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

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Preface

The research described in this paper and most of the biological commentary and discussion constituted a chapter of my dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Fish and Wildlife Biology. In this paper I expanded on the Abundance Estimation section under Methods by adding seven sections that describe in detail the following: the multinomial model in capture-recapture, maximum likelihood estimation, the estimation of sampling variance, and descriptions of the estimators Null M_o, Darroch M_t, Chao M_t, and Chao M_h (pages 6-17). I also added a description of the model selection procedure used in program CAPTURE (page 17).

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 m^2. 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. There is 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 Henrys Fork data sets.

Study Area

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

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 abundance estimators. Closed-population estimators included the following estimators in the computer program CAPTURE: Null M_o, Darroch M_t, Chao M_t, and Chao M_h (Otis et al. 1978; Chao 1989; Rexstad and Burnham 1991).

The Multinomial Model in Capture-Recapture

A mark-recapture data set consisted of the capture histories of each individual fish captured at least one time during the sampling period. Denote the capture history matrix $\boldsymbol{X}=(x_{ij})$ where $i=1, \ldots, N$ (i.e., the number of rows equals the number of individuals in the population) and $j=1, \ldots, t$ (i.e., the number of columns c equals the number of capture occasions). Let $x_{ij}=1$ if individual i is captured on occasion j and $x_{ij}=0$ if the individual is not captured. There is a row for each individual fish in the population and a column for each sampling occasion. The number of fish not captured (i.e., the number of rows of zeros) is unknown. For t sampling occasions there are 2^t possible capture histories w. Consider the scenario in which a population is sampled on 2 occasions. There are $2^2=4$ possible capture histories w where w is a series of 0's (no capture) and 1's (capture):

$w = 1\ 0$	captured first time only,
$w = 0\ 1$	captured second time only,
$w = 1\ 1$	captured both times,
$w = 0\ 0$	never captured.

Let n_w = the number of individuals with capture history w where $\sum_{w} n_w = N$ and $n_{(w=00)}$ is unknown; let $\{ n_w \}$ be the set of frequencies of each possible capture history w. If probabilities for these capture histories are the same for all individuals in the population and the capture events of one individual are independent of the capture events of any other individual, then the appropriate statistical model is the multinomial distribution with four probabilities of capture (i.e., for the two sampling occasion scenario):

(1) $$P[\{n_w\}|N,\boldsymbol{p}] = \left(\frac{N!}{\prod_w n_w!} \right) \prod_w p_w{}^{n_w}$$

where $\boldsymbol{p}$ represents the set of four capture probabilities (Otis et al. 1978).

Substituting for w and expanding the products yields

(2) $$P[\{n_w\}|N,\boldsymbol{p}] = \frac{N!}{n_{10}! \cdot n_{01}! \cdot n_{11}! \cdot n_{00}!} \cdot p_{10}^{n_{10}} \cdot p_{01}^{n_{01}} \cdot p_{11}^{n_{11}} \cdot p_{00}^{n_{00}} \; .$$

The fully parameterized model includes four parameters to estimate: the population size N and three of the four probabilities of capture p_w (the fourth equals 1-(the sum of the other three)). Additional assumptions can lead to model simplification.

Maximum Likelihood Estimation

Maximum likelihood estimation can be applied to obtain estimates of model parameters N and $\boldsymbol{p}$ if the model is a well-defined parametric model with fewer parameters than the dimension of the vector of minimal sufficient statistics (e.g., Model M_o and Model M_t) (Otis et al. 1978). Maximum likelihood estimation methods have been used extensively in mark-recapture theory (Burnham et al. 1987; Seber 1992). Maximum likelihood methods have well-known optimal properties, such as invariance, consistency, and preservation of the ranges of parameters (Casella and Berger 1990). Maximum likelihood methods also allow the derivation of approximate sampling variances for estimators, which for large samples are the smallest sampling variances possible in the class of consistent estimators (Otis et al. 1978). These sampling variances can be used to construct confidence intervals.

Maximum likelihood estimation in mark-recapture theory is based on the sampling probability distribution of mark-recapture data, which is represented as a function of the parameters N and $\boldsymbol{p}$ (e.g., equation (1)). The probability distribution is stated as $P[\boldsymbol{X}\,|N, \boldsymbol{p}]$ (i.e., the probability of mark-recapture sample data $\boldsymbol{X}$ given population size N and capture probabilities $\boldsymbol{p}$); the likelihood function is $\mathrm{L}(N, \boldsymbol{p} \mid X)$ (i.e., the likelihood of population size N and capture probabilities $\boldsymbol{p}$ given mark-recapture sample data X). Maximum likelihood estimates of N and $\boldsymbol{p}$ are values that maximize the likelihood function (i.e., the function is maximized over a set of possible values of the parameters N and $\boldsymbol{p}$).

The multinomial model with three or more sampling occasions requires the use of numerical methods to find the value of N that maximizes the likelihood function. (Taking the derivative of the log-likelihood function with respect to N and equating the result to zero does not result in a closed-form solution.) The values of $\boldsymbol{p}$, however, can be obtained from closed-form equations to maximize the likelihood function $\mathrm{L}(N, \boldsymbol{p} \mid X)$ for a fixed value of N, where N is greater than or equal to the total number of distinct individuals captured from the population. Given the maximum likelihood estimates of $\boldsymbol{p}$, the likelihood function is then maximized over N numerically in a one-dimensional search between two endpoints (i.e., the lower bound M_{t+1}, the number of distinct individuals captured, and the upper bound M_{t+1} plus a linear approximation to $\hat{N}$) (Otis et al. 1978). If the upper bound maximizes the likelihood function, then the search is continued over a new set of values with the lower bound being the previous upper bound. The search is conducted over real numbers, but the domain of $\hat{N}$ contains only integer values and therefore only integer values are appropriate. The real value found to maximize the likelihood function is truncated to an integer $\hat{N}$ and is checked against $\hat{N}+1$ to determine the integer that maximizes the likelihood function.

