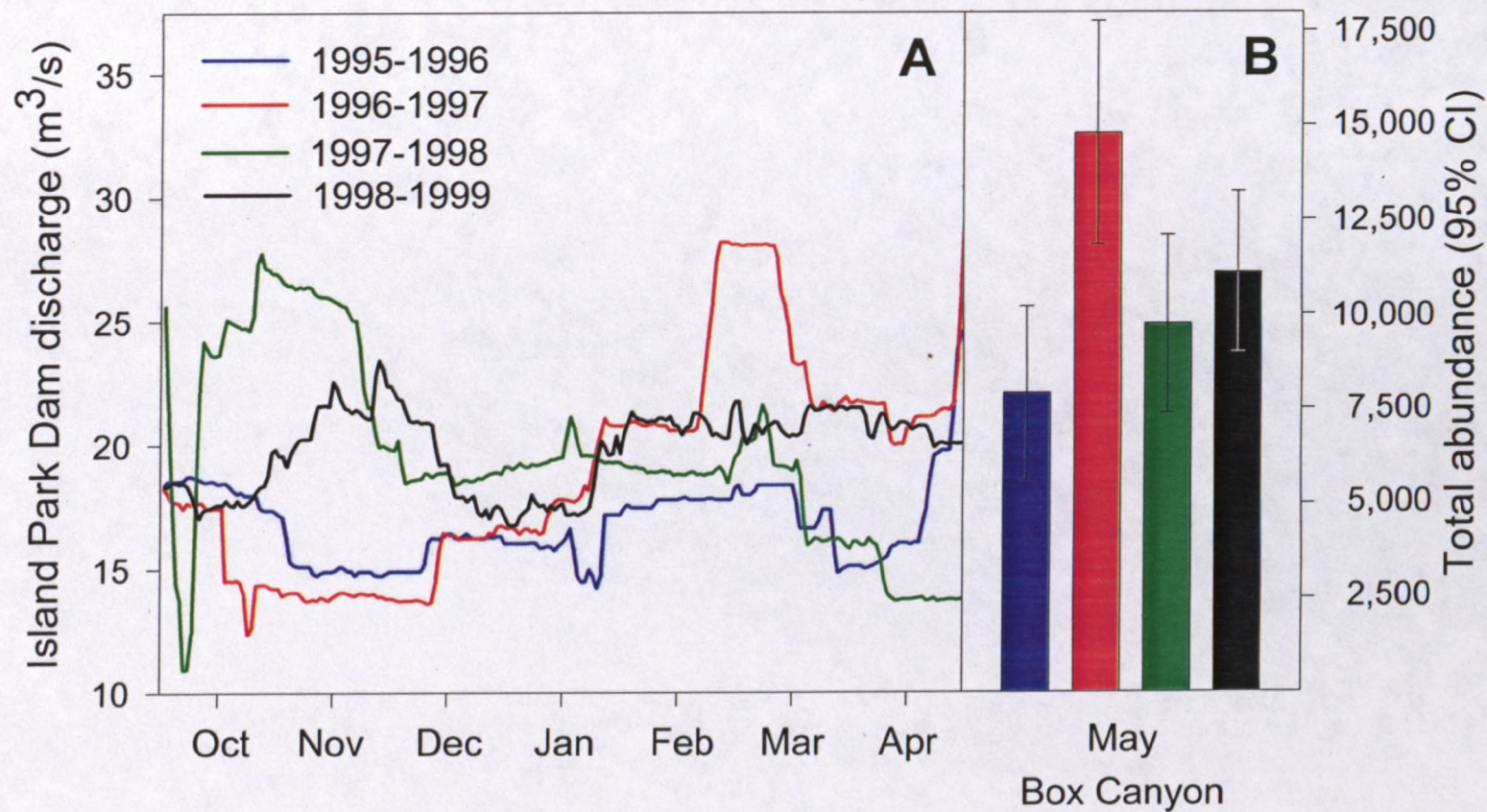


Figure 6.8.—(A) Discharge (m³/s) from Island Park Dam from October through April in four winters. Tick marks indicate the 15th day of each month. (B) Total abundance of age-0 rainbow trout and 95% confidence intervals (CI) for Box Canyon in springs 1996-1999.

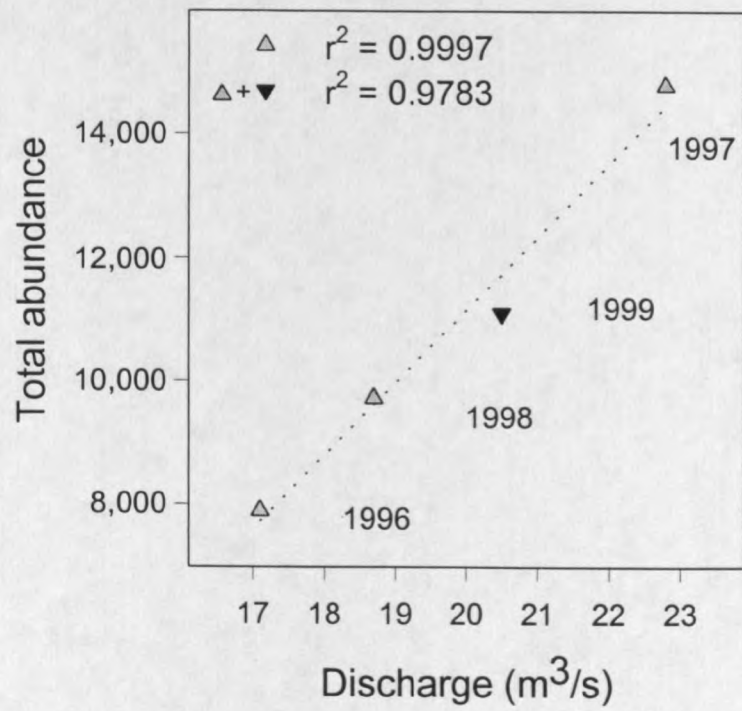


Figure 6.9.—Relation between discharge (m³/s) from Island Park Dam between 15 January and 31 March, and total abundance of age-0 rainbow trout in Box Canyon in spring. Grey symbols indicate data from the initial study and the black symbol indicates data from the validation study.

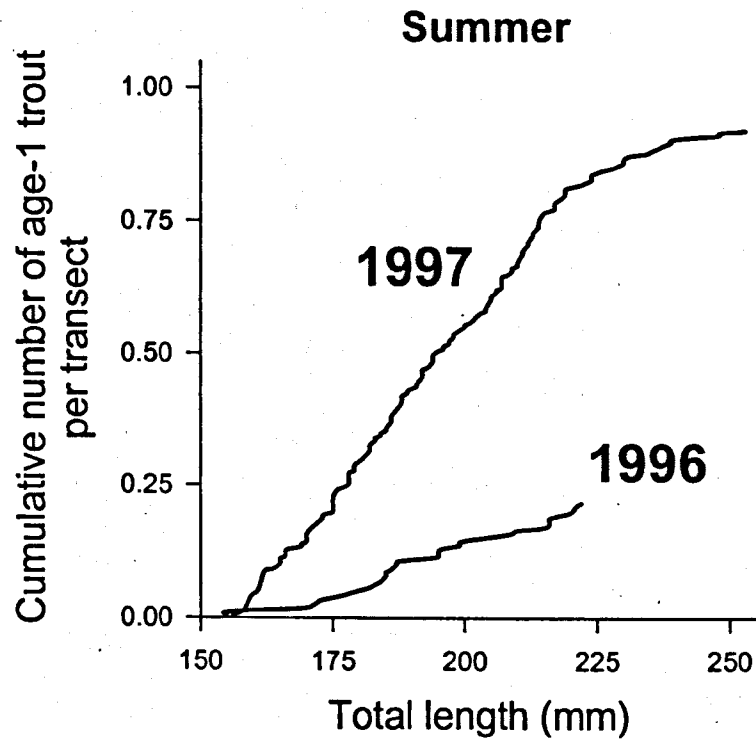


Figure 6.10.—Cumulative number of age-1 rainbow trout (standardized per transect) captured in Box Canyon and Last Chance in summers 1996 and 1997.

CHAPTER 7

CONCLUSION

Summary

Sampling and Analysis Techniques

Distance sampling was used, as an alternative to a traditional census, to sample large-scale areas of the Henrys Fork of the Snake River, Idaho, for rainbow trout spawning redds. Distance sampling provided an unbiased approach to sampling large-scale areas in a river for redds and was robust to changes in detectability. As discharge in the Henrys Fork increased between sampling dates, detectability of redds decreased and most observations were closer to the transects. The effective area sampled was smaller, but an increase in redd density was observed, indicating increased spawning activity and demonstrating the robustness of distance sampling to changes in detectability.

There were inherent difficulties in the sampling and analysis of large abundances of age-0 rainbow trout over a large spatial scale in the Henrys Fork. I developed and rigorously evaluated sampling and analysis techniques for such situations and used these results to quantify the age-0 rainbow trout production, apparent survival, movement, and habitat use in the Henrys Fork.

I developed and evaluated a mark-recapture sampling methodology for age-0 trout in the Henrys Fork. Sampling was concentrated in 100-m sample areas to improve capture efficiency and recapture rate and hence improve our ability to estimate abundance for the purpose of monitoring the age class. Low levels of emigration of marked trout

were observed in the Henrys Fork, but simulations indicated that some closed population abundance estimators were robust to minor violations of the closure assumption. The Chao M_t estimator performed best in terms of bias and coverage for simulations of sparse data generated under a temporal variation model. Capture diagnostic statistics identified temporal variation in Henrys Fork data sets. I therefore used the Chao M_t estimator to analyze mark-recapture data from sample areas in the Henrys Fork and found consistent trends in abundance for all river sections from year to year.

