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## Estimating Abundances of Age-0 Rainbow Trout by Mark–Recapture in a Medium-Sized River

MATTHEW G. MITRO\*<sup>1</sup> AND ALEXANDER V. ZALE

Montana Cooperative Fishery Research Unit, U.S. Geological Survey,  
Department of Ecology, Montana State University,  
Bozeman, Montana 59717, USA

**Abstract.**—We developed and evaluated a sampling methodology to obtain mark–recapture data to estimate abundances of age-0 rainbow trout *Oncorhynchus mykiss* in 70–125-m-wide reaches of the Henrys Fork of the Snake River, Idaho. Sampling by electrofishing was concentrated in sample areas that were 100 m long and extended from bank to bank; these areas were electrofished 3–5 times within periods of 3–17 d. Adjacent 50-m-long areas upstream and downstream were sampled to quantify movements out of the 100-m sample areas. We evaluated assumptions—closed population and equal catchability—using the field data, and we used simulation to identify the most appropriate abundance estimator for sparse data. Both closed and open population abundance estimators were evaluated. Most trout (84%) were recaptured in the area where they were marked, but about 10% had moved downstream and about 6% were recaptured upstream. Multistrata model analyses confirmed that apparent mortality rates, and hence movement rates, were low. The Chao  $M_i$  estimator, which assumes that capture probabilities vary with capture occasion, performed best for simulated closed populations; bias was minimal and interval coverage was near or at the nominal level. This estimator was also robust to minor violations of the closure assumption; performance was better for larger closure violations when capture probabilities were smaller. Application of the Chao  $M_i$  estimator to our field data resulted in a median capture probability of 0.036, a median capture efficiency of 16.7%, and a median recapture rate of 5.4%. Average abundance estimates in the sample areas provided indices of abundance and extrapolated estimates provided total abundance estimates for river sections 1–4 km long. Small capture probabilities and large confidence intervals made it possible to detect only relatively large changes in abundance, but this level of discrimination was sufficient to satisfy management needs.

The juvenile component of a salmonid population is inherently difficult to sample and quantify in large river systems and over large spatial scales. Estimates of juvenile salmonid abundance in such rivers are often required to quantify production and survival and to determine the effects of management on juvenile salmonid recruitment. 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 wider rivers is more difficult. Small capture probabilities and large abundances are often encountered in wider rivers, negating the use of the removal method for estimating abundance (i.e., if capture probabilities are less than 0.2 and abun-

dances are greater than 3,000; White et al. 1982). Use of mark–recapture is therefore necessitated. However, capture probabilities may be too small to get precise abundance estimates when sampling long reaches (e.g., >1 km) of wider rivers by electrofishing. For example, sampling a group of 20,000 juvenile trout in a 1-km section of a river 100 m wide would result in very small capture probabilities (e.g., <0.01) and possibly no trout recaptured.

The problem with estimating abundance of a large group of juvenile salmonids sampled in a long reach of a wide river (e.g., 4 km long) can be addressed by intensively sampling smaller areas (e.g., 100 m long) and extrapolating results to the river as a whole. A greater proportion of juvenile salmonids could be marked and thus recaptured in such areas than would generally be feasible in longer river sections.

The assumptions of a closed population and equal catchability of individual fish are important to consider when developing and evaluating a sampling methodology. The use of blocking nets across a wide river may be impractical, necessitating the use of physically open sample areas. However, contingent on a short study period, phys-

\* Corresponding author: mitro.matt@epa.gov

<sup>1</sup> Present address: U.S. Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Atlantic Ecology Division, 27 Tarzwell Drive, Narragansett, Rhode Island 02882, USA.

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ically open populations can sometimes be treated as closed (Pollock 1982). If juvenile salmonids restrict their activities to a defined area, sample areas may be considered biologically closed (Bohlin et al. 1989). However, empirical data should be collected to test the hypothesis of population closure and to quantify the extent to which the population closure assumption was violated should the hypothesis be rejected.

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. These include the Lincoln–Peterson estimator for two capture occasions and the Schumacher–Eschmeyer and Schnabel estimators for multiple capture occasions (Ricker 1975; Seber 1992). If the closure assumption is not satisfied, the Jolly–Seber estimator for open populations can be used (Jolly 1965; Seber 1965; Ricker 1975). There is also a set of closed-population abundance estimators for multiple capture occasions included in program CAPTURE (Otis et al. 1978; White et al. 1982; Rexstad and Burnham 1991). This set includes estimators for models that are parameterized for various violations of the equal catchability assumption.

We were interested in estimating age-0 rainbow trout *Oncorhynchus mykiss* abundance in an area of the Henrys Fork of the Snake River, Idaho, which is about 25 km in length and varies from about 50–150 m in width. A sampling methodology was needed to improve capture efficiency and recapture rate, hence improving estimates of age-0 rainbow trout abundance in the Henrys Fork and management capability of the river's trout fishery. We developed and evaluated mark–recapture sampling methods to estimate trout abundance; we used multiple sample areas that were 100 m long and extended from bank to bank. Our objectives were to (1) evaluate the sample area approach and related assumptions of population closure and equal catchability, and (2) identify the most appropriate estimator—that is, one that minimizes estimate bias and maximizes precision.