Estimation of Sampling Variance

There is a general method in maximum likelihood theory for obtaining the asymptotic formula for the true sampling variance of $\hat{N}$, which is a function of the unknown parameters N and $\boldsymbol{p}$:

(3) $$\operatorname{var}(\hat{N}) \approx Ng(\boldsymbol{p})$$

where $g(\boldsymbol{p})$ is a known function of $\boldsymbol{p}$ (Otis et al. 1978). We substitute $\hat{N}$ and $\hat{p}$ into equation (2) to estimate var($\hat{N}$):

(4) $$\hat{\operatorname{var}}(\hat{N}) \approx \hat{N}g(\hat{p}).$$

Therefore, to estimate var($\hat{N}$) we first estimate N and $\boldsymbol{p}$ and then estimate the resulting approximation (Casella and Berger 1990).

Darroch M_t Estimator

A simplification of the multinomial model (equations (1) and (2)) is such that the capture probability is the same for every individual on a given sampling occasion, but may vary by sampling occasion. Consider the scenario in which a population is sampled on 2 occasions. Let p_1 = the probability of capture in occasion 1 and p_2 = the probability of capture in occasion 2. Then

$$\begin{aligned}
p_{(w=10)} &= p_1(1-p_2)\\
p_{(w=01)} &= (1-p_1)\,p_2\\
p_{(w=11)} &= p_1\,p_2\\
p_{(w=00)} &= (1-p_1)(1-p_2)
\end{aligned}$$

and substituting into equation (2) yields

(5) $$\mathrm{P}[\{n_w\}|N,\boldsymbol{p}] =$$

$$\frac{N!}{n_{10}!\cdot n_{01}!\cdot n_{11}!\cdot n_{00}!}\cdot[p_1(1-p_2)]^{n_{10}}\cdot[(1-p_1)p_2]^{n_{01}}\cdot[p_1 p_2]^{n_{11}}\cdot[(1-p_1)(1-p_2)]^{n_{00}}.$$

Let n_1 = the number of individuals captured in occasion 1 and n_2 = the number captured in occasion 2 and substitute into equation (5):

(6) $$\mathrm{P}[\{n_w\}|N,\boldsymbol{p}] =$$

$$\frac{N!}{n_{10}!\cdot n_{01}!\cdot n_{11}!\cdot n_{00}!}\cdot\left[p_1^{\,n_1}(1-p_2)^{N-n_2}\right]\cdot\left[(1-p_1)^{N-n_1}p_2^{\,n_2}\right]\cdot\left[p_1^{\,n_1}p_2^{\,n_2}\right]\cdot\left[(1-p_1)^{N-n_1}(1-p_2)^{N-n_2}\right].$$

Equation (6) can be reduced to

(7) $$\mathrm{P}[\{n_w\}|N,\boldsymbol{p}] = \frac{N!}{n_{10}!\cdot n_{01}!\cdot n_{11}!\cdot n_{00}!}\cdot\prod_{j=1}^{2}p_j^{n_j}(1-p_j)^{N-n_j}\ .$$

This temporal variation model can be generalized for t sampling occasions and therefore has t+1 parameters, the population size N and t capture probabilities ($p_1, p_2, \ldots, p_t$). This model is designated Model M_t and parameter estimates can be obtained from the estimator Darroch M_t (Darroch 1958; Otis et al. 1978). In practice $n_{00}!$ is unknown and is estimated by subtracting the total number of distinct individuals captured from the population size N. The probability distribution of the set of possible capture histories $\{n_w\}$ for Model M_t is therefore

(8) $$\mathrm{P}[\{n_w\}|N,\boldsymbol{p}]=\frac{N!}{\left[\prod_{w(1)}n_{w(1)}!\right](N-M_{t+1})!}\prod_{j=1}^{t}p_j^{n_j}(1-p_j)^{N-n_j}$$

where n_w = the number of individuals with capture history w,

$w(1)$ is used to index capture histories that include at least one capture,

N = the total number of individuals in the population,

M_{t+1} = the number of distinct individuals captured (i.e., the number of non-zero rows in $\boldsymbol{X}$),

t = the number of sampling occasions,

p_j = the probability of capture in occasion j, and n_j = the number of animals caught on the j^{th} sampling occasion.

The estimator Darroch M_t is a maximum likelihood estimator of N that is derived from the log-likelihood of equation (8):

(9) $$\ln L(N,\boldsymbol{p}|X) = \ln\left(\frac{N!}{(N-M_{t+1})!}\right)+\sum_{j=1}^{t} n_j \ln(p_j)+\sum_{j=1}^{t}(N-n_j)\ln(1-p_j)$$

where $\boldsymbol{p}=\{p_1,p_2,\ldots,p_t\}$, $p_j\in[0,1]$ for $j=1$ to t, and $N\in\{M_{t+1}, M_{t+1}+1, M_{t+1}+2, \ldots\}$. (The log-likelihood function excludes components of the probability distribution not relevant to the estimation of N and p_j, i.e., $\prod_w n_w!$.) The maximum likelihood estimator of p_j given the value of N is the solution to the derivative of equation (9) with respect to $\boldsymbol{p}$, set equal to zero:

(10) $$\frac{\partial}{\partial p_j}\ln L(\boldsymbol{p}|N,X)=0, \quad j=1,\ldots,t,$$

which results in the closed-form solution

(11) $$\hat{p}_j(N)=\frac{n_j}{N}.$$

The maximum likelihood estimate $\hat{N}_t$ of N satisfies

(12) $$\ln L(\hat{N}_t, \hat{p}_1(\hat{N}_t),\ldots,\hat{p}_t(\hat{N}_t)\,|X) = \max_N$$

$$\left[\ln\left(\frac{N!}{(N-M_{t+1})!}\right)+\sum_{j=1}^{t} n_j \ln(n_j)+\sum_{j=1}^{t}(N-n_j)\ln(N-n_j)-tN\ln(tN)\right].$$

This estimator is a function of the minimal sufficient statistic $\{n_1, \ldots, n_t, M_{t+1}\}$.

