Fishery Manuscript No. 99-1

Estimating Natural Mortality and Abundance of Potamodromous Lake Dwelling Cutthroat Trout at Florence Lake, Alaska

by

Gregg Rosenkranz,

Robert P. Marshall,

Roger D. Harding,

and

David R. Bernard

March 1999

Alaska Department of Fish and Game **Division of Sport Fish**

Symbols and Abbreviations

The following symbols and abbreviations, and others approved for the Système International d'Unités (SI), are used in Division of Sport Fish Fishery Manuscripts, Fishery Data Series Reports, Fishery Management Reports, and Special Publications without definition. All others must be defined in the text at first mention, as well as in the titles or footnotes of tables and in figures or figure captions.

Weights and measures (metric)

centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
metric ton	mt
milliliter	ml
millimeter	mm

Weights and measures (English)

cubic feet per second	ft^3/s
foot	ft
gallon	gal
inch	in
mile	mi
ounce	oz
pound	lb
quart	qt
yard	yd

Spell out acre and ton.

Time and temperature

day	d
degrees Celsius	°C
degrees Fahrenheit	°F
hour (spell out for 24-hour clock)	h
minute	min
second	s

Spell out year, month, and week.

Physics and chemistry

all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General

All commonly accepted abbreviations.	e.g., Mr., Mrs., a.m., p.m., etc.
All commonly accepted professional titles.	e.g., Dr., Ph.D., R.N., etc.
and	&
at	@
Compass directions:	
east	E
north	N
south	S
west	W
Copyright	©
Corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
et alii (and other people)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.,
id est (that is)	i.e.,
latitude or longitude	lat. or long.
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
number (before a number)	# (e.g., #10)
pounds (after a number)	# (e.g., 10#)
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S. state and District of Columbia abbreviations	use two-letter abbreviations (e.g., AK, DC)

Mathematics, statistics, fisheries

alternate hypothesis	H_A
base of natural logarithm	e
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	F, t, χ^2, etc.
confidence interval	C.I.
correlation coefficient	R (multiple)
correlation coefficient	r (simple)
covariance	cov
degree (angular or temperature)	°
degrees of freedom	df
divided by	÷ or / (in equations)
equals	=
expected value	E
fork length	FL
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	$\log_2$, etc.
mideye-to-fork	MEF
minute (angular)	'
multiplied by	x
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	"
standard deviation	SD
standard error	SE
standard length	SL
total length	TL
variance	Var

FISHERY MANUSCRIPT NO. 99-1

ESTIMATING NATURAL MORTALITY AND ABUNDANCE OF POTAMODROMOUS LAKE DWELLING CUTTHROAT TROUT AT FLORENCE LAKE, ALASKA

by

Gregg Rosenkranz
University of Alaska Fairbanks

Robert P. Marshall
Division Sport Fish / RTS, Juneau

Roger D. Harding
Division Sport Fish, Juneau

and

David R. Bernard
Division Sport Fish / RTS, Anchorage

Alaska Department of Fish and Game
Division of Sport Fish
Anchorage, Alaska

March 1999

Development of this manuscript was partially financed by the Federal Aid in Sport Fish Restoration Act (16 U.S.C. 777-777K) under Project F-10-7, F-10-8, F-10-9, F-10-12 and F-10-14, Job No. R-T-1.

The Fishery Manuscript Series was established in 1987 for the publication of technically oriented results of several years' work undertaken on a project to address common objectives, provide an overview of work undertaken through multiple projects to address specific research or management goal(s), or new and/or highly technical methods. Fishery Manuscripts are intended for fishery and other technical professionals. Distribution is to state and local publication distribution centers, libraries and individuals and, on request, to other libraries, agencies, and individuals. This publication has undergone editorial and peer review.