### Study Site

The Henrys Fork, a medium-sized river, had a mean annual discharge of 24.3 m<sup>3</sup>/s (range, 6.9–78.4 m<sup>3</sup>/s) at Island Park Dam (elevation, 1,897 m) during 1995–1997. The Henrys Fork has a drainage area of 1,246 km<sup>2</sup>. The Buffalo River joins the Henrys Fork about 0.6 km downstream of Island Park Dam (Figure 1). The Buffalo River is spring-fed and has a relatively constant dis-

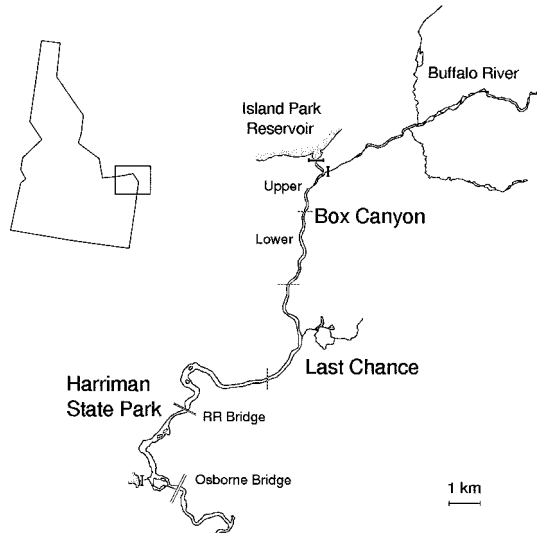


FIGURE 1.—Sections of the Henrys Fork, Idaho, downstream of Island Park Reservoir and the Buffalo River used to estimate abundance of age-0 rainbow trout; sections are Box Canyon (upper and lower), Last Chance, and Harriman State Park. Single solid lines with end-caps = dams, double parallel lines = bridges, and dashed lines = river section boundaries.

charge of 6 m<sup>3</sup>/s. We sampled juvenile rainbow trout from the Henrys Fork in three sections between its confluence with the Buffalo River and Osborne Bridge: (1) Box Canyon (length = 4 km, mean width = 70 m), (2) Last Chance (length = 4 km, mean width = 95 m), and (3) Harriman State Park (length = 8 km, mean width = 125 m; Figure 1). Box Canyon was further divided into upper (1.5 km) and lower sections (2.5 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 its 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 (>1 m deep), and large, uneven substrate. The methods described in this article were not used in upper Box Canyon. 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; it 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*

We obtained 29 mark–recapture data sets by intensively resampling multiple sample areas in each river section on three to five capture occasions lasting 3–17 d in summer (August) and autumn (October) 1995–1998. Captured trout were given a partial fin clip—a batch mark unique to each capture occasion. Thus, we could determine the capture history of each captured trout from the combination of fin clips. Fin clips were minimal in size to allow mark recognition within the summer or autumn sampling periods and regeneration thereafter (Gowan and Fausch 1996). 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. We 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, which 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. We sampled two sample areas in lower Box Canyon, two in Last Chance, and one in Harriman State Park. The same sample areas were used in each season and year.

In each 100-m sample area, juvenile rainbow trout along eight transects (about equally spaced) perpendicular to the current were collected 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*

We used length-frequency histograms to identify age-0 rainbow trout based on length. We also read scales to aid in the separation of age-0 and

age-1 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. We 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 from scales 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*

We compared the characteristics of different abundance estimators to select an appropriate estimator of age-0 rainbow trout abundance for sample areas. A candidate list of estimators included closed-population and open-population abundance estimators. Closed-population estimators included the following estimators in the computer program CAPTURE: Null  $M_o$ , Darroch  $M_p$ , Chao  $M_p$ , Chao  $M_h$ , and Chao  $M_{th}$  (Otis et al. 1978; White et al. 1982; Chao 1989; Rexstad and Burnham 1991; Chao et al. 1992). The Null estimator for model  $M_o$  assumes a constant capture probability for each fish on all capture occasions. The Darroch and Chao estimators for model  $M_i$  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; Seber 1992). 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 as-

sume a constant capture probability for each fish. No assumption is made about a constant capture probability with time. The Lincoln–Petersen estimator is 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 (Jolly 1965; Seber 1965; Ricker 1975), which estimates abundance for capture occasions 2, 3, and 4 for a data set including 5 capture occasions.

#### *Model and Estimator Selection*

We evaluated the utility of the model selection procedure in CAPTURE for analyzing juvenile rainbow trout mark–recapture data from the Henrys Fork. We 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 less than 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 five population sizes ( $N = 1,000, 1,500, 2,000, 2,500$ , and  $3,000$ ) and 1,000 replications. Capture probabilities and population sizes used in all simulations were based on 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  $M_t$ ) and does not consider the Lincoln–Petersen, Schumacher–Eschmeyer, Schnabel, or Jolly–Seber estimators. We 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 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 random number  $p_{\text{unif}}$  was selected from the uniform (0, 1) distribution for each individual in a population on each capture occasion. If  $p_{\text{unif}} \leq p_t$  for  $t = 1-5$ , then the individual was considered cap-

tured and marked. After five capture occasions, each individual had a capture history indicating the 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 (CI). Confidence intervals for Null  $M_o$ , Darroch  $M_p$ , Chao  $M_t$ , Chao  $M_h$ , and Chao  $M_{th}$  were constructed assuming the  $\log_e$ -transformation of the estimated number of fish not captured has an approximately normal distribution (Chao 1989; Rexstad and Burnham 1991). Confidence intervals for the Lincoln–Petersen and Schnabel estimators were constructed assuming the number of recaptures had 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.

We also examined the total number of individuals captured in each sample, the number of first captures in each sample, and recapture frequencies for Henrys Fork data to identify patterns consistent with models  $M_o$ ,  $M_p$ , and  $M_h$ . Data consistent with models  $M_o$  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  $M_o$ . 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, we wanted to determine how much movement occurred, upstream or downstream, out of a 100-m sample area 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. (There were four transects in 50-m areas versus eight transects in 100-m areas.) A unique partial fin clip was assigned to each adjacent area to identify movement. To detect movement out of the sample areas in Box Canyon and



Last Chance, adjacent 50-m areas were sampled on the last capture occasion for all 100-m sample areas in both summer and autumn 1997. We recorded the transect in which trout were recaptured to measure the distance moved outside of the area in which trout were marked and released. We could measure movements of 1–4 transects upstream or downstream from 100-m sample areas and movements of 1–12 transects from adjacent 50-m areas.