The asymptotic variance of $\hat{N}_t$ is

(13) $$\operatorname{var}(\hat{N}_t)\approx\frac{N_t}{\dfrac{1}{\prod_{j=1}^{t}(1-p_j)}+t-1-\sum_{j=1}^{t}(1-p_j)^{-1}},$$

which is estimated by

(14) $$\hat{\text{var}}(\hat{N}_t) \approx \frac{\hat{N}_t}{\dfrac{1}{\prod_{j=1}^{t}(1-\hat{p}_j)} + t - 1 - \sum_{j=1}^{t}(1-\hat{p}_j)^{-1}}.$$

Null M_o Estimator

A further simplification of the temporal variation Model Mt is such that every individual has an equal probability of capture on all sampling occasions. Consider the scenario in which a population is sampled on 2 occasions. Let $p = p_1 = p_2 =$ the probability of capture in either sampling occasion. Then substituting p and t=2 into equation (8) yields

(15) $$P[\{n_w\}|N,p] = \frac{N!}{\left[\prod_{w(1)} n_{w(1)}!\right](N-M_{t+1})!} \prod_{j=1}^{2} p^{n_j}(1-p)^{N-n_j}$$

or

(16) $$P[\{n_w\}|N,p] = \frac{N!}{\left[\prod_{w(1)} n_{w(1)}!\right](N-M_{t+1})!} \cdot p^{n_1}(1-p)^{N-n_1} \cdot p^{n_2}(1-p)^{N-n_2}.$$

Let $n. = n_1+n_2$ and substitute into equation (16):

(17) $$P[\{n_w\}|N,p] = \frac{N!}{\left[\prod_{w(1)} n_{w(1)}!\right](N-M_{t+1})!} \cdot p^{n.}(1-p)^{2N-n.}.$$

This model is designated Model M_o and has two parameters, the population size N and the capture probability p. Parameter estimates for Model M_o are obtained from the estimator designated Null M_o (Otis et al. 1978). Model M_o can be generalized to t sampling occasions.

The probability distribution of the set of possible capture histories $\{n_w\}$ for Model M_o is therefore

$$\mathrm{P}[\{n_w\}|N,p]=\frac{N!}{\left[\prod_{w(1)} n_{w(1)}!\right](N-M_{t+1})!}\cdot p^{n.}(1-p)^{tN-n.} \tag{18}$$

where n_w = the number of individuals with capture history w,

$w(1)$ is used to index capture histories that include at least one capture,

N = the total number of individuals in the population,

M_{t+1} = the number of distinct individuals captured (i.e., the number of non-zero rows in X),

p = the probability of capture,

t = the number of sampling occasions,

and $n.$ = the total number of captures in the study (i.e., the sum of the total number of times each individual was captured).

The estimator Null M_o is a maximum likelihood estimator of N that is derived from the log-likelihood of equation (18):

$$\mathrm{lnL}(N,p|X) = \ln\left(\frac{N!}{(N-M_{t+1})!}\right)+(n.)\ln(p)+(tN-n.)\ln(1-p) \tag{19}$$

where $p\in[0,1]$ and $N\in\{M_{t+1}, M_{t+1}+1, M_{t+1}+2, \ldots\}$. (The log-likelihood function excludes components of the probability distribution not relevant to the estimation of N and p, i.e., $\prod_{w} n_w!$.)

The maximum likelihood estimator of p given the value of N is the solution to the derivative of equation (19) with respect to p, set equal to zero:

$$\frac{\partial}{\partial p}\mathrm{lnL}(\mathrm{p}|\mathrm{N},\mathbf{X})=0, \tag{20}$$

which results in the closed-form solution

(21) $$\hat{p}(N) = \frac{n.}{tN}.$$

The maximum likelihood estimate $\hat{N}_o$ of N satisfies

(22) $$\ln L(\hat{N}_o, \hat{p}(\hat{N}_o) \mid X) = \max_N$$

$$\left[\ln\left(\frac{N!}{(N - M_{t+1})!} \right) + (n.)\ln(n.) + (tN - n.)\ln(tN - n.) - tN\ln(tN) \right].$$

This estimator is a function of the minimal sufficient statistic $\{n., M_{t+1}\}$.

The asymptotic variance of $\hat{N}_o$ is

(23) $$\operatorname{var}(\hat{N}_o) \approx \frac{N}{[(1-p)^{-t} - t(1-p)^{-1} + t - 1]},$$

which is estimated by

(24) $$\widehat{\operatorname{var}}(\hat{N}_o) \approx \frac{\hat{N}_o}{[(1-\hat{p})^{-t} - t(1-\hat{p})^{-1} + t - 1]}.$$

Chao M_t Estimator

Chao (1989) developed an alternative estimator for the temporal variation model for use in analyzing "sparse" data sets. A sparse data set is characterized by having few recaptures. The Chao M_t estimator is based on lower-order capture frequency counts (i.e., the number of individuals captured exactly once or twice).

The derivation of the Chao M_t estimator starts with the equation

(25) $$N = M_{t+1} + f_0$$

where M_{t+1} is the number of distinct individuals captured in the study and f_0 is the number of individuals never captured. A bias-corrected estimator of E(f_0) was developed using the number of individuals captured once and twice:

$$\text{(26)} \qquad \mathrm{E}(f_0) = \frac{f_1^2 - \sum_{j=1}^{t} Z_j^2}{2(f_2 + 1)}$$

where f_1 is the number of individuals captured once,

f_2 is the number of individuals captured twice,

Z_j is the number of individuals captured only on the j^{th} occasion,

and t is the total number of sampling occasions.

The bias-corrected Chao M_t estimate $\hat{N}_t$ of N is obtained by substituting equation (26) into equation (25):

$$\text{(27)} \qquad \hat{N}_t = M_{t+1} + \frac{f_1^2 - \sum_{j=1}^{t} Z_j^2}{2(f_2 + 1)}.$$

The minimal sufficient statistic for this estimator is $\{f_2, Z_1, \ldots, Z_t, M_{t+1}\}$. Unlike the Darroch M_t estimator for the temporal variation model, the Chao M_t estimator does not have a likelihood form. The asymptotic variance of $\hat{N}_t$ is

$$\text{(28)} \qquad \mathrm{var}(N_t) \approx (N_t - M_{t+1}) + (N_t - M_{t+1})^2 \left(\frac{1}{f_2 + 1} + \frac{4}{N_t}\right) + \frac{\sum_{j=1}^{t} (f_1 - Z_j)^2 - \dfrac{\left[\sum_{j=1}^{t} (f_1 - Z_j) Z_j\right]^2}{N_t}}{(f_2 + 1)^2}$$

which is estimated by

(29) $$\hat{\mathrm{var}}(\hat{N}_t) \approx (\hat{N}_t - M_{t+1}) + (\hat{N}_t - M_{t+1})^2 \left(\frac{1}{f_2+1} + \frac{4}{\hat{N}_t}\right) + \frac{\sum_{j=1}^{t} (f_1 - Z_j)^2 - \frac{\left[\sum_{j=1}^{t} (f_1 - Z_j) Z_j\right]^2}{\hat{N}_t}}{(f_2+1)^2}.$$

Chao M_h Estimator

Capture heterogeneity occurs when each individual has its own capture probability that remains constant for all sampling occasions. The capture heterogeneity model, designated Model M_h, has N+1 parameters, the population size N and N capture probabilities ($p_1, p_2, \ldots, p_N$) (Otis et al. 1978). Estimation of N under model M_h is not possible because there are too many nuisance parameters. Therefore, capture probabilities $p_1, p_2, \ldots, p_N$ are conceptually thought of as a sample from an unknown probability distribution function.