I also developed and rigorously evaluated models to predict abundance from single-pass removal data. The mean capture probability model with log-odds prediction intervals performed best for predicting abundance within a specific bank unit, in terms of achieving the nominal coverage level, but precision was poor (log-odds intervals were about 7.5 times greater than three-pass removal intervals). These models have the greatest utility for predicting total abundance in a large area from multiple samples within it. The models can be used to reduce data collection effort, or reallocation of effort from three-pass removal sampling to single-pass sampling can be used to increase the precision of prediction intervals. These models work particularly well for sampling large-scale areas and may be used to obtain estimates of total abundance for a single stream or for all streams in a watershed.

I used a maximum likelihood method originally developed for quantifying movement in an ocean fishery to quantify movement (or lack thereof) of juvenile trout among sections of a river that varied by habitat type. This was a more rigorous approach to the analysis of movement data that complemented the traditional qualitative approach of showing the direction of movement by drawing arrows on maps.

Rainbow Trout Recruitment in the Henrys Fork

Although relatively few redds were observed in the Henrys Fork, estimates of age-0 rainbow trout abundance indicated that spawning and production were not limiting factors in recruitment. However, it was not possible to quantify the number of redds produced during the entire spawning season because spawning coincided with spring runoff, thereby making it difficult to find redds.

The installation of a fish ladder in the Buffalo River increased the availability of spawning habitat for rainbow trout in the Henrys Fork beginning in 1997. Trout may have been able to pass the dam spillover in the Buffalo River prior to 1997 during high discharge, but the fish ladder now allows access during the spawning season when discharge is not high. Redd sampling indicated that trout were likely spawning in the Buffalo River rather than in the Henrys Fork after the installation of the fish ladder. The Buffalo River has the potential to improve recruitment in the Henrys Fork if some age-0 rainbow trout remain in the Buffalo River during their first winter. The Buffalo River is spring fed and may therefore provide a more moderate aquatic environment during winter.

Rainbow trout fry were consistently captured along the east bank in Box Canyon downstream of the confluence of the Henrys Fork and the Buffalo River each spring; trout fry were rarely captured along the west bank at that time. Rainbow trout fry may have historically dispersed from the Buffalo River upon emergence and probably will continue to do so with the installation of the fish ladder. There was no evidence in this study that the fish ladder improved recruitment in the Henrys Fork in the first two years

of its operation. Whether or not the fish ladder will improve recruitment in the Henrys Fork is an open question that should be investigated.

Many age-0 rainbow trout were found throughout Box Canyon, Last Chance, and Harriman State Park during summer and autumn. Summer growth habitat was not limiting the number of age-0 trout entering each winter. Macrophytes in particular provided much of the summer growth habitat. More age-0 trout were captured in center channel macrophytes in Last Chance than along the banks in Box Canyon in summer and autumn.

First-winter survival is a limiting factor for rainbow trout recruitment in the Henrys Fork. The number of age-0 rainbow trout surviving their first winter in the Henrys Fork was limited by the availability of winter habitat in the form of rocks and woody debris along the banks. This type of complex habitat is found primarily in Box Canyon, and to a lesser extent in Pinehaven-Riverside, and is absent in Last Chance, Harriman State Park, and Harriman East.

Harriman East was generally not used by age-0 rainbow trout at any time of the year. Age-0 trout were captured there each autumn, but they were likely there only temporarily. No trout were ever recaptured in Harriman East the following spring, but one marked in autumn was recaptured downstream in Pinehaven-Riverside in spring. Pinehaven-Riverside was the only river section in addition to Box Canyon that provided suitable winter habitat for age-0 trout. Few age-0 trout were captured there in summer, suggesting that age-0 trout moved to Pinehaven-Riverside from summer growth habitat in other river sections upstream. More importantly, this suggests that age-0 trout were also

moving downstream of Pinehaven-Riverside and contributing to recruitment in a 25-km reach extending to Mesa Falls.

I identified a flow-survival relation in which the number of age-0 rainbow trout surviving winter in Box Canyon was related to higher discharge in the latter half of winter. Increasing discharge from Island Park Dam in the latter half of winter raises the water level in Box Canyon and floods rocks and woody debris along the banks, thereby creating more available winter habitat at a critical time for survival. There is much evidence to support this conclusion. The loss of age-0 trout from Last Chance was initiated during mid-winter in each year of this study. The loss from Last Chance occurred from center channel habitat (i.e., macrophytes) and there was relatively consistent use of available bank habitat. Bank habitat was the primary habitat used by age-0 trout in Box Canyon throughout the year. The loss of age-0 trout from Last Chance could not be attributed only to mortality. Trout marked in Last Chance in autumn were recaptured in Box Canyon in spring, indicating winter movement from river sections with simple bank habitat to river sections with complex bank habitat. A plot of mean discharge from Island Park Dam from 15 January to 31 March versus the total abundance of age-0 rainbow trout along the banks in Box Canyon in springs 1996-1999 showed a strong linear positive relation. The large number of age-0 trout surviving winter 1996-1997 was evident in age-1 catch-per-unit-effort data the following summer.

Production, as well as discharge, was related to the number of age-0 rainbow trout surviving winter in Box Canyon during the first three years of this study. Spring abundance in Box Canyon was greater in 1997 than in 1996 or 1998; autumn abundance was greater in 1996 than in 1995 or 1997. I believe this correlation was spurious. In the

winter 1998-1999 validation study, autumn abundance was lower than abundances in the three previous autumns and spring abundance was the second greatest recorded. This supported higher discharge in the latter half of winter, rather than pre-winter production, as the determinant of first-winter survival in Box Canyon.

Management Recommendations

If excess water in Island Park Reservoir can be released during winter, I recommend that it be released during the latter half of winter to improve the survival of age-0 rainbow trout in Box Canyon and thereby improve recruitment to the Henrys Fork rainbow trout fishery. Monitoring of age-0 trout should continue for the purpose of further validation of the flow-survival relation, whether discharge is high or low during the latter half of winter. Estimating the abundance of age-0 rainbow trout in Box Canyon in spring by sampling 50 bank units using a removal methodology and obtaining winter discharge data from the U.S.G.S. gauging station at Island Park Dam would be sufficient to further evaluate the flow-survival relation. The mean capture probability (MCP) model developed for the Henrys Fork in chapter three could be used to reduce data collection effort. Rather than sampling 50 bank units by three-pass removal, they could be sampled by single-pass removal and abundance could be estimated using the MCP model. Alternatively, a portion of bank units could be sampled by three-pass removal to further calibrate the model for use with the single-pass removal data from the other bank units.

If discharge will be purposely increased in the latter half of winter to improve age-0 rainbow trout survival in Box Canyon, I would caution that the timing of the

increase should coincide approximately with the initiation of loss of age-0 trout. The timing of the loss in Last Chance was related to discharge in the first half of winter. The loss occurred between November and December at low discharge (about $7 \text{ m}^3/\text{s}$) and between December and January at high discharge ($> 15 \text{ m}^3/\text{s}$). The catch-per-unit-effort methodology used in Last Chance during winter could be used to confirm when the loss was occurring. I recommend sampling ten random bank-to-bank transects in Last Chance once per month until the loss of age-0 trout is detected. The sampling should begin in October if autumn discharge is low and in November if discharge is high.

If there is debate as to the importance of pre-winter age-0 trout production to winter survival, I recommend estimating abundance in Box Canyon in October using a combination of mark-recapture sampling in sample areas and removal sampling in bank units. The two sample areas in lower Box Canyon should be sampled on four or five days in about a ten-day period, preferably every other day. A different fin clip should be used on each sampling date such that the data can be analyzed using estimators in program CAPTURE. I recommend the use of the Chao- M_t estimator, which was found to perform best in simulations of data analogous to that obtained in the Henrys Fork. At least ten bank units should be sampled in upper Box Canyon using three-pass or single-pass removal sampling as described earlier.

This study showed the importance of complex bank habitat, which provides interstitial shelter, to winter survival of age-0 rainbow trout in the Henrys Fork. The input of sediment into the Henrys Fork and into Box Canyon in particular should be limited such that complex bank habitat is preserved. There has been some discussion about improving bank habitat in other river sections by planting willows, increasing the

amount of woody debris, or installing artificial structures. I suspect that such efforts will have limited value to winter survival of age-0 trout. Freezing conditions during winter would negate the utility of such habitat modifications in Harriman State Park and Harriman East. The embedded substrate and the inability of higher discharge to raise the water level in Last Chance may negate habitat modifications in that river section. I recommend managing winter discharge as the best approach to improving the recruitment of age-0 rainbow trout in the Henrys Fork.

APPENDICES

Table A.1—Detection function model, value of probability distribution function at 0 for the detection function ($f(o)$), probability of observing a redd in a river section (p), effective strip width (ESW), and redd encounter rate (n/L or number per total length of transects sampled) for 1995 and 1996 sampling in the river section between Island Park Dam and the United States Geological Survey gauging station.

	Mean	95% Confidence interval
27 April 1995		
Model	Half-normal/cosine	
$f(o)$	0.133	[0.086—0.204]
p	0.660	[0.429—1]
ESW	7.5 m	[4.9—11.6]
n/L	0.031	[0.014—0.068]
9 April 1996		
Model	Half-normal/cosine	
$f(o)$	0.150	[0.068—0.333]
p	0.803	[0.362—1]
ESW	6.7 m	[3.0—14.8]
n/L	0.012	[0.003—0.040]

Table A.1—Continued.