We analyzed mark–recapture data from the 100-m and adjacent 50-m sample areas using the multistrata model in program MARK (White and Burnham 1999). The multistrata model is an open-population model that simultaneously estimates apparent survival, capture probabilities, and movement probabilities among strata or sample areas (Hestbeck et al. 1991; Brownie et al. 1993). We used this analysis to quantify how much movement was occurring from a 100-m sample area to the adjacent 50-m sample areas and how much movement might be occurring to beyond the adjacent 50-m sample areas. If apparent mortality rates were low, after accounting for movement among adjacent sample areas, then movement beyond the adjacent 50-m sample areas was probably minimal. This analysis was performed for 100-m sample areas and adjacent 50-m areas that were each sampled on five dates. We used models in which apparent survival was constant among capture occasions, capture probability was either constant or varied among occasions, and movement was either constant or varied upstream versus downstream. Models were compared and weighted using Akaike's information criterion, and model-averaged estimates were obtained for apparent survival, capture probabilities, and movement probabilities.

*Simulation.*—We simulated the movement of marked fish out of a sample area to determine the effect of violating the population closure assumption on abundance estimation. The following rates of permanent emigration of marked fish were examined: 0 (i.e., the simulations described earlier), 5, 10, 15, 20, and 35%. The range of emigration rates was based on observed movement out of Henrys Fork sample areas by age-0 rainbow trout and on the upper bounds of movement rate confidence intervals from the multistrata model analyses. The capture probability was set to zero for the remaining sampling occasions for a percentage of captured fish. That is, if  $p_{\text{unif}} \leq p_t e$  for  $t = 1-5$  and  $e = 0.05, 0.10, 0.15, 0.20$ , or  $0.35$ , then that individual fish was permanently removed from the population by setting  $p_t$  equal to zero for the re-

maining sampling occasions. Estimator statistics were computed as described earlier.

#### *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. We 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. We analyzed 17 mark–recapture data sets that included five capture occasions by 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.

We 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 1). Confidence intervals for total abundance estimates included within-sample area, among-sample area, and extrapolation error terms.

#### *Variables Affecting Capture Probability*

We 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 the value 1 (e.g., five capture occasions that occurred every other day would be assigned dates 1, 3, 5, 7, and 9.) We 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

TABLE 1.—Percent selection of models  $M_o$ ,  $M_b$ ,  $M_{bh}$ ,  $M_p$ ,  $M_{th}$ ,  $M_{tb}$ , and  $M_{tbb}$  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. 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  $M_{tbb}$ .

Model	Population size				
	1,000	1,500	2,000	2,500	3,000
<b>Scenario 1: <math>p_1 = 0.01, p_2 = 0.04, p_3 = 0.02,</math> <math>p_4 = 0.02, p_5 = 0.01, \bar{p} = 0.02</math></b>					
—No model selection results—					
<b>Scenario 2: <math>p_1 = 0.03, p_2 = 0.03, p_3 = 0.05,</math> <math>p_4 = 0.05, p_5 = 0.07; \bar{p} = 0.046</math></b>					
$M_o$	1.8	0	0	0	0
$M_b$	2.9	0.5	2.2	3.1	3.3
$M_{bh}$	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
$M_{tbb}$	78.3	73.4	64.6	58.4	52.0
<b>Scenario 3: <math>p_1 = 0.08, p_2 = 0.07, p_3 = 0.10, p_4 = 0.06,</math> <math>p_5 = 0.08; \bar{p} = 0.078</math></b>					
$M_o$	20.7	6.5	1.4	0.6	0
$M_b$	4.1	1.8	0.3	0	0
$M_p$	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
$M_{tbb}$	2.2	0.7	0.8	0.3	0.2
<b>Scenario 4: <math>p_1 = 0.10, p_2 = 0.13, p_3 = 0.08, p_4 = 0.10,</math> <math>p_5 = 0.12; \bar{p} = 0.106</math></b>					
$M_o$	10.4	1.7	0.1	0.1	0
$M_b$	0.9	0.3	0	0	0
$M_p$	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
$M_{tbb}$	0.7	0.5	0.3	0.3	0.1

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 1). Model  $M_{tbb}$  was selected most frequently at  $\bar{p} = 0.046$  (52.0% to 78.3%; note, there is no estimator in CAPTURE for model  $M_{tbb}$ ). 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. Average bias, expressed as a percentage of the true abundance, was generally smaller than  $\pm 1\%$  for closed populations (Figure 2). There was increasing positive bias as the emigration rate increased; average bias was about equal to the emigration rate for simulations up to 20% (e.g., average bias was about 15% at a 15% emigration rate). However, the average bias was about 46% at a 35% 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 at or about the nominal level of 95% for all simulations with closed populations and for simulations with emigration rates up to 35% at  $\bar{p} = 0.02$ , 15% at  $\bar{p} = 0.046$ , and 5% at  $\bar{p} = 0.078$  and 0.106 (Figure 3). Percent interval coverage tended to decrease as  $N$  and  $\bar{p}$  increased and as the emigration rate increased from 5% to 35%. Average interval length, expressed as a percentage of the true abundance, decreased as  $N$  and  $\bar{p}$  increased but increased as the emigration rate increased (Figure 4).