Address correspondence to:

Robert P. Marshall
Alaska Department of Fish and Game, Division of Sport Fish / RTS,
POB 240020, Douglas, AK 99824-0020, USA
Telephone: (907) 465-4303 e-mail: BobM@fishgame.state.ak.us

This document should be cited as:
Rosenkranz, Gregg, Robert P. Marshall, Roger D. Harding, and David R. Bernard. 1999. Estimating natural mortality and abundance of potamodromous lake dwelling cutthroat trout at Florence Lake, Alaska. Alaska Department of Fish and Game, Fishery Manuscript No. 99-1, Anchorage.

The Alaska Department of Fish and Game administers all programs and activities free from discrimination on the basis of sex, color, race, religion, national origin, age, marital status, pregnancy, parenthood, or disability. For information on alternative formats available for this and other department publications, contact the department ADA Coordinator at (voice) 907-465-4120, or (TDD) 907-465-3646. Any person who believes s/he has been discriminated against should write to: ADF&G, P.O. Box 25526, Juneau, AK 99802-5526, or O.E.O., U.S. Department of the Interior, Washington, DC 20240.

TABLE OF CONTENTS

Page

LIST OF TABLES ii

LIST OF FIGURES ii

ABSTRACT 1

INTRODUCTION 1

METHODS 2

Compiling Data 2
Model and Assumptions 3
Testing Model Assumptions 4

- Detecting heterogeneous capture and survival probabilities 4
- Detecting heterogeneity in capture probabilities related to size 5
- Detecting heterogeneity in survival probabilities related to size/age 6
- Detecting effects related to handling 6
- Effects of tag loss 6
- Instantaneous sampling 6

RESULTS 6

Estimates 6
Heterogeneity in Survival and Capture Probabilities 10
Heterogeneity in Capture Probabilities by Size 10
Heterogeneity in Survival Probabilities by Size/Age 11
Effect of Handling 12
Tag Loss 13

DISCUSSION 14

RECOMMENDATIONS 18

The Spawning Season Straddle 19
The Summer Strategy 19
The Spring Stretch 19

ACKNOWLEDGMENTS 19

LITERATURE CITED 20

APPENDIX A 21

LIST OF TABLES

Table **Page**

1. Estimates from the 4-event and 16-event versions of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 7
2. Summary of GOF tests to the model used in the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 11
3. Summary of GOF tests to the model used in the 16-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 11
4. Breakdown for 1992 and 1993 of statistics for component 1 of the GOF tests to the model used in the 4-event version of the JS experiment on cutthroat trout in Florence Lake 12
5. Breakdown for 1993 of statistics for component 2 of the GOF tests to the model used in the 4-event version of the JS experiment on cutthroat trout in Florence Lake 12
6. Residuals from the fitting the log-linear model to capture histories for the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 13
7. Results of likelihood ratio tests from log-linear models to test two-level length-stratification in the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 13
8. Results of likelihood ratio testing of three-level stratification by size in 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake 14
9. Estimates of cutthroat trout abundance, survival rate, surviving recruitment, and probability of capture from Jolly-Seber and log-linear models, 1991–1994 study at Florence Lake 14
10. Estimated cutthroat trout abundance and survival rates at Florence Lake, 1991–1994, and associated analytical standard errors SE_A, bootstrap standard errors SE_B, and bootstrap confidence intervals for the 4-event JS experiment, optimally stratified by fork length 15
11. Estimates of cutthroat trout abundance and survival rates and goodness-of-fit (GOF) statistics for the 4-event version of the JS experiment at Florence Lake, 1991–1994: data stratified by size of fish at the time of the initial marking 16
12. Estimates for the 4-event version JS experiment from 1991–1994 on cutthroat trout in Florence Lake, fitted to analytical and log-linear models after multiple recaptures within a year were deleted 16
13. Standard errors and confidence intervals of the Jolly-Seber abundance and survival estimates for Florence Lake cutthroat trout, derived from the data after multiple recaptures within a year were deleted 16
14. Comparison of standardized residuals from log-linear models of cutthroat trout capture histories at Florence Lake in the 4-event version of the 1991–1994 JS experiment between the full (original) analysis and the analysis after all fish captured more than once within a year were deleted 17