	Mean	95% Confidence interval
14 April 1996		
Model	Half-normal/cosine	
$f(o)$	0.080	[0.042—0.153]
p	1	[0.523—1]
ESW	12.5 m	[6.5—23.9]
n/L	0.020	[0.008—0.050]
21 April 1996		
Model	Half-normal/cosine	
$f(o)$	0.150	[0.072—0.314]
p	0.900	[0.430—1]
ESW	6.7 m	[3.2—13.9]
n/L	0.016	[0.007—0.033]

Table A.2.—Simulation results for comparing closed-population abundance estimators (Lincoln-Petersen, Schumacher-Eschmeyer, Schnabel, Null M_0 , Darroch M_t , Chao M_t , Chao M_h , and Chao M_{th}). Mark-recapture data were simulated under model M_t for 4 closed populations with average capture probabilities ranging from 0.02 to 0.106 ($t=5$ capture occasions; 1,000 replications). % cov. = percent coverage for 95% confidence intervals; ne = no estimate.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Lincoln-Petersen							Schumacher-Eschmeyer					
1.	$p_1=0.01, p_2=0.04,$	1,000	861.0	(517.0)	1,296.5	(389.4)	87.4	ne	ne	ne	ne	ne
	$p_3=0.02, p_4=0.02,$	1,500	1,401.0	(816.2)	2,449.6	(852.1)	93.7	ne	ne	ne	ne	ne
	$p_5=0.01$	2,000	1,865.7	(1,054.8)	3,430.7	(1,481.6)	93.2	ne	ne	ne	ne	ne
	$[\bar{p}=0.02]$	2,500	2,415.7	(1,260.1)	4,455.0	(2,227.4)	94.2	ne	ne	ne	ne	ne
		3,000	2,894.0	(1,303.8)	5,189.3	(2,807.1)	95.2	ne	ne	ne	ne	ne
Schnabel estimator							Null M_0					
		1,000	ne	ne	ne	ne	ne	880.5	(162.3)	1,732.7	(419.8)	97.0
		1,500	ne	ne	ne	ne	ne	1,339.0	(207.0)	2,106.9	(432.4)	97.3
		2,000	ne	ne	ne	ne	ne	1,812.5	(235.4)	2,442.0	(421.2)	97.9
		2,500	ne	ne	ne	ne	ne	2,295.0	(268.1)	2,753.0	(422.6)	97.7
		3,000	1,995.3	(828.1)	9,247.7	(5,046.0)	85.4	2,754.6	(300.9)	3,000.0	(442.0)	98.3
Darroch M_1							Chao M_1					
		1,000	854.1	(178.3)	1,738.5	(494.0)	95.6	1,002.0	(618.9)	2,621.0	(3,134.9)	91.0
		1,500	1,300.7	(231.0)	2,111.7	(520.0)	95.6	1,529.0	(850.0)	3,118.6	(3,752.7)	92.0
		2,000	1,758.7	(268.2)	2,438.0	(519.6)	96.0	1,956.5	(789.1)	3,146.5	(2,591.3)	93.8
		2,500	2,232.7	(309.8)	2,753.5	(528.5)	96.7	2,528.8	(973.0)	3,631.7	(2,673.1)	93.8
		3,000	2,681.0	(350.8)	3,002.6	(558.1)	95.9	3,003.0	(968.3)	3,824.5	(2,086.9)	93.4

Table A.2.—Continued.

		Average		Average		%	Average		Average		%
		estimate	(SE)	interval	(SE)	cov.	estimate	(SE)	interval	(SE)	cov.
		Chao M_h					Chao M_{th}				
	1,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
	1,500	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
	2,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
	2,500	3,866.7	(2,095.8)	6,470.0	(8,509.9)	88.0	3,401.0	(1,864.1)	5,759.0	(7,445.5)	92.9
	3,000	4,431.8	(1,689.5)	6,227.4	(4,097.4)	88.0	3,906.7	(1,552.2)	5,585.8	(3,814.4)	93.3
		Lincoln-Petersen					Schumacher-Eschmeyer				
2.	$p_1=0.03, p_2=0.03,$	1,000	876.0	(273.3)	1,132.2	(578.8)	89.3	ne	ne	ne	ne
	$p_3=0.05, p_4=0.05,$	1,500	1,329.8	(317.8)	1,351.8	(524.5)	90.0	ne	ne	ne	ne
	$p_5=0.07$	2,000	1,750.6	(374.6)	1,508.8	(505.3)	86.9	ne	ne	ne	ne
	$[\bar{p}=0.046]$	2,500	2,215.1	(415.7)	1,692.1	(485.1)	88.4	ne	ne	ne	ne
		3,000	2,649.8	(464.4)	1,838.7	(505.8)	87.2	ne	ne	ne	ne
		Schnabel					Null M_0				
	1,000	591.0	(159.2)	1,858.3	(928.4)	83.9	1,060.6	(238.4)	917.8	(346.2)	95.3
	1,500	865.6	(180.1)	2,226.4	(837.7)	70.2	1,588.8	(283.2)	1,098.5	(332.5)	95.1
	2,000	1,124.1	(199.1)	2,493.3	(810.2)	58.6	2,077.0	(319.0)	1,223.4	(310.9)	94.5
	2,500	1,412.1	(229.7)	2,795.2	(779.9)	46.3	2,622.7	(367.7)	1,377.9	(319.5)	93.1
	3,000	1,682.5	(246.9)	3,041.9	(810.6)	36.1	3,124.4	(397.9)	1,493.0	(325.6)	94.3

Table A.2.—Continued.

	<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Darroch M_t					Chao M_t				
	1,000	1,030.4	(232.0)	887.9	(336.8)	95.0	994.8	(232.6)	899.0	(342.9)	94.9
	1,500	1,543.7	(274.1)	1,062.8	(322.3)	95.1	1,503.3	(274.9)	1,092.6	(328.9)	95.1
	2,000	2,020.6	(310.0)	1,185.2	(302.0)	93.8	1,986.0	(324.5)	1,239.9	(328.5)	92.5
	2,500	2,551.1	(357.3)	1,334.8	(310.1)	93.9	2,521.8	(373.7)	1,408.3	(334.2)	93.8
	3,000	3,042.1	(386.3)	1,447.8	(316.0)	95.5	3,011.7	(411.1)	1,532.2	(345.6)	94.6
		Chao M_h					Chao M_{th}				
	1,000	1,288.0	(333.2)	1,262.9	(517.5)	85.7	1,122.7	(293.9)	1,098.0	(478.7)	94.0
	1,500	1,912.2	(381.3)	1,487.4	(471.6)	81.4	1,657.5	(333.5)	1,287.7	(445.3)	94.5
	2,000	2,500.4	(438.7)	1,660.5	(454.9)	77.6	2,163.5	(385.2)	1,436.4	(442.6)	93.1
	2,500	3,161.4	(499.3)	1,870.7	(455.1)	68.1	2,730.2	(437.9)	1,619.5	(442.2)	91.3
	3,000	3,760.0	(548.5)	2,022.3	(468.0)	66.2	3,242.5	(483.9)	1,745.3	(458.2)	92.8
		Lincoln-Petersen					Schumacher-Eschmeyer				
3. $p_1=0.08, p_2=0.07,$	1,000	823.3	(144.9)	625.5	(174.4)	81.5	705.0	(101.0)	1,986.0	(15,686)	94.0
$p_3=0.10, p_4=0.06,$	1,500	1,231.3	(167.2)	741.2	(162.0)	71.3	1,042.0	(114.0)	1,884.0	(1,172.0)	97.0
$p_5=0.08$	2,000	1,637.9	(207.1)	821.8	(163.7)	58.1	1,377.0	(141.0)	2,300.0	(1,070.0)	97.0
$[\bar{p}=0.078]$	2,500	2,053.6	(226.7)	914.8	(151.2)	52.8	1,718.0	(153.0)	2,850.0	(1,229.0)	99.0
	3,000	2,455.0	(244.1)	999.5	(149.2)	46.8	2,050.0	(161.0)	3,300.0	(1,070.0)	99.0

Table A.2.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Schnabel						Null M_0				
1,000	605.1	(82.2)	1,230.6	(333.2)	18.1	1,019.3	(115.2)	467.6	(91.5)	95.7
1,500	899.0	(94.9)	1,458.7	(309.3)	3.3	1,525.0	(140.6)	566.1	(90.9)	95.6
2,000	1,192.8	(118.1)	1,622.2	(313.2)	1.2	2,021.0	(168.4)	646.8	(92.3)	94.6
2,500	1,488.5	(128.4)	1,808.2	(296.6)	0.1	2,529.7	(185.7)	720.5	(90.7)	95.2
3,000	1,777.7	(134.4)	1,979.3	(286.5)	0	3,020.8	(196.6)	784.2	(89.1)	95.5
Darroch M_t						Chao M_t				
1,000	1,010.5	(114.0)	462.4	(90.4)	95.5	1,002.9	(127.1)	512.6	(109.9)	96.0
1,500	1,512.5	(139.2)	560.1	(89.9)	95.8	1,501.2	(154.2)	620.9	(108.1)	95.5
2,000	2,005.6	(166.7)	640.4	(91.4)	94.3	1,998.8	(189.2)	715.6	(113.5)	94.5
2,500	2,510.4	(184.2)	713.3	(89.9)	95.3	2,504.9	(201.4)	798.6	(106.6)	95.7
3,000	2,998.5	(194.7)	776.8	(88.2)	95.5	2,991.7	(221.0)	869.8	(108.5)	94.7
Chao M_h						Chao M_{th}				
1,000	1,198.9	(165.1)	663.8	(146.4)	77.0	1,055.5	(146.0)	560.0	(148.1)	94.5
1,500	1,783.2	(198.0)	795.5	(141.3)	67.5	1,562.2	(172.0)	666.8	(147.0)	94.3
2,000	2,366.9	(241.2)	911.8	(146.9)	59.3	2,069.0	(208.8)	764.0	(156.6)	93.2
2,500	2,961.3	(255.2)	1,014.6	(137.1)	51.5	2,585.6	(221.1)	848.7	(148.4)	92.2
3,000	3,531.7	(280.1)	1,102.6	(139.1)	44.1	3,080.7	(243.4)	918.5	(156.6)	93.4

Table A.2.—Continued.