Burnham and Overton (1978) derived a jackknife estimator of N for data generated under Model M_h. The jackknife estimator performs well for data sets including large numbers of recaptures and performs poorly for sparse data sets (Otis et al. 1978). Chao (1989) derived an alternative estimator of N for sparse data generated under Model M_h. Chao (1989) began with the following equation from Burnham and Overton (1978):

(30) $$E(f_i) = N \int_0^1 \binom{t}{i} p^i (1-p)^{t-i}\, dF(p), \quad i=0, \ldots, t.$$

Combining this equation with the Cauchy-Schwarz inequality

(31) $$\left[\int (1-p)^t\, dF(p)\right] \cdot \left[\int p^2 (1-p)^{t-2}\, dF(p)\right] \geq \left[\int p(1-p)^{t-1}\, dF(p)\right]^2$$

yielded

(32) $$E(f_0) \leq \left(\frac{t-1}{t}\right)\left(\frac{[E(f_1)]^2}{2E(f_2)}\right).$$

If t (the number of sampling occasions) is large, then a lower bound $\hat{N}_h$, an estimate of N, is

$$(33) \qquad \hat{N}_h = M_{t+1} + \frac{f_1^2}{2f_2}.$$

The minimal sufficient statistic for this estimator is $\{f_1, f_2, M_{t+1}\}$. Like the Chao M_t estimator for the temporal variation model, the Chao M_h estimator does not have a likelihood form. The asymptotic variance of $\hat{N}_h$ is

$$(34) \qquad \operatorname{var}(\hat{N}_h) \approx f_2\left[0.25\left(\frac{f_1}{f_2}\right)^4 + \left(\frac{f_1}{f_2}\right)^3 + 0.5\left(\frac{f_1}{f_2}\right)^2\right]$$

which is estimated by

$$(35) \qquad \widehat{\operatorname{var}}(\hat{N}_h) \approx f_2\left[0.25\left(\frac{f_1}{f_2}\right)^4 + \left(\frac{f_1}{f_2}\right)^3 + 0.5\left(\frac{f_1}{f_2}\right)^2\right].$$

Model and Estimator Selection

Model Selection in Program CAPTURE

I evaluated the utility of the model selection procedure in CAPTURE for analyzing juvenile rainbow trout mark-recapture data from the Henrys Fork. The model selection procedure uses a classification function based on the significance or probability levels of seven tests and nine additional variables based on all possible products of probability levels from the three tests against Model M_o and the three goodness-of-fit tests. The three tests against Model Mo are likelihood ratio tests of Model M_o versus Models M_b (i.e., behavioral response to capture), M_t, and M_h. There is also a likelihood ratio test of Model M_h versus Model M_{bh} (i.e., behavioral response in the presence of heterogeneity). The three goodness-of-fit tests are for

Models M_b, M_t, and M_h. The sixteen variables (p) are transformed by $\log(p+0.01)$, which weights smaller probabilities more heavily than larger probabilities closer to 1. The classification function was constructed by a discriminant function analysis of mark-recapture data simulated to represent real studies (Otis et al. 1978).

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; 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.

Estimator Selection by Simulation

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). I performed simulations to evaluate the performance of each closed-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 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 estimator to provide an abundance estimate and 95% confidence interval. Confidence intervals 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). 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_o, 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_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, 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 detect movement out of the sample areas.

Simulation

I simulated the movement of marked fish out of a sample area to determine the effect on abundance estimation of violating the population closure assumption. The following rates of permanent emigration of marked fish were examined: 0% (i.e., the simulations described earlier), 5%, and 10%. The range of emigration rates was based on observed movement out of Henrys Fork sample areas by age-0 rainbow trout. The capture probability was set to zero for the remaining sampling occasions for a percentage of captured fish. That is, if $p_{unif} \leq p_t \cdot e$ for $t = 1$ to 5 and $e = 0.05$ or 0.10, then that individual fish was permanently removed from the population by setting p_t equal to zero for the remaining sampling occasions. Estimator statistics were computed as described earlier.

Representative Sample Areas

A comparison of catch-per-unit-effort for an equal number of transects within and outside of sample areas was used to determine if sample areas in the Henrys Fork were representative of a river section. Sixteen transects outside of sample areas were randomly selected and sampled on the same date as the first capture occasion for the two sample areas in Box Canyon and Last Chance in summer and autumn 1997. Comparisons were performed using the *t*-test procedure in

SAS (PROC TTEST; SAS Institute 1994).

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 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 $\overline{p}$=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 $\overline{p}$ increased from 0.046 to 0.106 (Table 3). Model M_{tbh} was selected most frequently at $\overline{p}$=0.046 (52.0% to 78.3%). (There is no estimator in CAPTURE for model M_{tbh}.) Model M_t was selected most frequently at $\overline{p}$=0.078 (49.5% to 86.5%) and $\overline{p}$=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.1-A.3). Average bias, expressed as a percentage of the true abundance, was generally smaller than ±1% for closed populations (Figure 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). 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 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 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). 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 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 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). 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_o 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 as low as 2.1% as N, $\bar{p}$, and emigration rate increased.

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 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 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 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 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 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 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.4). These patterns of captures were consistent with model M_t. 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 captured four times, and none were recaptured five times (Appendix Table A.4). 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 5). There were more trout captured per transect within versus outside of sample areas for Box Canyon in autumn 1997 (Table 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.4). The mean capture probability ranged from 0.01 to 0.126 with a median of 0.036 (Appendix Table A.4). 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.4).

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 6 and 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 6); density was lowest in Harriman State Park (Appendix Table

A.4).