The Darroch  $M_t$  estimator performed about as well as the Chao  $M_t$  estimator at  $\bar{p} = 0.046, 0.078$  and 0.106, but performed poorly at  $\bar{p} = 0.02$ . The Darroch  $M_t$  estimator had a negative bias that was greater than 10% at  $\bar{p} = 0.02$  for closed populations and decreased as  $N$  and the emigration rate increased (Figure 2). Percent interval coverage exceeded the nominal level of 95% at  $\bar{p} = 0.02$  and increased as  $N$  and the emigration rate increased (Figure 3). Average interval length was shorter than that of the Chao  $M_t$  estimator at  $\bar{p} = 0.02$  (Figure 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 negative bias that was greater than 8% at  $\bar{p} = 0.02$  and decreased as  $N$  and the emigration rate increased (Figure 2). Average bias was positive at  $\bar{p} = 0.046$ ; bias was about 5% for a closed population and increased as the emigration rate increased. Percent interval coverage exceeded the nominal level of 95% at  $\bar{p} = 0.02$ , similar to the Darroch  $M_t$  estimator (Figure 3). Coverage was about at the nominal level at higher values of  $\bar{p}$  for closed populations but decreased to a greater extent, compared with the Chao  $M_t$  estimator, as the emigration rate increased from 5% to 35%. Average interval length was shorter than that of the Chao  $M_t$  estimator and

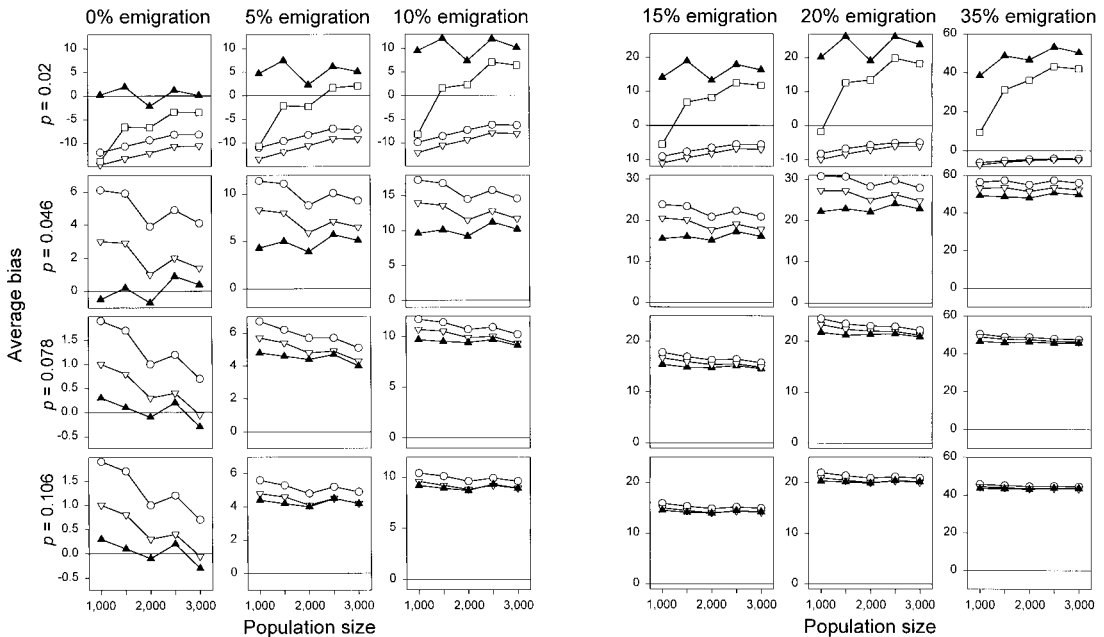


FIGURE 2.—Average bias expressed as a percentage of the true abundance for closed population abundance estimators, as applied to age-0 rainbow trout in the Henrys Fork (black triangles pointing up = Chao  $M_p$ , open triangles pointing down = Darroch  $M_p$ , circles = Null  $M_p$ , and squares = Lincoln–Petersen). Mark–recapture data were simulated under model  $M_t$  for four populations having average capture probabilities of 0.02, 0.046, 0.078, and 0.106; permanent emigration rates were 0, 5, 10, 15, 20, or 35% of marked fish ( $t = 5$  capture occasions; 1,000 replications).

about the same as that of the Darroch  $M_t$  estimator (Figure 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 0% 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  $\bar{p} = 0.02$  and for emigration rates of

5% and 10% (Figures 2–4), but performed poorly elsewhere. Unlike the estimators in program CAPTURE, negative bias increased as  $\bar{p}$  increased, and average interval length increased as  $N$  increased at  $\bar{p} = 0.02$  (Figure 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. 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  $N \leq 2,500$  at  $\bar{p} = 0.02$ . 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.