	<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Lincoln-Petersen					Schumacher-Eschmeyer				
4. $p_1=0.10, p_2=0.13,$	1,000	753.4	(95.8)	392.3	(79.4)	36.9	658.1	(67.7)	1,049.9	(442.7)	96.2
$p_3=0.08, p_4=0.10,$	1,500	1,130.6	(122.6)	477.0	(75.9)	22.4	979.0	(81.1)	1,527.6	(503.9)	98.2
$p_5=0.12$	2,000	1,497.6	(141.5)	544.8	(74.7)	14.3	1,298.3	(98.9)	1,934.0	(487.8)	98.1
$[\bar{p}=0.106]$	2,500	1,884.4	(160.7)	613.9	(75.6)	9.4	1,627.2	(107.6)	2,410.9	(564.0)	99.4
	3,000	2,248.2	(166.9)	667.7	(72.0)	3.7	1,948.1	(111.1)	2,872.3	(578.3)	99.8
		Schnabel					Null M_0				
	1,000	571.9	(57.4)	776.0	(147.2)	8.6	1,012.8	(79.8)	322.2	(46.5)	95.8
	1,500	851.6	(68.4)	946.3	(140.8)	1.0	1,515.7	(100.1)	392.5	(47.5)	94.4
	2,000	1,132.7	(84.1)	1,083.1	(138.9)	0.2	2,012.2	(117.8)	448.4	(48.0)	94.0
	2,500	1,420.6	(91.2)	1,220.2	(141.8)	0.0	2,523.9	(131.8)	502.9	(47.2)	94.5
	3,000	1,700.7	(94.0)	1,330.3	(134.6)	0.0	3,020.7	(133.5)	548.3	(44.4)	96.1
		Darroch M_t					Chao M_t				
	1,000	1,005.2	(79.1)	318.8	(46.1)	96.3	1,001.9	(94.0)	366.4	(62.3)	95.1
	1,500	1,504.9	(99.2)	388.5	(47.0)	95.0	1,499.3	(112.7)	445.9	(60.0)	95.4
	2,000	1,998.3	(116.9)	443.9	(47.5)	94.4	1,995.6	(136.4)	512.3	(62.8)	94.0
	2,500	2,507.3	(130.7)	498.1	(46.8)	94.5	2,509.9	(149.2)	577.4	(60.5)	94.5
	3,000	3,000.9	(132.4)	543.1	(44.1)	96.3	3,000.2	(159.2)	628.0	(59.4)	94.9

Table A.2.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
	Chao M_h					Chao M_{th}				
1,000	1,162.4	(119.6)	466.9	(80.9)	68.6	1,040.2	(106.4)	388.2	(85.0)	92.7
1,500	1,733.6	(142.2)	564.7	(77.0)	57.7	1,545.7	(123.5)	467.3	(84.1)	92.8
2,000	2,303.4	(171.5)	646.8	(80.3)	46.4	2,051.7	(149.2)	534.7	(89.4)	92.6
2,500	2,895.4	(186.6)	727.7	(77.0)	34.0	2,575.6	(164.5)	603.5	(90.1)	90.8
3,000	3,457.9	(199.2)	790.6	(75.5)	28.4	3,074.1	(175.4)	653.6	(93.6)	92.4

Table A.3.—Simulation results for comparing closed-population abundance estimators (Lincoln-Petersen, Schumacher-Eschmeyer, Schnabel, Null M_0 , Darroch M_t , Chao M_t , Chao M_h , and Chao M_{th}). Mark-recapture data were simulated under model M_t for 4 open populations (i.e., permanent emigration of 5% of marked fish) with average capture probabilities ranging from 0.02 to 0.106 ($t=5$ capture occasions; 1,000 replications). % cov. = percent coverage for 95% confidence intervals; ne = no estimate.

	<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Lincoln-Petersen					Schumacher-Eschmeyer				
1. $p_1=0.01, p_2=0.04,$	1,000	893.3	(530.0)	1,315.8	(382.6)	88.5	ne	ne	ne	ne	ne
$p_3=0.02, p_4=0.02,$	1,500	1,468.8	(868.2)	2,520.9	(849.3)	95.0	ne	ne	ne	ne	ne
$p_5=0.01$	2,000	1,954.6	(1,136.7)	3,570.2	(1,497.1)	94.3	ne	ne	ne	ne	ne
$[\bar{p}=0.02]$	2,500	2,541.5	(1,366.0)	4,701.4	(2,281.5)	95.8	ne	ne	ne	ne	ne
	3,000	3,062.1	(1,548.4)	5,516.0	(2,907.7)	95.9	ne	ne	ne	ne	ne
		Schnabel estimator					Null M_0				
	1,000	ne	ne	ne	ne	ne	890.4	(156.7)	1,764.5	(401.2)	97.8
	1,500	ne	ne	ne	ne	ne	1,356.1	(196.5)	2,150.6	(404.5)	98.0
	2,000	ne	ne	ne	ne	ne	1,833.8	(220.8)	2,488.4	(385.6)	98.8
	2,500	ne	ne	ne	ne	ne	2,324.4	(248.6)	2,810.4	(378.9)	98.1
	3,000	2,131.8	(933.1)	9,829.4	(5,235.6)	82.8	2,785.2	(277.7)	3,054.9	(396.6)	98.8
		Darroch M_t					Chao M_t				
	1,000	866.0	(172.8)	1,777.8	(476.1)	96.5	1,046.9	(645.7)	2,818.9	(3,313.2)	92.3
	1,500	1,322.1	(220.3)	2,167.6	(492.1)	96.7	1,612.5	(921.5)	3,425.8	(4,187.0)	93.3
	2,000	1,787.3	(254.2)	2,501.2	(486.1)	97.2	2,045.4	(843.8)	3,386.6	(2,787.2)	94.9
	2,500	2,271.7	(287.9)	2,830.6	(482.3)	97.4	2,656.1	(1,049.5)	3,937.1	(2,986.7)	94.9
	3,000	2,724.0	(326.8)	3,080.3	(512.5)	97.4	3,154.4	(1,037.3)	4,140.1	(2,299.4)	94.5

Table A.3.—Continued.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Chao M_h					Chao M_{th}					
		1,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		1,500	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		2,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		2,500	4,109.2	(2,331.3)	7,176.9	(9,831.9)	85.0	3,609.6	(2,064.7)	6,367.1	(8,563.4)	91.7
		3,000	4,693.7	(1,837.9)	6,825.4	(4,617.8)	83.6	4,134.2	(1,675.6)	6,107.7	(4,243.9)	91.4
		Lincoln-Petersen					Schumacher-Eschmeyer					
2.	$p_1=0.03, p_2=0.03,$	1,000	926.4	(301.1)	1,237.1	(655.2)	92.1	ne	ne	ne	ne	ne
	$p_3=0.05, p_4=0.05,$	1,500	1,402.5	(344.0)	1,469.8	(591.1)	93.8	ne	ne	ne	ne	ne
	$p_5=0.07$	2,000	1,848.0	(405.7)	1,640.1	(567.3)	90.8	ne	ne	ne	ne	ne
	$[\bar{p}=0.046]$	2,500	2,339.1	(447.8)	1,839.0	(542.2)	93.4	ne	ne	ne	ne	ne
		3,000	2,796.4	(498.2)	1,997.2	(558.4)	91.9	ne	ne	ne	ne	ne
		Schnabel					Null M_0					
		1,000	626.9	(183.7)	2,023.6	(1,050.5)	78.6	1,114.0	(259.0)	998.0	(387.6)	94.7
		1,500	913.1	(192.6)	2,412.6	(943.3)	63.3	1,666.3	(303.0)	1,190.6	(365.0)	93.5
		2,000	1,184.1	(212.9)	2,701.4	(906.4)	49.7	2,176.9	(343.3)	1,324.3	(343.9)	92.7
		2,500	1,489.4	(249.6)	3,028.4	(871.5)	34.9	2,751.6	(397.4)	1,494.1	(356.4)	90.7
		3,000	1,774.2	(263.9)	3,293.9	(894.4)	25.0	3,278.8	(424.9)	1,619.1	(357.6)	92.1

Table A.3.—Continued.

	<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Darroch M_t					Chao M_t				
	1,000	1,082.7	(252.8)	966.5	(378.5)	95.3	1,043.2	(255.6)	973.0	(393.7)	94.9
	1,500	1,619.5	(293.0)	1,152.6	(353.3)	94.8	1,574.5	(293.0)	1,178.3	(360.4)	95.4
	2,000	2,118.6	(333.6)	1,283.9	(333.9)	93.6	2,078.6	(345.3)	1,335.0	(357.9)	93.7
	2,500	2,677.5	(386.4)	1,448.3	(346.2)	92.0	2,643.1	(398.9)	1,519.8	(365.9)	94.5
	3,000	3,193.6	(412.7)	1,571.1	(347.2)	93.4	3,154.2	(434.7)	1,651.0	(374.7)	94.3
		Chao M_h					Chao M_{th}				
	1,000	1,357.7	(370.5)	1,374.4	(607.4)	81.7	1,181.2	(324.2)	1,191.9	(553.1)	92.8
	1,500	2,010.2	(408.7)	1,608.5	(520.1)	74.1	1,739.6	(357.3)	1,391.9	(489.6)	92.0
	2,000	2,625.0	(468.1)	1,791.1	(497.5)	67.7	2,267.1	(410.0)	1,547.6	(481.5)	91.0
	2,500	3,323.0	(534.0)	2,021.5	(499.5)	55.2	2,863.4	(466.2)	1,748.2	(479.9)	86.7
	3,000	3,948.2	(581.1)	2,181.4	(508.7)	51.8	3,396.1	(510.5)	1,877.8	(492.7)	88.6
		Lincoln-Petersen					Schumacher-Eschmeyer				
3. $p_1=0.08, p_2=0.07,$	1,000	870.5	(160.2)	682.1	(197.4)	88.7	743.0	111.0	2136.0	16242.0	95.0
$p_3=0.10, p_4=0.06,$	1,500	1,298.4	(181.1)	807.9	(179.0)	82.3	1095.0	122.0	2004.0	1348.0	98.0
$p_5=0.08$	2,000	1,729.9	(223.1)	897.2	(186.8)	75.3	1447.0	153.0	2423.0	1104.0	98.0
$[\bar{p}=0.078]$	2,500	2,168.5	(244.9)	993.6	(168.9)	73.5	1805.0	166.0	3033.0	1419.0	99.0
	3,000	2,588.5	(259.4)	1,082.8	(162.0)	67.8	2150.0	171.0	3495.0	1163.0	99.0