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, $\overline{p}=0.046$ 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 erythophthalmus*, 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 four 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. 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_o 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.

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.

References Cited

Bohlin, T., S. Hamrin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. Electrofishing–theory and practice with special emphasis on salmonids. Hydrobiologia 173:9-43.

Bohlin, T., and B. Sundstrom. 1977. Influence of unequal catchability on population estimates using the Lincoln index and the removal method applied to electro-fishing. Oikos 28:123-129.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information theoretic approach. Springer, New York.

Burnham, K. P., and W. S. Overton. 1978. Estimating the size of a closed population when capture probabilities vary among animals. Biometrika 65:625-633.

Chao, A. 1988. Estimating animal abundance with capture frequency data. Journal of Wildlife Management 52:295-300.

Chao, A. 1989. Estimating population size for sparse data in capture-recapture experiments. Biometrics 45:427-438.

Chao, A., S-M. Lee, and S-L. Jeng. 1992. Estimating population size for capture recapture data when capture probabilities vary by time and individual animal. Biometrics 48:201-216.

Cormack, R. M. 1992. Interval estimation for mark-recapture studies of closed populations. Biometrics 48:567-576.

Cross, D. G., and B. Stott. 1975. The effect of electric fishing on subsequent capture of fish. Journal of Fish Biology 7:349-357.

Darroch, J. N. 1958. The multiple-recapture census: I. Estimation of a closed population. Biometrika 45:343-359.

Elliott, J. M. 1994. Quantitative ecology and the brown trout. Oxford University Press, New York.

Jones, M. L., and J. D. Stockwell. 1995. A rapid assessment procedure for the enumeration of salmonine populations in streams. North American Journal of Fisheries Management 15:551-562.

Kennedy, G. J. A., and C. D. Strange. 1981. Efficiency of electric fishing for salmonids in relation to river width. Fisheries Management 12:55-60.

Koenig, C. C., and F. C. Coleman. 1998. Absolute abundance and survival of juvenile gags in sea grass beds of the northeastern Gulf of Mexico. Transactions of the American Fisheries Society 127:44-55.

Kruse, C. G., W. A. Hubert, and F. J. Rahel. 1998. Single-pass electrofishing predicts trout abundance in mountain streams with sparse habitat. North American Journal of Fisheries Management 18:940-946.

Magurran, A. E. 1986. Individual differences in fish behavior. Pages 338-365, *in* T. J. Pitcher, editor. The behavior of teleost fishes. Croom Helm, London.

MathWorks, Inc. 1998. MATLAB version 5. The MathWorks, Inc., Natick, Massachusetts.

Menkins, G. E., Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69:1952-1959.

Mesa, M. G., and C. B. Schreck. 1989. Electrofishing mark-recapture and depletion methodologies evoke behavioral and physiological changes in cutthroat trout. Transactions of the American Fisheries Society 118:644-658.

Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46:752-757.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107.

Rexstad, E., and K. Burnham. 1991. User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO.

Riley, S. C., and K. D. Fausch. 1992. Underestimation of trout population size by maximum likelihood removal estimates in small streams. North American Journal of Fisheries Management 12:768-776.

SAS Institute. 1994. SAS/STAT user's guide, version 6, fourth edition. SAS Institute, Cary, North Carolina.

Seber, G. A. F. 1992. A review of estimating animal abundance II. International Statistical Review 60:129-166.

Stanley, T. R., and K. P. Burnham. 1998. Estimator selection for closed-population capture recapture. Journal of Agricultural, Biological, and Environmental Statistics 3:131-150.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA 8787-NERP, Los Alamos, NM.

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

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	--
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 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 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*(age 0 | age 0) = probability of classifying a trout as age 0 given that the trout is age 0 (*P*(age 1 | 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 Season	River section	Number of age-0 trout	Number of age-1 trout		Parameter estimate	(SE)	*P*	*P*(age 0 | age 0)	*P*(age 1 | age 1)	Classification 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 2—Continued.

Sampling Season	River section	Number of age-0 trout	Number of age-1 trout		Parameter estimate	(SE)	P	P(age 0 | age 0)	P(age 1 | age 1)	Classification 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 2—Continued.

Sampling Season	River section	Number of age-0 trout	Number of age-1 trout		Parameter estimate	(SE)	*P*	*P*(age 0 | age 0)	*P*(age 1 | age 1)	Classification 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.—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}.

	Population size				
Model	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.—Continued.

	Population size				
Model	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 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

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

Table 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 4.—Continued.

			Recapture area		
Capture area	Total captured	d	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 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).

	Within sample areas		Outside of sample areas		
River section	*n*	(SE)	*n*	(SE)	*P*
		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 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	$\bar{\hat{N}}$	(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 6.—Continued.

Year	$\bar{\hat{N}}$	(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 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	$\hat{N}$	(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 7.—Continued.

Year	$\overline{\hat{N}}$	(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.