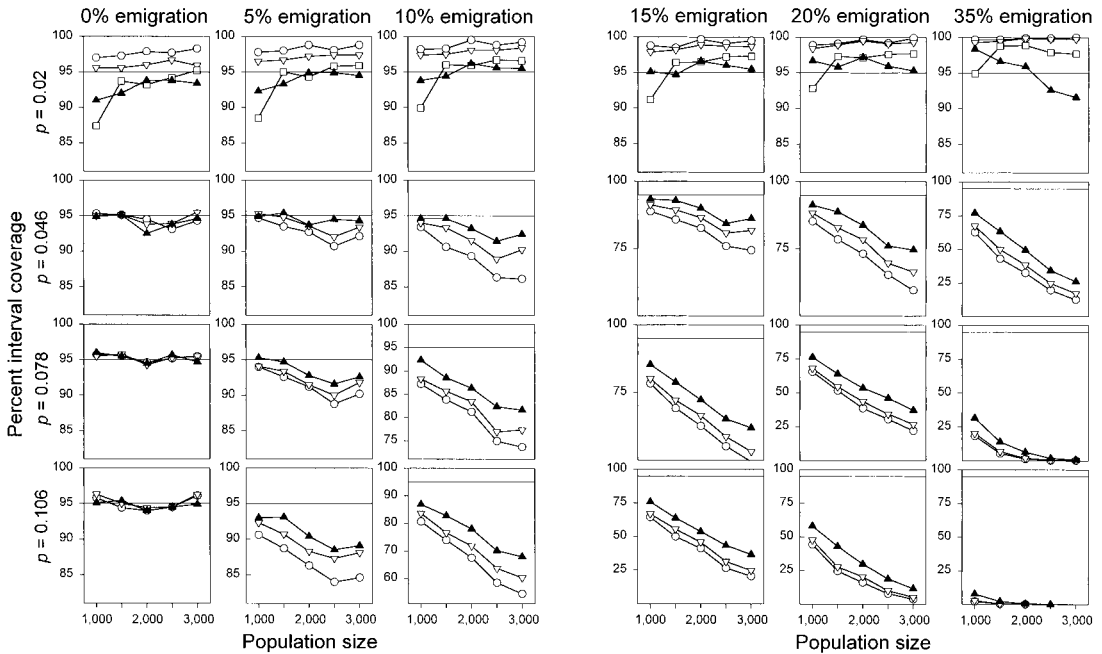


FIGURE 3.—Percent coverage of the true abundance for 95% confidence intervals for closed population abundance estimators, as applied to age-0 rainbow trout in the Henrys Fork (black triangles pointing up = Chao  $M_n$ , open triangles pointing down = Darroch  $M_n$ , circles = Null  $M_n$ , and squares = Lincoln-Petersen). Mark-recapture data were simulated under model  $M_1$  for four populations having average capture probabilities of 0.02, 0.046, 0.078, and 0.106; permanent emigration rates were 0, 5, 10, 15, 20, or 35% of marked fish ( $t = 5$  capture occasions; 1,000 replications).

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

#### Henrys 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 length-frequency histograms and by reading scales in Box Canyon and Last Chance in summer 1995 and 1996, in Last Chance in autumn 1996, and in Hariman State Park in all sampling seasons and years (Figure 5). 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 in summer and autumn 1997 and for Box Canyon in autumn 1996 (Figure 5). The probability of correctly classifying a rainbow trout to age 0 ranged from 0.93 to 1 and the probability of correctly classifying a rainbow trout to age 1 ranged from 0.60 to 0.97.

*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 in which they were marked (Table 2). About 84% (145 of 173) of trout recaptured on dates when three adjacent areas were sampled were in the area they were marked; about 10% (17 of 173) were recaptured downstream and about 6% (11 of 173) were recaptured upstream. There was a decreasing trend in the number of trout recaptured as the distance from the marking area increased both upstream and downstream.

Multistrata model results indicated that apparent mortality, and hence movement, were low for sample area 1 in Last Chance in summers 1996 and 1997 (Table 3). Capture probabilities were low, ranging from 0.017 to 0.032 in 1996 and from 0.008 to 0.026 in 1997. Apparent survival rates were high: 0.847 in 1996 (95% CI = 0.515–0.966) and 0.975 in 1997 (0.0006–0.999). Therefore, apparent mortality was 0.153 in 1996 and 0.025 in 1997. Movement probabilities in 1996 were 0.092 downstream (95% CI = 0.042–0.188) and 0.054 upstream (0.017–0.161); movement probabilities in 1997 were 0.026 downstream (0.007–0.094) and 0.028 upstream (0.008–0.091). Therefore, the emigration rate was about 15% in 1996 and 5% in 1997.