Table A.3.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Schnabel						Null M_0				
1,000	636.6	(90.9)	1,335.5	(375.6)	11.9	1,066.7	(127.8)	508.4	(104.9)	94.0
1,500	943.7	(101.8)	1,581.9	(340.4)	1.7	1,593.7	(151.0)	613.6	(100.5)	92.6
2,000	1,252.1	(127.3)	1,762.0	(356.4)	0.3	2,113.0	(183.7)	701.7	(103.8)	91.2
2,500	1,562.0	(138.9)	1,954.4	(330.1)	0	2,643.7	(201.0)	781.0	(101.4)	88.8
3,000	1,862.2	(143.4)	2,133.6	(310.0)	0	3,153.8	(210.1)	848.5	(97.5)	90.2
Darroch M_t						Chao M_t				
1,000	1,057.2	(126.4)	502.7	(103.7)	94.1	1,048.2	(138.9)	553.7	(122.7)	95.3
1,500	1,580.5	(149.5)	607.2	(99.4)	93.4	1,568.4	(166.1)	670.1	(119.5)	94.7
2,000	2,096.6	(181.7)	694.8	(102.7)	91.5	2,088.9	(204.8)	772.5	(125.7)	92.8
2,500	2,623.2	(199.3)	773.3	(100.5)	90.0	2,616.7	(217.7)	861.4	(118.6)	91.6
3,000	3,130.1	(208.1)	840.4	(96.5)	91.8	3,120.5	(234.4)	935.6	(117.6)	92.6
Chao M_h						Chao M_{th}				
1,000	1,258.5	(180.8)	718.4	(163.8)	65.4	1,104.9	(158.8)	607.6	(164.3)	91.0
1,500	1,870.3	(213.7)	859.6	(156.4)	49.6	1,634.1	(186.0)	720.2	(162.4)	89.5
2,000	2,482.9	(261.6)	985.4	(163.0)	42.2	2,163.9	(225.8)	827.2	(171.6)	88.3
2,500	3,104.5	(276.4)	1,095.4	(152.7)	30.6	2,702.2	(239.1)	916.0	(162.4)	85.9
3,000	3,696.4	(297.3)	1,187.1	(150.9)	24.1	3,213.9	(256.7)	989.2	(167.9)	88.3

Table A.3.—Continued.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
			Lincoln-Petersen					Schumacher-Eschmeyer				
4.	$p_1=0.10, p_2=0.13,$	1,000	798.8	(104.2)	430.9	(91.1)	54.5	691.4	(73.5)	1,112.6	(490.1)	98.2
	$p_3=0.08, p_4=0.10,$	1,500	1,198.9	(132.8)	520.4	(84.8)	42.9	1,028.6	(87.4)	1,619.2	(569.1)	98.9
	$p_5=0.12$	2,000	1,587.4	(151.7)	594.0	(82.7)	28.3	1,362.8	(106.0)	2,036.3	(520.8)	99.0
	$[\bar{p}=0.106]$	2,500	1,997.3	(171.8)	669.4	(83.6)	24.8	1,707.7	(115.4)	2,536.8	(623.4)	99.6
		3,000	2,382.3	(180.3)	727.6	(80.3)	16.0	2,044.1	(120.3)	3,023.9	(629.4)	100
			Schnabel					Null M_0				
		1,000	600.1	(62.2)	844.0	(168.2)	4.0	1,056.1	(87.3)	350.1	(52.6)	90.6
		1,500	893.4	(73.3)	1,022.1	(156.2)	0.1	1,580.2	(107.9)	426.3	(52.8)	88.7
		2,000	1,187.5	(90.0)	1,169.6	(153.5)	0	2,096.4	(127.2)	486.4	(53.4)	86.3
		2,500	1,489.1	(97.3)	1,318.0	(156.4)	0	2,629.2	(140.5)	545.3	(51.9)	84.0
		3,000	1,782.2	(101.3)	1,435.6	(149.5)	0	3,147.3	(144.9)	594.8	(49.7)	84.6
			Darroch M_1					Chao M_1				
		1,000	1,048.1	(86.5)	346.4	(52.0)	92.3	1,044.1	(101.3)	395.8	(68.3)	93.0
		1,500	1,568.8	(107.0)	422.0	(52.4)	90.7	1,563.0	(122.1)	482.0	(66.6)	93.1
		2,000	2,081.8	(126.2)	481.6	(53.0)	88.3	2,079.6	(145.5)	553.3	(68.6)	90.4
		2,500	2,611.6	(139.2)	540.2	(51.4)	87.3	2,613.4	(158.9)	622.5	(66.1)	88.5
		3,000	3,126.4	(143.7)	589.2	(49.2)	88.1	3,125.2	(171.4)	677.8	(65.4)	89.1

Table A.3.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
	Chao M_h					Chao M_{th}				
1,000	1,216.8	(129.1)	505.0	(88.9)	53.1	1,084.7	(113.8)	421.4	(93.2)	88.4
1,500	1,815.1	(154.4)	611.1	(85.6)	36.3	1,612.7	(133.9)	506.8	(93.8)	86.4
2,000	2,410.5	(183.2)	699.3	(87.7)	26.6	2,139.0	(158.8)	579.8	(98.7)	83.5
2,500	3,027.0	(199.3)	785.3	(84.2)	14.7	2,683.0	(174.6)	651.5	(99.3)	79.4
3,000	3,616.6	(214.8)	853.9	(83.2)	9.3	3,202.8	(188.0)	707.3	(102.1)	80.8

Table A.4.—Simulation results for comparing closed-population abundance estimators (Lincoln-Petersen, Schumacher-Eschmeyer, Schnabel, Null M_0 , Darroch M_t , Chao M_t , Chao M_h , and Chao M_{th}). Mark-recapture data were simulated under model M_t for 4 open populations (i.e., permanent emigration of 10% of marked fish) with average capture probabilities ranging from 0.02 to 0.106 ($t=5$ capture occasions; 1,000 replications). % cov. = percent coverage for 95% confidence intervals; ne = no estimate.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Lincoln-Petersen							Schumacher-Eschmeyer					
1. $p_1=0.01, p_2=0.04,$ $p_3=0.02, p_4=0.02,$ $p_5=0.01$ [$\bar{p}=0.02$]	1,000	917.9	(539.3)	1,335.8	(374.6)	89.9	ne	ne	ne	ne	ne	
	1,500	1,523.3	(891.9)	2,580.3	(844.7)	96.0	ne	ne	ne	ne	ne	
	2,000	2,045.1	(1,205.1)	3,721.3	(1,501.9)	95.9	ne	ne	ne	ne	ne	
	2,500	2,676.9	(1,455.0)	4,962.4	(2,312.5)	96.7	ne	ne	ne	ne	ne	
	3,000	3,191.1	(1,597.0)	5,802.0	(2,979.0)	96.6	ne	ne	ne	ne	ne	
Schnabel estimator							Null M_0					
	1,000	ne	ne	ne	ne	ne	900.9	(148.9)	1,798.4	(376.6)	98.2	
	1,500	ne	ne	ne	ne	ne	1,371.5	(186.5)	2,189.7	(372.9)	98.3	
	2,000	ne	ne	ne	ne	ne	1,853.7	(204.3)	2,533.0	(346.0)	99.5	
	2,500	ne	ne	ne	ne	ne	2,344.1	(232.8)	2,851.4	(344.0)	98.8	
	3,000	2,285.0	(1,163.0)	10,334	(5,363.0)	80.0	2,809.8	(252.8)	3,099.9	(349.0)	99.2	
Darroch M_1							Chao M_1					
	1,000	879.4	(165.4)	1,822.1	(452.1)	97.4	1,095.3	(682.6)	3,043.4	(3,568.0)	93.8	
	1,500	1,340.6	(209.5)	2,215.5	(459.9)	97.5	1,682.2	(965.3)	3,670.4	(4,479.2)	94.4	
	2,000	1,812.9	(236.9)	2,559.2	(445.9)	98.1	2,148.4	(900.0)	3,668.9	(2,999.5)	96.2	
	2,500	2,302.6	(269.6)	2,894.4	(443.2)	98.1	2,800.8	(1,117.3)	4,288.0	(3,233.7)	95.6	
	3,000	2,757.8	(300.5)	3,142.4	(463.5)	98.4	3,307.3	(1,132.6)	4,480.2	(2,675.0)	95.5	