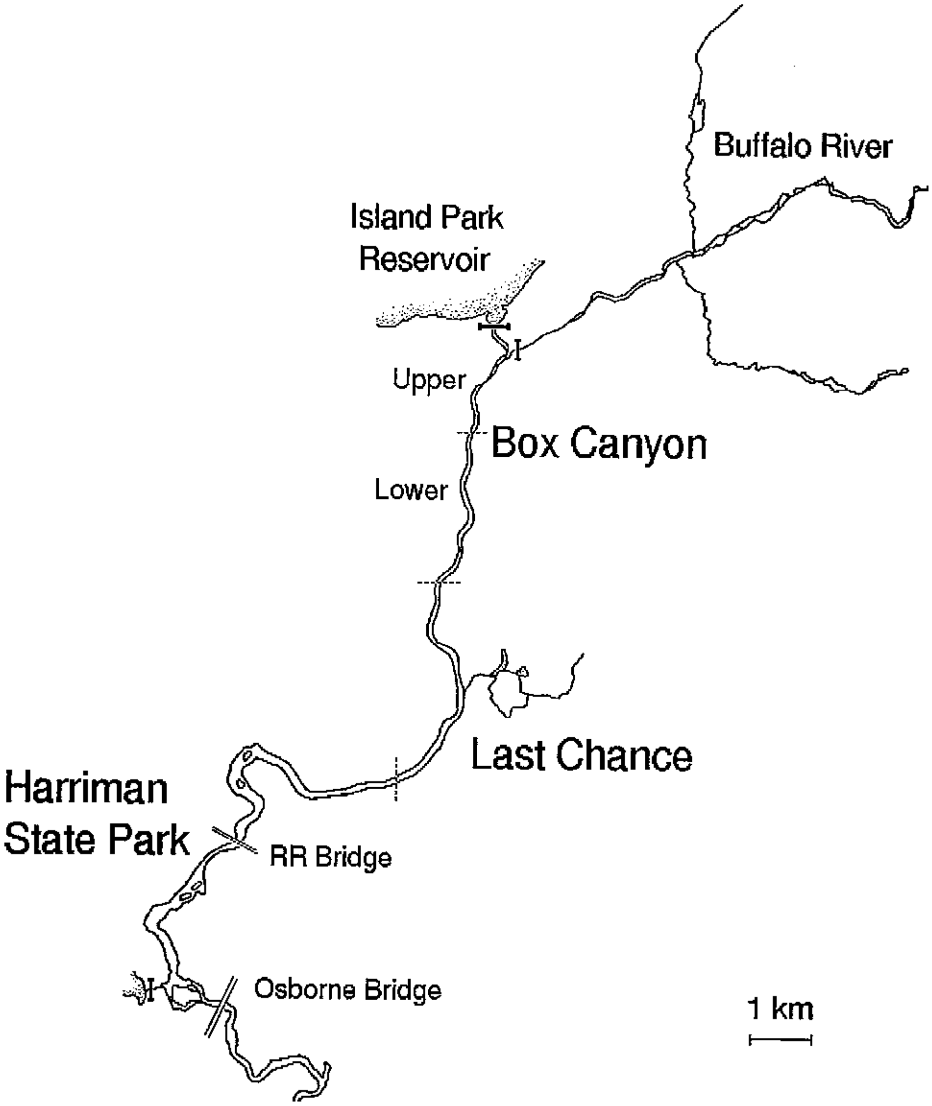

Figure 1.—Study sections of the Henrys Fork downstream of Island Park Reservoir and the Buffalo River: Box Canyon (upper and lower), Last Chance, and Harriman State Park. Lines with end-caps = dams, dashed lines = river section boundaries, and parallel lines = bridges.

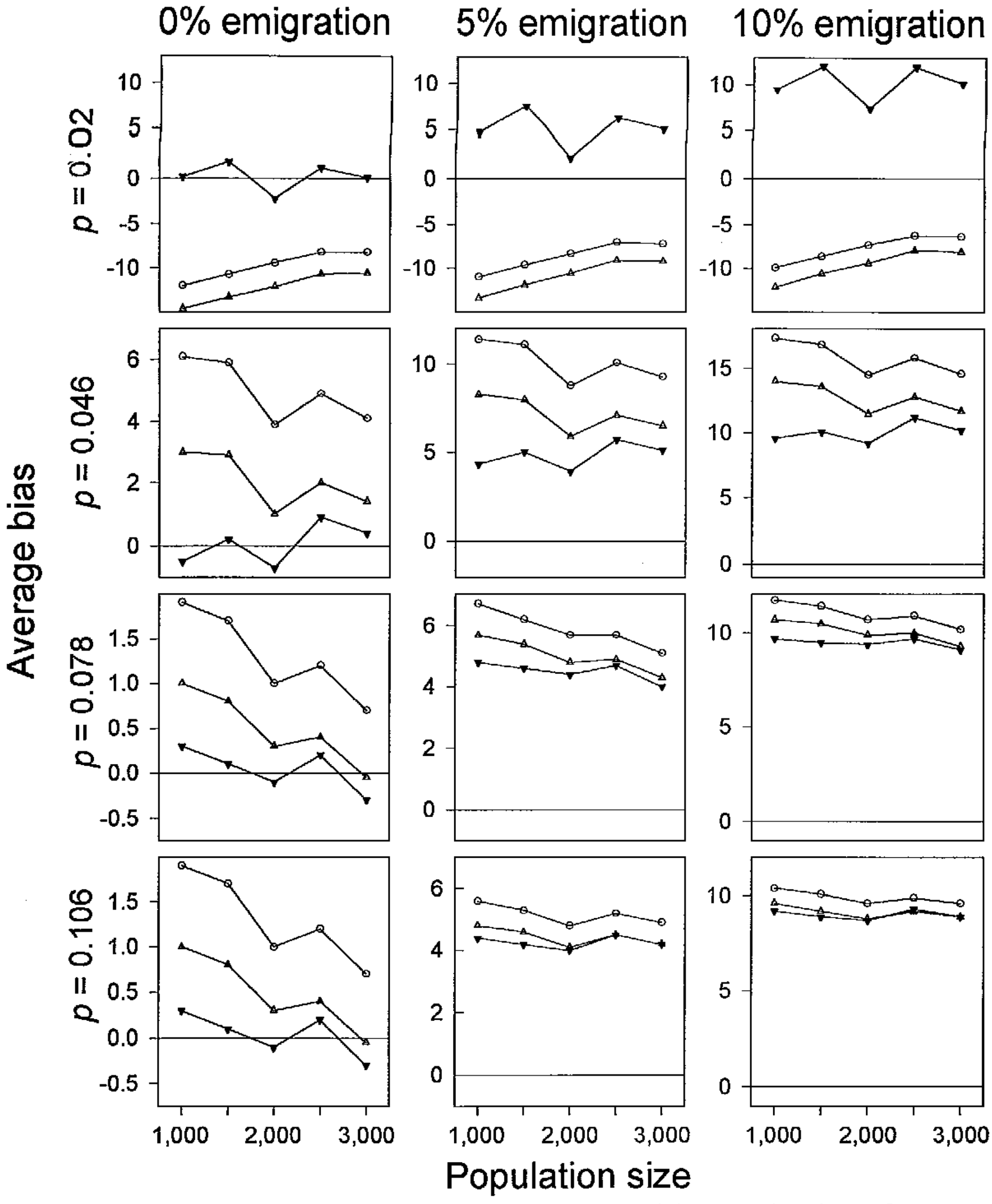

Figure 2.—Average bias expressed as a percentage of the true abundance for closed population abundance estimators (black triangles = Chao M_t, open triangles = Darroch M_t, and circles = Null M_o). Mark-recapture data were simulated under model M_t for four populations with permanent emigration of 0%, 5%, or 10% of marked fish. Average capture probabilities ranged from 0.02 to 0.106; t=5 capture occasions; 1,000 replications.