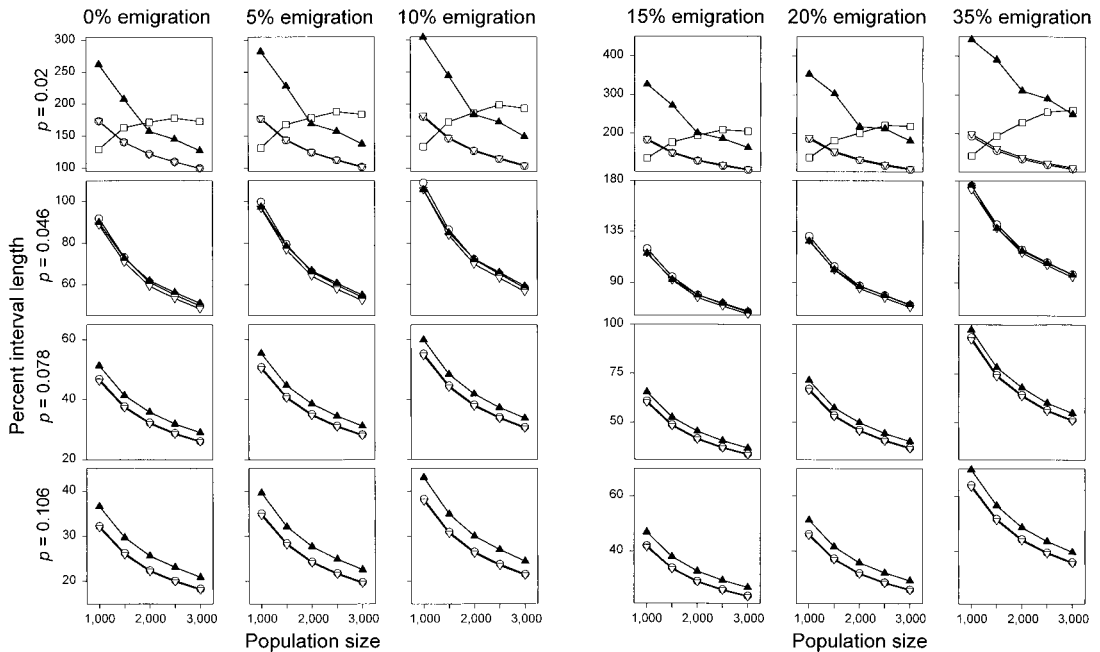


FIGURE 4.—Average interval length expressed as a percentage of the true abundance for closed-population abundance estimators, as applied to age-0 rainbow trout in the Henrys Fork (black triangles pointing up = Chao  $M_p$ , open triangles pointing down = Darroch  $M_p$ , circles = Null  $M_p$ , and squares = Lincoln-Petersen). Mark-recapture data were simulated under model  $M_t$  for four populations having average capture probabilities of 0.02, 0.046, 0.078, and 0.106; permanent emigration were 0, 5, 10, 15, 20, or 35% of marked fish ( $t = 5$  capture occasions; 1,000 replications).

*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. These patterns of captures were consistent with model  $M_p$ . Most age-0 rainbow trout were captured one time (92.7%; sample size = 10,065); 6.7% were captured two times, 0.5% were recaptured three times, 0.03% were recaptured four times, and none were recaptured five times. These small frequencies of multiple recaptures were not consistent with model  $M_p$ .

*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; bias was minimal and interval coverage was near or at the nominal level. Abundance estimates ranged from 778 to 8,175 (median 2,383). The mean capture probability ranged from 0.01 to 0.126 (median 0.036). The capture efficiency ranged from 4.2% to 62.4% (median 16.7%), and the recapture rate ranged from 0.7 to 22.4% (median 5.4%).

The average capture efficiency increased from

14.2% to 17.4% to 20.0% as the number of capture occasions increased from 3 to 4 to 5; the average standard error for abundance estimates decreased from 817.4 to 551.8 to 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 4, 5). 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 was higher in Last Chance versus Box Canyon in all seasons and years (Table 4); density was lowest in Harriman State Park.

*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 ( $r^2 = 0.03$ ) or relative sampling date ( $r^2 = 0.03$ ). The correlation between capture

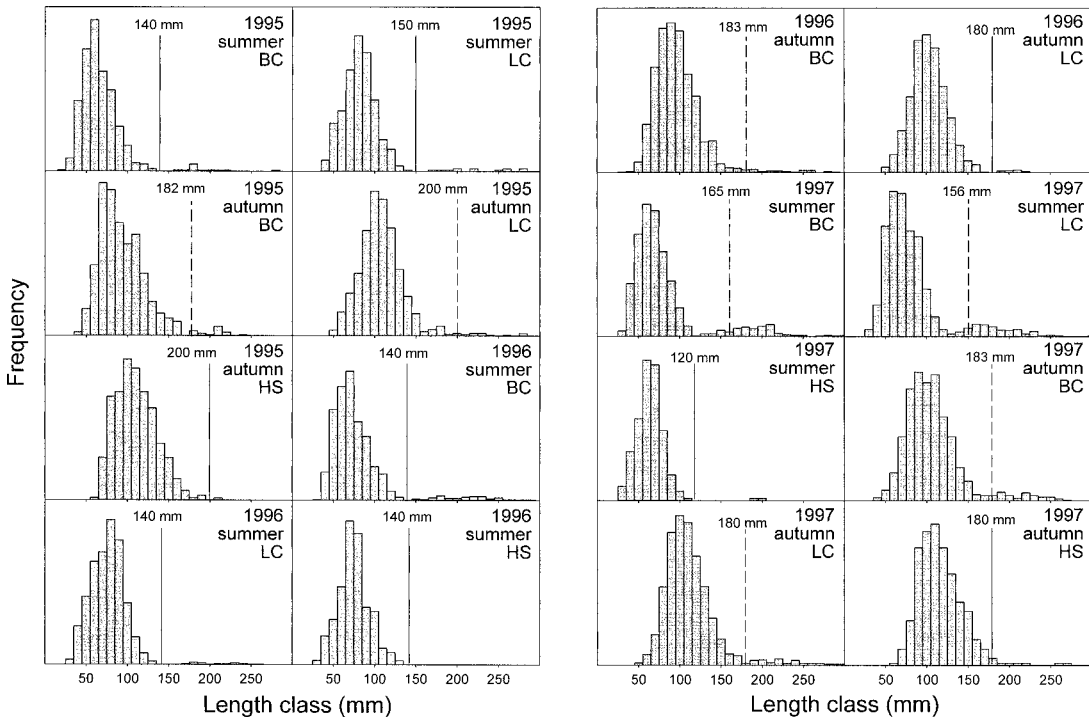


FIGURE 5.—Length-frequency histograms for the Box Canyon (BC), Last Chance (LC), and Harriman State Park (HS) study sections of the Henrys Fork in summer and autumn, 1995–1997. Vertical lines indicate the estimated length separating age-0 and age-1 rainbow trout, as determined by either length-frequencies (solid lines) or logistic regression of length and age data (dashed lines).

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, making the proportion of marked trout recaptured in studies of large populations relatively small, which produces 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. We 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

We estimated the emigration rate of marked trout out of 100-m sample areas based on the recapture of marked trout in sample areas and adjacent 50-m areas. The recapture rates we observed were low. Recapture rates may be low because emigration rates are high or capture probabilities are small. Gowan et al. (1994) and Gowan and Fausch (1996) argued that movement rate estimates, based on recapturing marked trout when recapture rates are low, are suspect because the behavior of trout not recaptured cannot be known. We contend that age-0 trout in the Henrys Fork that were not recaptured behaved similarly to recaptured trout. There was insufficient time, relative to the area sampled, for a significant number of trout to move beyond the areas we sampled. In other words, the large spatial scale and short temporal scale of our sampling efforts at each site were

TABLE 2.—Distribution of recaptured age-0 rainbow trout in 100-m sample areas and adjacent 50-m areas (downstream and upstream) of the Henrys Fork in summer and autumn of 1996 and 1997. Numbers of recaptures are for days on which all three areas were sampled; arrows indicated direction of movement from the capture area to the recapture area.