Table A.4.—Continued.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Chao M_h						Chao M_{th}				
		1,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		1,500	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		2,000	ne	ne	ne	ne	ne	ne	ne	ne	ne	ne
		2,500	4,384.0	(2,524.0)	7,970.0	(10,850)	82.0	3,845.7	(2,222.5)	7,025.5	(9,133.2)	89.7
		3,000	4,969.0	(2,088.0)	7,526.0	(5,866.0)	80.0	4,371.7	(1,884.8)	6,708.6	(5,238.4)	89.2
		Lincoln-Petersen						Schumacher-Eschmeyer				
2.	$p_1=0.03, p_2=0.03,$	1,000	980.5	(324.6)	1,351.4	(718.9)	93.8	ne	ne	ne	ne	ne
	$p_3=0.05, p_4=0.05,$	1,500	1,481.8	(378.0)	1,604.2	(696.8)	95.7	ne	ne	ne	ne	ne
	$p_5=0.07$	2,000	1,958.2	(444.6)	1,794.7	(656.3)	93.5	ne	ne	ne	ne	ne
	$[\bar{p}=0.046]$	2,500	2,479.3	(485.3)	2,009.5	(610.9)	96.0	ne	ne	ne	ne	ne
		3,000	2,950.8	(532.2)	2,167.0	(610.3)	94.9	ne	ne	ne	ne	ne
		Schnabel						Null M_0				
		1,000	666.6	(208.0)	2,203.1	(1,145.4)	73.1	1,172.6	(278.3)	1,089.0	(430.9)	93.4
		1,500	966.8	(210.4)	2,625.4	(1,108.4)	54.1	1,752.1	(323.9)	1,295.7	(402.8)	90.6
		2,000	1,252.6	(235.8)	2,946.7	(1,047.2)	39.0	2,289.7	(373.5)	1,441.7	(385.5)	89.3
		2,500	1,575.3	(270.5)	3,298.2	(979.9)	24.6	2,895.8	(429.8)	1,627.7	(398.9)	86.3
		3,000	1,868.5	(282.5)	3,562.6	(976.1)	15.7	3,438.6	(451.0)	1,752.9	(389.0)	86.1

Table A.4.—Continued.

	<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
		Darroch M_t					Chao M_t				
	1,000	1,140.4	(272.9)	1,055.9	(423.6)	94.0	1,096.2	(281.2)	1,056.7	(456.8)	94.6
	1,500	1,703.6	(313.5)	1,255.2	(390.4)	93.3	1,652.2	(314.1)	1,274.5	(400.2)	94.6
	2,000	2,229.4	(363.9)	1,398.9	(376.1)	91.5	2,183.4	(377.2)	1,446.1	(404.5)	93.2
	2,500	2,818.9	(418.4)	1,578.8	(387.7)	88.9	2,779.8	(427.4)	1,648.7	(403.1)	91.4
	3,000	3,350.6	(439.3)	1,702.1	(379.5)	90.2	3,305.6	(462.5)	1,780.3	(408.6)	92.4
		Chao M_h					Chao M_{th}				
	1,000	1,434.8	(413.7)	1,502.2	(726.1)	74.9	1,244.8	(358.5)	1,295.8	(646.7)	91.0
	1,500	2,117.6	(440.9)	1,745.3	(582.6)	64.1	1,828.2	(384.6)	1,508.5	(541.2)	89.3
	2,000	2,766.7	(513.3)	1,944.2	(565.6)	55.1	2,382.8	(446.1)	1,676.5	(535.6)	86.5
	2,500	3,505.5	(573.1)	2,196.3	(551.5)	43.0	3,014.2	(497.1)	1,898.0	(523.6)	80.5
	3,000	4,148.5	(619.9)	2,355.0	(556.5)	37.4	3,560.6	(544.0)	2,023.9	(537.0)	82.9
		Lincoln-Petersen					Schumacher-Eschmeyer				
3. $p_1=0.08, p_2=0.07,$	1,000	919.9	(178.7)	743.8	(233.5)	93.4	783.0	(122.0)	1,116.0	(13,871)	96.0
$p_3=0.10, p_4=0.06,$	1,500	1,372.9	(197.0)	884.1	(198.8)	91.3	1,155.0	(135.0)	2,161.0	(1,579.0)	99.0
$p_5=0.08$	2,000	1,831.8	(240.4)	985.7	(213.0)	87.6	1,524.0	(165.0)	2,600.0	(1,377.0)	99.0
$[\bar{p}=0.078]$	2,500	2,297.0	(267.5)	1,084.8	(192.9)	87.6	1,902.0	(181.0)	3,221.0	(1,470.0)	100
	3,000	2,743.0	(284.6)	1,182.1	(183.5)	85.9	2,264.0	(188.0)	3,693.0	(1,264.0)	100

Table A.4.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Schnabel						Null M_0				
1,000	669.8	(98.3)	1,448.8	(440.6)	7.7	1,117.3	(138.8)	553.1	(118.0)	87.2
1,500	994.7	(112.3)	1,722.9	(376.9)	0.9	1,671.6	(167.2)	669.2	(115.2)	83.8
2,000	1,317.7	(137.2)	1,926.3	(404.7)	0.2	2,214.8	(198.6)	764.1	(116.0)	81.2
2,500	1,644.5	(150.8)	2,123.3	(374.1)	0	2,771.5	(219.2)	850.7	(114.7)	74.9
3,000	1,959.7	(156.9)	2,317.5	(350.0)	0	3,304.6	(230.5)	923.4	(110.6)	73.6
Darroch M_t						Chao M_t				
1,000	1,107.3	(137.3)	546.9	(116.6)	88.3	1,097.4	(149.5)	599.3	(136.2)	92.3
1,500	1,657.6	(165.5)	662.2	(114.0)	85.6	1,643.2	(180.1)	726.0	(132.8)	88.5
2,000	2,197.4	(196.6)	756.6	(114.8)	83.4	2,187.8	(220.0)	836.3	(138.5)	86.3
2,500	2,749.7	(217.3)	842.3	(113.7)	76.9	2,741.9	(237.9)	933.5	(133.5)	82.3
3,000	3,279.4	(228.4)	914.6	(109.5)	77.3	3,271.9	(254.9)	1,015.0	(131.5)	81.6
Chao M_h						Chao M_{th}				
1,000	1,323.4	(195.3)	779.3	(182.6)	52.9	1,158.0	(171.1)	658.4	(182.3)	84.5
1,500	1,967.3	(232.3)	932.8	(174.2)	35.4	1,713.9	(200.4)	781.3	(177.9)	80.2
2,000	2,610.3	(281.5)	1,068.2	(179.8)	25.9	2,267.8	(242.1)	898.0	(186.5)	78.6
2,500	3,265.2	(302.8)	1,188.3	(172.1)	13.2	2,834.4	(261.2)	995.7	(183.3)	72.7
3,000	3,890.1	(323.8)	1,289.1	(168.9)	9.4	3,372.7	(277.9)	1,076.8	(185.7)	71.5

Table A.4.—Continued.

		<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
Lincoln-Petersen							Schumacher-Eschmeyer					
4.	$p_1=0.10, p_2=0.13,$	1,000	849.9	(112.8)	477.1	(103.9)	73.5	728.7	(79.3)	1,189.1	(570.4)	98.7
	$p_3=0.08, p_4=0.10,$	1,500	1,273.8	(144.6)	569.6	(95.8)	64.5	1,083.0	(95.8)	1,715.1	(626.9)	99.6
	$p_5=0.12$	2,000	1,687.5	(165.7)	650.6	(93.4)	55.0	1,435.2	(115.5)	2,149.2	(570.1)	99.5
	$[\bar{p}=0.106]$	2,500	2,123.9	(189.0)	733.7	(95.3)	49.9	1,798.4	(126.4)	2,688.9	(689.1)	100
		3,000	2,532.5	(197.0)	796.9	(90.8)	40.9	2,151.5	(131.8)	3,190.7	(697.1)	100
Schnabel							Null M_0					
		1,000	631.5	(66.8)	925.6	(191.2)	1.3	1,104.4	(93.6)	382.0	(58.4)	80.6
		1,500	939.5	(80.7)	1,108.6	(175.6)	0	1,650.8	(118.7)	464.2	(60.1)	73.9
		2,000	1,249.0	(97.7)	1,269.1	(173.0)	0	2,191.1	(138.7)	530.2	(60.3)	67.5
		2,500	1,566.0	(106.2)	1,431.5	(177.5)	0	2,747.4	(153.4)	594.2	(58.8)	58.5
		3,000	1,873.7	(110.6)	1,557.7	(168.1)	0	3,288.3	(159.0)	647.9	(56.2)	54.5
Darroch M_1							Chao M_1					
		1,000	1,095.9	(92.7)	378.0	(57.9)	83.6	1,092.2	(108.6)	430.1	(75.7)	86.9
		1,500	1,638.7	(117.6)	459.6	(59.5)	76.6	1,633.7	(133.6)	522.9	(74.7)	82.7
		2,000	2,175.6	(137.5)	525.0	(59.8)	71.8	2,173.7	(156.7)	600.3	(75.6)	78.0
		2,500	2,728.9	(152.1)	588.6	(58.3)	63.7	2,731.4	(172.3)	675.2	(73.6)	70.1
		3,000	3,266.2	(157.6)	641.9	(55.7)	60.3	3,267.6	(187.0)	735.6	(73.2)	67.9

Table A.4.—Continued.