Table A.1.—Simulation results for comparing closed-population abundance estimators (Null M_o, Darroch M_t, Chao M_t, and Chao M_h). 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.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
1. $p_1=0.01$, $p_2=0.04$,	1,000	880.5	(162.3)	1,732.7	(419.8)	97.0	ne	ne	ne	ne	ne
$p_3=0.02$, $p_4=0.02$,	1,500	1,339.0	(207.0)	2,106.9	(432.4)	97.3	ne	ne	ne	ne	ne
$p_5=0.01$	2,000	1,812.5	(235.4)	2,442.0	(421.2)	97.9	ne	ne	ne	ne	ne
[$\bar{p}=0.02$]	2,500	2,295.0	(268.1)	2,753.0	(422.6)	97.7	3,866.7	(2,095.8)	6,470.0	(8,509.9)	88.0
	3,000	2,754.6	(300.9)	3,000.0	(442.0)	98.3	4,431.8	(1,689.5)	6,227.4	(4,097.4)	88.0
				Darroch M_t					**Chao M_t**		
	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
				Null M_o					**Chao M_h**		
2. $p_1=0.03$, $p_2=0.03$,	1,000	1,060.6	(238.4)	917.8	(346.2)	95.3	1,288.0	(333.2)	1,262.9	(517.5)	85.7
$p_3=0.05$, $p_4=0.05$,	1,500	1,588.8	(283.2)	1,098.5	(332.5)	95.1	1,912.2	(381.3)	1,487.4	(471.6)	81.4
$p_5=0.07$	2,000	2,077.0	(319.0)	1,223.4	(310.9)	94.5	2,500.4	(438.7)	1,660.5	(454.9)	77.6
[$\bar{p}=0.046$]	2,500	2,622.7	(367.7)	1,377.9	(319.5)	93.1	3,161.4	(499.3)	1,870.7	(455.1)	68.1
	3,000	3,124.4	(397.9)	1,493.0	(325.6)	94.3	3,760.0	(548.5)	2,022.3	(468.0)	66.2

Table A.1.—Continued.

	N	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
				Null M_o					**Chao M_h**		
3. p_1=0.08, p_2=0.07,	1,000	1,019.3	(115.2)	467.6	(91.5)	95.7	1,198.9	(165.1)	663.8	(146.4)	77.0
p_3=0.10, p_4=0.06,	1,500	1,525.0	(140.6)	566.1	(90.9)	95.6	1,783.2	(198.0)	795.5	(141.3)	67.5
p_5=0.08	2,000	2,021.0	(168.4)	646.8	(92.3)	94.6	2,366.9	(241.2)	911.8	(146.9)	59.3
[$\overline{p}$ =0.078]	2,500	2,529.7	(185.7)	720.5	(90.7)	95.2	2,961.3	(255.2)	1,014.6	(137.1)	51.5
	3,000	3,020.8	(196.6)	784.2	(89.1)	95.5	3,531.7	(280.1)	1,102.6	(139.1)	44.1
				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

Table A.1.—Continued.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
4. p_1=0.10, p_2=0.13,	1,000	1,012.8	(79.8)	322.2	(46.5)	95.8	1,162.4	(119.6)	466.9	(80.9)	68.6
p_3=0.08, p_4=0.10,	1,500	1,515.7	(100.1)	392.5	(47.5)	94.4	1,733.6	(142.2)	564.7	(77.0)	57.7
p_5=0.12	2,000	2,012.2	(117.8)	448.4	(48.0)	94.0	2,303.4	(171.5)	646.8	(80.3)	46.4
[$\overline{p}$ =0.106]	2,500	2,523.9	(131.8)	502.9	(47.2)	94.5	2,895.4	(186.6)	727.7	(77.0)	34.0
	3,000	3,020.7	(133.5)	548.3	(44.4)	96.1	3,457.9	(199.2)	790.6	(75.5)	28.4
				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.—Simulation results for comparing closed-population abundance estimators (Null M_o, Darroch M_t, Chao M_t, and Chao M_h). 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.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
1. p_1=0.01, p_2=0.04,	1,000	890.4	(156.7)	1,764.5	(401.2)	97.8	ne	ne	ne	ne	ne
p_3=0.02, p_4=0.02,	1,500	1,356.1	(196.5)	2,150.6	(404.5)	98.0	ne	ne	ne	ne	ne
p_5=0.01	2,000	1,833.8	(220.8)	2,488.4	(385.6)	98.8	ne	ne	ne	ne	ne
[$\overline{p}$ =0.02]	2,500	2,324.4	(248.6)	2,810.4	(378.9)	98.1	4,109.2	(2,331.3)	7,176.9	(9,831.9)	85.0
	3,000	2,785.2	(277.7)	3,054.9	(396.6)	98.8	4,693.7	(1,837.9)	6,825.4	(4,617.8)	83.6
				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
				Null M_o					**Chao M_h**		
2. p_1=0.03, p_2=0.03,	1,000	1,114.0	(259.0)	998.0	(387.6)	94.7	1,357.7	(370.5)	1,374.4	(607.4)	81.7
p_3=0.05, p_4=0.05,	1,500	1,666.3	(303.0)	1,190.6	(365.0)	93.5	2,010.2	(408.7)	1,608.5	(520.1)	74.1
p_5=0.07	2,000	2,176.9	(343.3)	1,324.3	(343.9)	92.7	2,625.0	(468.1)	1,791.1	(497.5)	67.7
[$\overline{p}$ =0.046]	2,500	2,751.6	(397.4)	1,494.1	(356.4)	90.7	3,323.0	(534.0)	2,021.5	(499.5)	55.2
	3,000	3,278.8	(424.9)	1,619.1	(357.6)	92.1	3,948.2	(581.1)	2,181.4	(508.7)	51.8

Table A.2.—Continued.