Capture area	Numbers of fish by recapture area		
	Downstream	Sample area	Upstream
<b>Box Canyon, summer 1997</b>			
Sample area 1 <sup>a</sup>	0	7	1 ↑
Sample area 2 <sup>a</sup>	0	2	1 ↑
<b>Box Canyon, autumn 1997</b>			
Sample area 1 <sup>a</sup>	1 ↓	23	2 ↑
<b>Last Chance, summer 1996</b>			
Upstream <sup>b</sup>	0	4 ↓	7
Sample area 1	3 ↓	14	2 ↑
Downstream	7	0	0
<b>Last Chance, autumn 1996</b>			
Upstream <sup>c</sup>	0	1 ↓	12
Sample area 1	5 ↓	24	0
Downstream	12	2 ↑	0
<b>Last Chance, summer 1997</b>			
Upstream <sup>b</sup>	0	1 ↓	3
Sample area 1	0	13	1 ↑
Downstream	9	0	1 ↑
Sample area 2 <sup>a</sup>	1 ↓	2	0
<b>Last Chance, autumn 1997</b>			
Sample area 1 <sup>a</sup>	1 ↓	10	1 ↑

<sup>a</sup> All adjacent areas sampled over 1 d.  
<sup>b</sup> All adjacent areas sampled over 5 d.  
<sup>c</sup> All adjacent areas sampled over 3 d.

such that the concerns of Gowan et al. (1994) and Gowan and Fausch (1996) were adequately addressed in our study design. We did not recapture many marked trout, not because marked trout moved beyond the adjacent areas we were sampling, but because capture probabilities were small.

The results of the multistrata model analyses supported our contentions that we adequately addressed the issue of emigration in our study design and that movement was minimal. Capture probability estimates were small in the multistrata models, as were similar estimates in the closed-population abundance models. Estimates of apparent survival were high and corresponding estimates of apparent mortality were low. The low apparent mortality estimates were indicative of low rates of movement.

We sampled age-0 rainbow trout in the Henrys Fork during the summer and autumn growth periods when environmental conditions were stable and mass seasonal movements were not occurring. Movement rates of trout reported in the literature suggest that rates of age-0 trout movement in the Henrys Fork would be amenable to detection by sampling 50-m areas upstream and downstream of sample areas during the short time frames of our sampling efforts in each season. Young (1994) reported median weekly movements of telemetered brown trout *Salmo trutta* (<340 mm total length [TL]) to be 20 m in Douglas Creek and 8 m in South French Creek, Wyoming. Corresponding median weekly movements for brown trout greater than 340 mm TL were 53 and 55 m. Radiotelemetry studies of Colorado River cutthroat trout *On-*

TABLE 3.—Multistrata model results for the Last Chance section of Henrys Fork in summers 1996 and 1997.  $S(.)$  = constant survival rates,  $p(.)$  = constant capture probabilities,  $p(t)$  = time-specific capture probabilities;  $\Psi(.)$  = constant movement probabilities, and  $\Psi(d)$  = direction-specific movement probabilities (i.e., downstream and upstream). Apparent mortality equals one minus apparent survival.

Model	Weight	Apparent survival		Apparent mortality	Movement downstream		Movement upstream	
		Estimate	(SE)		Estimate	(SE)	Estimate	(SE)
<b>1996</b>								
$S(.) p(.) \Psi(d)$	0.31	0.880	(0.104)		0.106	(0.037)	0.037	(0.026)
$S(.) p(.) \Psi(.)$	0.26	0.880	(0.104)		0.075	(0.025)	0.075	(0.025)
$S(.) p(t) \Psi(d)$	0.24	0.803	(0.100)		0.106	(0.037)	0.037	(0.026)
$S(.) p(t) \Psi(.)$	0.20	0.803	(0.100)		0.075	(0.025)	0.075	(0.025)
Weighted average		0.847	(0.102)	0.153	0.092	(0.032)	0.054	(0.025)
<b>1997</b>								
$S(.) p(t) \Psi(.)$	0.52	0.981	(0.140)		0.027	(0.016)	0.027	(0.016)
$S(.) p(.) \Psi(.)$	0.21	0.963	(0.126)		0.027	(0.016)	0.027	(0.016)
$S(.) p(t) \Psi(d)$	0.19	0.981	(0.140)		0.022	(0.022)	0.031	(0.021)
$S(.) p(.) \Psi(d)$	0.08	0.963	(0.126)		0.022	(0.022)	0.031	(0.021)
Weighted average		0.975	(0.136)	0.025	0.026	(0.018)	0.028	(0.017)

TABLE 4.—Average age-0 rainbow trout abundance estimates for summer and autumn in two sample areas within two sections of the Henrys Fork. Lower (LB) and upper bounds (UB) of normal 95% confidence intervals include error within and among sample areas.

Year	Abundance ( $\hat{N}$ )	SE	LB-UB
<b>Summer, Box Canyon</b>			
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
<b>Summer, Last Chance</b>			
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
<b>Autumn, Box Canyon</b>			
1995 <sup>a</sup>	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
<b>Autumn, Last Chance</b>			
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

<sup>a</sup> One sample area.