<i>N</i>	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.	
	Chao <i>M_h</i>						Chao <i>M_{th}</i>				
1,000	1,279.0	(138.8)	549.6	(98.6)	34.5	1,135.9	(122.7)	459.6	(104.1)	78.0	
1,500	1,905.7	(169.3)	663.8	(96.2)	19.1	1,687.4	(146.8)	551.6	(104.9)	71.8	
2,000	2,530.5	(197.7)	759.4	(96.8)	11.3	2,237.2	(171.1)	631.6	(107.7)	65.6	
2,500	3,177.1	(216.6)	852.4	(93.9)	4.7	2,804.9	(189.1)	708.2	(111.2)	55.6	
3,000	3,797.5	(234.9)	927.6	(93.2)	2.1	3,350.9	(205.8)	773.0	(113.2)	53.3	

Table A.5.—Mark-recapture statistics for Henrys Fork age-0 trout data for Box Canyon, Last Chance, and Harriman State Park sample areas. Sample areas were 100 m long and extended bank-to-bank. T = number of capture occasions; M_{t+1} = number of individual trout captured at least once; $n(T)$ = total number of captures; $f(t)$ = number of trout captured t times (i.e., capture frequencies); $z(t)$ = number of trout captured only on capture occasion t ; $\hat{p}_t$ = estimated capture probability for capture occasion t ; LB and UB = lower and upper bounds of $\log_e$ -based 95% confidence interval; Capt. eff. = capture efficiency (i.e., $\{n(T)/\hat{N}\} \cdot 100$ (%)); and Recap. rate = recapture rate (i.e., $\{ \{f(2)+f(3) \cdot 2 + f(4) \cdot 3 + f(5) \cdot 4\} / n(T) \} \cdot 100$ (%)).

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)					eff.	rate
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Box Canyon—sample area 1—Summer														
1995	3	182	186	178	4	0				2,264	(983.6)	[1,047—5,200]	8.2%	2.2%
				70	46	62								
				0.03	0.02	0.03			0.027					
1996	5	420	454	389	28	3	0	0		2,497	(442.0)	[1,796—3,557]	18.2%	7.5%
				88	89	80	71	61						
				0.04	0.04	0.04	0.03	0.03	0.036					
1997	5	313	331	295	18	0	0	0		2,126	(468.4)	[1,415—3,296]	15.6%	5.4%
				74	55	64	38	64						
				0.04	0.03	0.03	0.02	0.03	0.03					

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
				z(1)	z(2)	z(3)	z(4)	z(5)						
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Box Canyon—sample area 2—Summer														
1995	3	244	259	230	13	1				1,496	(375.0)	[950—2,468]	17.3%	5.8%
				78	86	66								
				0.06	0.07	0.05			0.06					
1996	3	236	243	230	5	1				3,117	(1,237.6)	[1,522—6,689]	7.8%	2.9%
				98	69	63								
				0.03	0.02	0.02			0.023					
1997	5	258	267	249	9	0	0	0		2,717	(839.3)	[1,541—4,971]	9.8%	3.4%
				67	41	50	43	48						
				0.03	0.02	0.02	0.02	0.02	0.022					

Table A.5.—Continued.

				f(1)	f(2)	f(3)	f(4)	f(5)							
				z(1)	z(2)	z(3)	z(4)	z(5)						Capt.	Recap.
Year	T	Mt+1	n(T)	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	eff.	rate	
Last Chance—sample area 1—Summer															
1995	4	294	310	278	16	0	0			1,988	(460.2)	[1,298—3,151]	15.6%	5.2%	
				65	86	61	66								
				0.04	0.05	0.04	0.04		0.043						
1996	5	493	506	481	11	1	0	0		8,175	(2,327.2)	[4,791—14,223]	6.2%	2.6%	
				112	82	103	82	102							
				0.01	0.01	0.01	0.01	0.01	0.01						
1997	5	373	386	361	11	1	0	0		4,668	(1,321.7)	[2,756—8,117]	8.3%	3.4%	
				102	70	60	62	67							
				0.02	0.02	0.01	0.01	0.02	0.016						

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
				z(1)	z(2)	z(3)	z(4)	z(5)						
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Last Chance—sample area 2—Summer														
1995	3	145	146	144	1	0				3,496	(2,435.7)	[1,080—12,155]	4.2%	0.7%
				49	62	33								
				0.01	0.02	0.01			0.013					
1996	4	276	287	266	9	1	0			2,919	(897.9)	[1,659—5,327]	9.8%	3.8%
				77	68	57	64							
				0.03	0.02	0.02	0.02		0.018					
1997	5	202	207	198	3	1	0	0		4,075	(2,014.2)	[1,687—10,306]	5.1%	2.4%
				33	34	53	31	47						
				0.01	0.01	0.01	0.01	0.01	0.01					

Table A.5.—Continued.

				f(1)	f(2)	f(3)	f(4)	f(5)						
				z(1)	z(2)	z(3)	z(4)	z(5)					Capt.	Recap.
Year	T	Mt+1	n(T)	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	eff.	rate
Harriman State Park—Summer														
1995														
1996	5	99	102	96	3	0	0	0		1,008	(492.0)	[436—2,553]	10.1%	2.9%
				17	17	14	21	27						
				0.02	0.02	0.01	0.02	0.03	0.02					
1997	5	170	178	162	8	0	0	0		1,252	(401.1)	[706—2.356]	14.2%	4.5%
				19	22	36	20	65						
				0.02	0.02	0.03	0.02	0.06	0.03					

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)					eff.	rate
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Box Canyon—sample area 1—Autumn														
1995	5	287	322	256	27	4	0	0		1,205	(210.3)	[877—1,716]	26.7%	10.9%
				69	52	60	49	26						
				0.07	0.06	0.06	0.05	0.03	0.054					
1996	5	542	598	491	46	5	0	0		2,555	(348.5)	[1,980—3,361]	23.4%	9.4%
				79	119	141	77	75						
				0.04	0.05	0.07	0.04	0.03	0.046					
1997	4	365	399	334	28	3	0			1,716	(294.4)	[1,251—2,425]	23.3%	8.5%
				141	88	59	46							
				0.09	0.06	0.05	0.03		0.058					

Table A.5.—Continued.

				f(1)	f(2)	f(3)	f(4)	f(5)						Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)							
Year	T	Mt+1	n(T)	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	eff.	rate	
1998	5	495	638	376	98	18	3	0		1,022	(79.7)	[888—1,202]	62.4%	22.4%	
				148	89	64	50	25							
				0.21	0.16	0.12	0.09	0.05	0.126						

Table A.5.—Continued.

				f(1)	f(2)	f(3)	f(4)	f(5)					Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)						
Year	T	Mt+1	n(T)	$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	eff.	rate
Box Canyon—sample area 2—Autumn														
1995														
1996	5	472	505	441	29	2	0	0		3,031	(529.6)	[2,185—4,294]	16.7%	6.5%
				126	88	74	85	68						
				0.05	0.03	0.03	0.03	0.03	0.034					
1997	4	336	364	308	28	0	0			1,514	(259.5)	[1,105—2,141]	24.0%	7.7%
				120	78	55	55							
				0.09	0.06	0.04	0.05		0.06					

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
				z(1)	z(2)	z(3)	z(4)	z(5)					
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$	$\hat{p}_{mean}$				
1998	5	278	322	235	42	1	0	0	778	(103.0)	[614—1,023]	41.4%	13.7%
				61	69	40	34	31					
				0.11	0.12	0.07	0.06	0.06	0.084				

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)					eff.	rate
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Last Chance—sample area 1—Autumn														
1995	5	578	642	517	58	3	0	0		2,383	(286.8)	[1,903—3,037]	26.9%	10.0%
				128	93	107	93	96						
				0.07	0.05	0.05	0.05	0.05	0.054					
1996	5	848	916	783	62	3	0	0		4,705	(562.3)	[3,751—5,972]	19.5%	7.4%
				201	181	146	136	119						
				0.05	0.04	0.04	0.03	0.03	0.038					
1997	4	479	502	457	21	1	0			4,005	(823.4)	[2,725—6,018]	12.5%	4.6%
				142	111	116	88							
				0.04	0.03	0.03	0.02		0.03					

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)					eff.	rate
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Last Chance—sample area 2—Autumn														
1995	5	370	395	345	25	0	0	0		2,183	(407.9)	[1,543—3,172]	18.1%	6.3%
				84	80	76	50	55						
				0.04	0.04	0.04	0.03	0.03	0.036					
1996	5	499	536	464	33	2	0	0		3,024	(495.0)	[2,225—4,193]	17.7%	6.9%
				108	75	93	96	92						
				0.04	0.03	0.03	0.04	0.04	0.036					
1997	4	312	326	298	14	0	0			2,505	(622.7)	[1,583—4,097]	13.0%	4.3%
				99	68	66	65							
				0.04	0.03	0.03	0.03		0.033					

Table A.5.—Continued.

Year	T	Mt+1	n(T)	f(1)	f(2)	f(3)	f(4)	f(5)	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt.	Recap.
				z(1)	z(2)	z(3)	z(4)	z(5)					eff.	rate
				$\hat{p}_1$	$\hat{p}_2$	$\hat{p}_3$	$\hat{p}_4$	$\hat{p}_5$						
Harriman State Park—Autumn														
1995	4	226	242	211	14	1	0			1,329	(324.5)	[853—2,165]	18.2%	6.6%
				56	61	38	56							
				0.05	0.05	0.03	0.05		0.045					
1996														
1997	3	228	240	216	12	0				1,380	(358.1)	[864—2,317]	17.4%	5.0%
				97	70	49								
				0.08	0.06	0.04			0.045					

Table A.6.—Bias and interval statistics for three-pass estimates (normal and $\log_e$ 95% confidence intervals), simple linear regression (SLR) model predictions (normal and $\log_e$ 95% prediction intervals), and mean capture probability (MCP) model predictions (normal and log-odds 95% prediction intervals) for 10 groups of known size (n) ranging from 10 to 100 (1,000 replications). $\bar{n}$ = mean estimated size of group; LB and UB = lower and upper bounds of intervals.

n	$\bar{n}$	Mean	SE	Percent	Mean	Mean	Mean	SE
		bias	bias	coverage	LB	UB	interval length	interval length

Three-pass estimates (normal 95% confidence intervals)

10	9.8	-0.2	0.6	96.4	8.3	11.3	3.0	2.9
20	19.6	-0.4	1.3	94.5	17.5	22.0	4.6	5.9
30	29.6	-0.4	2.1	94.2	27.0	32.7	5.7	9.3
40	39.4	-0.6	1.7	93.8	36.7	42.5	5.8	6.1
50	49.5	-0.5	3.7	94.5	46.5	53.4	6.9	11.6
60	59.2	-0.8	2.1	94.6	56.0	63.0	7.1	6.7
70	69.3	-0.7	2.6	94.7	65.4	73.7	8.3	9.4
80	79.3	-0.7	2.8	95.6	75.1	84.1	8.9	10.9
90	89.2	-0.8	3.8	93.3	84.7	94.2	9.5	13.9
100	99.3	-0.7	3.8	94.5	94.9	104.3	9.3	12.6

Table A.6.—Continued.