	N	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
				Null M_o					**Chao M_h**		
3. p_1=0.08, p_2=0.07,	1,000	1,066.7	(127.8)	508.4	(104.9)	94.0	1,258.5	(180.8)	718.4	(163.8)	65.4
p_3=0.10, p_4=0.06,	1,500	1,593.7	(151.0)	613.6	(100.5)	92.6	1,870.3	(213.7)	859.6	(156.4)	49.6
p_5=0.08	2,000	2,113.0	(183.7)	701.7	(103.8)	91.2	2,482.9	(261.6)	985.4	(163.0)	42.2
[$\bar{p}$ =0.078]	2,500	2,643.7	(201.0)	781.0	(101.4)	88.8	3,104.5	(276.4)	1,095.4	(152.7)	30.6
	3,000	3,153.8	(210.1)	848.5	(97.5)	90.2	3,696.4	(297.3)	1,187.1	(150.9)	24.1
				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

Table A.2.—Continued.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
4. p_1=0.10, p_2=0.13,	1,000	1,056.1	(87.3)	350.1	(52.6)	90.6	1,216.8	(129.1)	505.0	(88.9)	53.1
p_3=0.08, p_4=0.10,	1,500	1,580.2	(107.9)	426.3	(52.8)	88.7	1,815.1	(154.4)	611.1	(85.6)	36.3
p_5=0.12	2,000	2,096.4	(127.2)	486.4	(53.4)	86.3	2,410.5	(183.2)	699.3	(87.7)	26.6
[$\overline{p}$ =0.106]	2,500	2,629.2	(140.5)	545.3	(51.9)	84.0	3,027.0	(199.3)	785.3	(84.2)	14.7
	3,000	3,147.3	(144.9)	594.8	(49.7)	84.6	3,616.6	(214.8)	853.9	(83.2)	9.3
				Darroch M_t					**Chao M_t**		
	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.—Simulation results for comparing closed-population abundance estimators (Null M_o, Darroch M_t, Chao M_t, and Chao M_h). 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.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
1. p_1=0.01, p_2=0.04,	1,000	900.9	(148.9)	1,798.4	(376.6)	98.2	ne	ne	ne	ne	ne
p_3=0.02, p_4=0.02,	1,500	1,371.5	(186.5)	2,189.7	(372.9)	98.3	ne	ne	ne	ne	ne
p_5=0.01	2,000	1,853.7	(204.3)	2,533.0	(346.0)	99.5	ne	ne	ne	ne	ne
[$\overline{p}$ =0.02]	2,500	2,344.1	(232.8)	2,851.4	(344.0)	98.8	4,384.0	(2,524.0)	7,970.0	(10,850)	82.0
	3,000	2,809.8	(252.8)	3,099.9	(349.0)	99.2	4,969.0	(2,088.0)	7,526.0	(5,866.0)	80.0
				Darroch M_t					**Chao M_t**		
	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
				Chao M_h					**Null M_o**		
2. p_1=0.03, p_2=0.03,	1,000	1,434.8	(413.7)	1,502.2	(726.1)	74.9	1,172.6	(278.3)	1,089.0	(430.9)	93.4
p_3=0.05, p_4=0.05,	1,500	2,117.6	(440.9)	1,745.3	(582.6)	64.1	1,752.1	(323.9)	1,295.7	(402.8)	90.6
p_5=0.07	2,000	2,766.7	(513.3)	1,944.2	(565.6)	55.1	2,289.7	(373.5)	1,441.7	(385.5)	89.3
[$\overline{p}$ =0.046]	2,500	3,505.5	(573.1)	2,196.3	(551.5)	43.0	2,895.8	(429.8)	1,627.7	(398.9)	86.3
	3,000	4,148.5	(619.9)	2,355.0	(556.5)	37.4	3,438.6	(451.0)	1,752.9	(389.0)	86.1

Table A.3.—Continued.

	N	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
				Null M_o					**Chao M_h**		
3. p_1=0.08, p_2=0.07,	1,000	1,117.3	(138.8)	553.1	(118.0)	87.2	1,323.4	(195.3)	779.3	(182.6)	52.9
p_3=0.10, p_4=0.06,	1,500	1,671.6	(167.2)	669.2	(115.2)	83.8	1,967.3	(232.3)	932.8	(174.2)	35.4
p_5=0.08	2,000	2,214.8	(198.6)	764.1	(116.0)	81.2	2,610.3	(281.5)	1,068.2	(179.8)	25.9
[$\overline{p}$ =0.078]	2,500	2,771.5	(219.2)	850.7	(114.7)	74.9	3,265.2	(302.8)	1,188.3	(172.1)	13.2
	3,000	3,304.6	(230.5)	923.4	(110.6)	73.6	3,890.1	(323.8)	1,289.1	(168.9)	9.4
				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

Table A.3.—Continued.

	N	Average estimate	(SE)	Average interval length	(SE)	% cov.	Average estimate	(SE)	Average interval length	(SE)	% cov.
				Null M_o					**Chao M_h**		
4. p_1=0.10, p_2=0.13,	1,000	1,104.4	(93.6)	382.0	(58.4)	80.6	1,279.0	(138.8)	549.6	(98.6)	34.5
p_3=0.08, p_4=0.10,	1,500	1,650.8	(118.7)	464.2	(60.1)	73.9	1,905.7	(169.3)	663.8	(96.2)	19.1
p_5=0.12	2,000	2,191.1	(138.7)	530.2	(60.3)	67.5	2,530.5	(197.7)	759.4	(96.8)	11.3
[$\bar{p}$=0.106]	2,500	2,747.4	(153.4)	594.2	(58.8)	58.5	3,177.1	(216.6)	852.4	(93.9)	4.7
	3,000	3,288.3	(159.0)	647.9	(56.2)	54.5	3,797.5	(234.9)	927.6	(93.2)	2.1
				Darroch M_t					**Chao M_t**		
	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.—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; Mt+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., $\{\{f(2)+f(3)\cdot 2+f(4)\cdot 3+f(5)\cdot 4\}/n(T)\}\cdot 100$ (%)).

				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
								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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. 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.4.—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 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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. 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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
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.4.—Continued.

				f(1)	f(2)	f(3)	f(4)	f(5)						
				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]	Capt. eff.	Recap. 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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. 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.4.—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
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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
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.4.—Continued.

Year	T	Mt+1	n(T)	f(1) z(1) $\hat{p}_1$	f(2) z(2) $\hat{p}_2$	f(3) z(3) $\hat{p}_3$	f(4) z(4) $\hat{p}_4$	f(5) z(5) $\hat{p}_5$	$\hat{p}_{mean}$	$\hat{N}$	(SE)	[LB—UB]	Capt. eff.	Recap. rate
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					