*corrhynchus clarki pleuriticus* (size range 185–242 mm TL) indicated mean home-range lengths of 27, 21, and 9 m during three summer observation periods (Young et al. 1997) and mean summer and autumn home-range lengths of 32 and 38 m (Young 1998) in the North Fork Little Snake River, Wyoming. Gowan and Fausch (1996) used weirs to estimate median movement rates of brook trout *Salvelinus fontinalis* of 16.7 m/d upstream and 10.0 m/d downstream in Jack Creek and 16.9 m/d upstream and 6.6 m/d downstream in the North Fork Cache la Poudre River, Colorado. The median length of fish in the general population was about 150 mm TL in each river, and the median length was about 1.5–24.8 mm greater for fish moving upstream or downstream versus fish not moving. Given the lower rates of movement by smaller trout in these studies, we inferred that age-0 trout in the Henrys Fork, being considerably smaller, could be expected to move even less.

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). 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 movement in juvenile gag *Mycteroperca microlepis*

TABLE 5.—Extrapolated abundance estimates (summer and autumn) for age-0 rainbow trout in three sections of the Henrys Fork: lower Box Canyon (2.5 km), Last Chance (4 km), and Harriman State Park (1 km). Lower (LB) and upper bounds (UB) of normal 95% prediction intervals include error within and among sample areas and extrapolation error.

Year	Abundance ( $\hat{N}$ )	SE	LB-UB
<b>Summer, Box Canyon</b>			
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
<b>Summer, Last Chance</b>			
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
<b>Summer, Harriman State Park</b>			
1996 <sup>a</sup>	10,080	1,556	7,030–13,130
1997 <sup>a</sup>	12,520	1,268	10,033–15,006
<b>Autumn, Box Canyon</b>			
1995 <sup>a</sup>	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
<b>Autumn, Last Chance</b>			
1995	91,320	4,490	85,520–100,120
1996	154,580	32,940	90,020–219,140
1997	130,200	29,600	72,180–188,220
<b>Autumn, Harriman State Park</b>			
1995 <sup>a</sup>	13,290	1,026	11,278–15,302
1997 <sup>a</sup>	13,800	1,132	11,580–16,020

<sup>a</sup> One sample area.

found in physically open, but with seagrass, 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 used specific habitats and tended to conceal themselves in interstitial spaces therein, particularly in rocky substrates, woody debris, and macrophytes (Mitro 1999). The slow, methodical process of electrofishing along transects across the river was particularly effective at capturing juveniles versus adults 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.

We sampled in reaches of the Henrys Fork that were wide, shallow, and cover-rich. Trout moving from one suitable location to another could, in addition to moving upstream or downstream, move across the approximately 100-m-wide channel. Trout would not leave a sample area by making such lateral shifts. However, movements would have to be essentially upstream or downstream in the smaller streams referred to above (mean widths 4.0–13.9 m; Young 1994, 1998; Gowan and Fausch 1996; Young et al. 1997).

The emigration of unmarked fish may have occurred, but we could not measure such movement. 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. We observed few juvenile trout that were stunned and drifted downstream past the netter.

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. We showed by simulation that 95% confidence intervals achieved a coverage level of about 90–95% for the Chao  $M_t$  estimator when  $N = 1,000$ – $3,000$ ,  $\bar{p} = 0.046$  and the emigration rate ranged up to 15%.

#### *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 a netter's visibility of juvenile trout and change the probability that an individual trout is susceptible to electrofishing. The cooler water temperatures 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 TL). Age-0 trout were larger in autumn than they were in summer and therefore may have been more susceptible in autumn.

Fish have been observed to respond behaviorally to electrofishing mark–recapture. Capture probabilities decreased in subsequent capture periods following 2-h intervals for marked roach *Rutilus rutilus*, gudgeon *Gobio gobio*, and rudd *Scardinius erythrophthalmus* (Cross and Stott 1975), and such a behavioral response is also likely for rainbow trout. 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, which reduced 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 (Figure 5).

On the contrary, the capture of large trout appeared to be less likely. This may have resulted from the slow, methodical approach to electrofishing that we used in these areas. Larger trout tended to react to the slowly approaching intermittent electric field by attempting to escape it, whereas juvenile trout tended to seek or remain 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. Only one individual was captured four times and no individuals were captured more than four times. Estimated abundances were usually greater than 2,000 and capture probabilities were usually less than 0.05. Such data are 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 (Menkins and Anderson 1988; Pollock et al. 1990; Seber 1992). We 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 because some models in CAPTURE have likelihood equations with nonidentifiable 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.

We 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 process to select the probable 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.

We found that the Chao  $M_t$  estimator performed best for sparse data generated under model  $M_t$ . However, results from the Chao  $M_t$  estimator were poor for combinations of high capture probabilities and high emigration rates. 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, capture probabilities were small (median = 0.036), and observed emigration rates were less than 20%.

The Null  $M_o$  and Darroch  $M_t$  estimators performed about as well as the Chao  $M_t$  estimator for certain simulated capture scenarios. However, we 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 consistently perform as well as the Chao  $M_t$  estimator. We 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. We also do not recommend 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 pikeminnow *Ptychocheilus lucius* (estimates of capture probability ranged 0.074–0.194).

The Darroch and Chao  $M_t$  estimators both reduce to the Lincoln–Petersen estimator for the spe-

cial 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 our 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 if 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. We recommend analyzing multiple capture data as multiple capture data and not pooling capture occasions for use with the Lincoln–Petersen estimator.

#### *Henry's 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 Henry's Fork. The small capture probabilities and large confidence intervals associated with our abundance estimates made it possible to detect only relatively large changes in abundances. For example, summer and autumn abundance estimates were high compared with spring abundance estimates, which were low (Mitro and Zale 2002). This allowed us to infer that poor recruitment was probably caused by high overwinter mortality and emigration.

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