<i>n</i>	$\bar{n}$	Mean	SE	Percent	Mean	Mean	Mean	SE
		bias	bias	coverage	LB	UB	interval length	interval length

Three-pass estimates (log_e 95% confidence intervals)

10	9.8	-0.2	0.6	93.5	9.7	11.5	1.9	4.8
20	19.6	-0.4	1.3	92.0	19.4	23.8	4.4	9.8
30	29.6	-0.4	2.1	93.0	29.1	35.4	6.3	20.3
40	39.4	-0.6	1.7	92.1	38.9	44.9	5.9	8.6
50	49.5	-0.5	3.7	93.2	48.7	56.8	8.1	36.0
60	59.2	-0.8	2.1	93.7	58.4	66.1	7.6	8.7
70	70.2	-0.8	2.5	95.3	69.1	78.2	9.2	11.2
80	79.3	-0.7	2.8	94.3	77.9	88.0	10.1	13.2
90	89.2	-0.8	3.8	95.4	87.6	98.1	10.6	16.8
100	99.3	-0.7	3.8	94.2	97.7	108.0	10.3	14.9

SLR model predictions (normal 95% prediction intervals)

10	9.2	-0.8	2.3	99.4	3.9	17.9	14.0	1.8
20	18.9	-1.1	3.8	97.5	10.7	30.0	19.3	1.9

Table A.6.—Continued.

<i>n</i>	$\bar{\hat{n}}$	Mean	SE	Percent	Mean	Mean	Mean	SE
		bias	bias	coverage	LB	UB	interval length	interval length
30	28.7	-1.3	5.4	95.3	18.5	42.0	23.5	2.1
40	38.5	-1.5	6.7	94.9	26.6	53.5	26.9	2.3
50	48.1	-1.9	8.1	94.5	34.7	64.6	29.9	2.5
60	57.6	-2.4	9.4	91.7	42.8	75.4	32.6	2.7
70	66.5	-3.5	11.2	88.4	50.5	85.7	35.1	3.1
80	76.1	-3.9	12.7	87.5	58.8	96.4	37.6	3.3
90	85.9	-4.1	14.4	84.8	67.5	107.5	40.0	3.6
100	96.4	-3.6	14.8	85.9	76.8	119.2	42.4	3.5

SLR model predictions (log_e 95% prediction intervals)

10	9.2	-0.8	2.3	100	7.4	31.9	24.4	1.0
20	18.9	-1.1	3.8	98.4	15.1	42.8	27.7	1.1
30	28.7	-1.3	5.4	95.7	23.5	54.3	30.9	1.8
40	38.5	-1.5	6.7	96.1	31.8	65.3	33.5	1.8
50	48.1	-1.9	8.1	93.4	40.3	76.2	36.0	2.1
60	57.6	-2.4	9.4	94.3	48.6	86.9	38.4	2.4

Table A.6.—Continued.

<i>n</i>	$\bar{n}$	Mean	SE	Percent	Mean	Mean	Mean	SE
		bias	bias	coverage	LB	UB	interval length	interval length
70	66.5	-3.5	11.2	89.6	56.5	97.0	40.5	2.7
80	76.1	-3.9	12.7	90.2	65.0	107.7	42.6	2.9
90	85.9	-4.1	14.4	85.6	73.8	118.6	44.8	3.2
100	96.4	-3.6	14.8	87.7	83.2	130.3	47.0	3.1
MCP model predictions (normal 95% prediction intervals)								
10	9.7	-0.3	2.2	94.8	5.8	13.7	8.0	0.9
20	19.2	-0.8	3.8	85.3	13.9	24.6	10.7	1.0
30	29.1	-0.9	5.4	77.5	22.7	35.5	12.8	1.2
40	38.8	-1.2	6.7	78.8	31.5	46.1	14.6	1.3
50	48.4	-1.6	8.0	75.3	40.3	56.6	16.3	1.4
60	57.9	-2.1	9.4	70.6	49.1	66.7	17.7	1.4
70	66.9	-3.1	11.2	62.1	57.4	76.3	18.9	1.6
80	76.4	-3.6	12.7	59.6	66.3	86.5	20.2	1.8
90	86.2	-3.8	14.4	55.4	75.5	96.9	21.4	1.9
100	96.7	-3.3	14.9	55.4	85.4	108.1	22.7	1.8

Table A.6.—Continued.

							Mean	SE
		Mean	SE	Percent	Mean	Mean	interval	interval
<i>n</i>	$\bar{\hat{n}}$	bias	bias	coverage	LB	UB	length	length
MCP model predictions (log-odds 95% prediction intervals)								
10	9.7	-0.3	2.2	94.8	7.4	15.9	8.4	1.7
20	19.2	-0.8	3.8	93.8	15.5	31.2	15.7	2.8
30	29.1	-0.9	5.4	92.4	23.7	47.0	23.3	4.1
40	38.8	-1.2	6.7	94.0	31.7	62.5	30.8	5.1
50	48.4	-1.6	8.0	94.2	39.7	77.9	38.1	6.2
60	57.9	-2.1	9.4	96.3	47.6	92.9	45.3	7.2
70	66.9	-3.1	11.2	95.7	55.0	107.3	52.3	8.6
80	76.4	-3.6	12.7	95.7	62.9	122.4	59.5	9.8
90	86.2	-3.8	14.4	95.5	71.1	138.1	67.1	11.0
100	96.7	-3.3	14.9	95.6	79.8	154.9	75.1	11.4

Table A.7.—Estimated total abundance of age-0 rainbow trout for five river sections in summer (1995-1997), autumn (1995-1997), and spring (1996-1998). Captures is the total number of age-0 trout used to obtain a mark-recapture abundance estimate and the number of trout captured in the first pass for three-pass removal estimates. Effort is the number of kilometers sampled by electrofishing for mark-recapture and the first pass for three-pass removal. LB and UB = lower and upper bounds of a 95% confidence interval. NE = no estimate.

Year	$\hat{N}$	[LB—UB]	Captures	Effort
Summer				
Box Canyon				
1995	48,730	[27,959—69,501]	500	3.9 km
1996	74,488	[55,038—93,937]	842	5.2 km
1997	64,923	[47,954—81,893]	715	6.4 km
Last Chance				
1995	109,680	[48,100—171,260]	456	5.3 km
1996	221,880	[19,870—423,890]	793	6.8 km
1997	174,860	[143,890—205,830]	593	7.6 km
Harriman State Park				
1995	NE	NE	72	2.1 km
1996	10,080	[7,030—13,130]	102	3.2 km
1997	12,520	[10,033—15,006]	178	3.2 km

Table A.7.—Continued.

Year	$\hat{N}$	[LB—UB]	Captures	Effort
Harriman East				
1995	NE	NE	19	3.0 km
1996	NE	NE	51	9.0 km
1997	NE	NE	1	9.0 km
Pinehaven-Riverside				
1995	NE	NE	150	15.1 km
1996	742	[243—2,603]	60	30.0 km
1997	NE	NE	6	30.0 km
Autumn				
Box Canyon				
1995	34,353	[29,781—38,924]	489	3.3 km
1996	81,165	[61,858—100,471]	1,431	6.5 km
1997	45,723	[37,335—54,110]	944	5.2 km

Table A.7.—Continued.

Year	$\hat{N}$	[LB—UB]	Captures	Effort
Last Chance				
1995	91,320	[82,520—100,120]	1,037	7.6 km
1996	154,580	[90,020—219,140]	1,452	7.6 km
1997	130,800	[72,180—188,220]	828	6.1 km
Harriman State Park				
1995	13,290	[11,278—15,302]	242	2.6 km
1996	13,130	[9,596—16,664]	143	1.9 km
1997	13,800	[11,580—16,020]	240	1.9 km
Harriman East				
1995	14,957	[4,532—27,194]	344	12.0 km
1996	2,752	[1,228—6,881]	236	12.0 km
1997	9,820	[4,027—24,734]	348	18.0 km
Pinehaven-Riverside				
1995	NE	NE	42	3.0 km
1996	NE	NE	59	12.0 km
1997	NE	NE	91	18.0 km

Table A.7.—Continued.

Year	$\hat{N}$	[LB—UB]	Captures	Effort
Spring				
Box Canyon				
1996	7,903	[5,608—10,197]	188	0.25 km
1997	14,788	[11,835—17,740]	684	0.55 km
1998	9,730	[7,372—12,082]	652	0.71 km
Last Chance				
1996	NE	NE	31	2.3 km
1997	NE	NE	18	1.2 km
1998	NE	NE	63	0.6 km
Harriman State Park				
1996	NE	NE	5	15.6 km
1997	NE	NE	1	12.0 km
1998	NE	NE	8	15.0 km

Table A.7.—Continued.

Year	$\hat{N}$	[LB—UB]	Captures	Effort
Harriman East				
1996	NE	NE	2	15.0 km
1997	NE	NE	0	12.0 km
1998	NE	NE	4	15.0 km
Pinehaven-Riverside				
1996	NE	NE	104	30.4 km
1997	3,538	[1,303—10,154]	164	30.3 km
1998	4,100	[1,697—10,372]	205	30.0 km

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