LIST OF FIGURES

Figure **Page**

1. Bathymetric map of Florence Lake on Admiralty Island, Southeast Alaska, showing location of the nine sampling areas in 1991–1994 2
2. Design of trap used at Florence Lake 3
3. Diagram of contingency table for the first component of the goodness-of-fit test 5
4. Diagram of the second component of the goodness-of-fit test 5
5. Abundance estimates for 1991–1994 under three experimental designs 8
6. Estimated survival rates from 1991–1994 under two experimental designs 9

LIST OF APPENDICES

Appendix **Page**

A1. Statistics for 4-event Jolly-Seber estimates for the Florence Lake data 23
A2. Statistics for 16-event Jolly-Seber estimates for the Florence Lake data 23
A3. Location of sampling data and file containing this report 24

ABSTRACT

Independent mark-recapture experiments were conducted annually at Florence Lake in Southeast Alaska from 1991 through 1994 to estimate abundance of potamodromous cutthroat trout *Oncorhynchus clarki* using models for closed populations (CP). These data were recompiled to estimate abundance and survival using two Jolly-Seber (JS) experiments: a 4-event (annual) version and a 16-event (trip-by-trip) version.

Estimated abundance from both versions of the JS experiment were about 24–64% lower than their comparable CP estimates for 1991 and 1992 and 63% lower to 6% higher in 1993 and 1994. Estimated abundances from the 16-event version were relatively stable within 1991 and 1992, but dropped precipitously during sampling in 1993 and 1994. Estimates of survival rates and surviving recruitment from the 16-event version implied unusually high turnover in the population during sampling in 1991 and 1992. In contrast, similar estimates in 1993 and 1994 indicated high loss to the population with no balancing recruitment. We found little evidence for age or size-specific mortality or capture rates, tag loss, or effects of handling. Evidence for some mortality related to dart tagging was present, but it could not explain the discrepant estimates.

Discrepancies between CP and JS estimates resulted largely because of where sampling occurred in 1991 and 1992, and when sampling occurred in later years. Sampling in 1991 and 1992 was limited to littoral areas ≤ 14 m in depth, but extended to depths ≤ 30 m in 1993 and 1994. Sampling dates changed also: from July and June in 1991 and 1992 to April and May in 1993 and 1994. Bias in the early CP estimates was caused by simultaneous migrations between sampled and unsampled lake areas (depths) and bias in the later estimates resulted from fish leaving the lake temporarily to spawn, in streams where they were not subject to capture. Procedures are recommended to provide accurate, efficient estimates of annual abundance, survival rates, and surviving recruitment for lacustrine populations of cutthroat trout.

INTRODUCTION

Independent mark-recapture experiments were conducted annually at Florence Lake (Figure 1) from 1991 through 1994 to estimate abundance of cutthroat trout *Oncorhynchus clarki*. The lake covers about 320 hectares, is about 7 km in length, and varies in width from about 0.4 to 0.8 km. About 60% of the lake is ≤14 m (45 ft) in depth and the maximum depth is 27 m. Cutthroat trout in the lake are potamodromous, and support a sport fishery that harvested an estimated 464, 175, 197, and 326 fish annually from 1991 through 1994 (Jones et al. 1992; Jones 1993, 1994, 1995).

Each summer and/or spring, fish were captured during four 9- to-10-day sampling trips usually separated by 4 to 10 days. Traps baited with salmon eggs were the primary sampling gear (Figure 2), and hook and line sport fishing gear served as a secondary gear. Fyke nets and hoop nets were also used occasionally in 1991, and an additional 9-day sampling trip preceded the usual series of (four) sampling trips in 1992. Beginning in 1992, weirs were also placed on two very small creeks discharging into Florence Lake to capture fish migrating to and from presumed spawning areas. All unmarked cutthroat trout ≥180 mm FL captured in good condition were tagged with a uniquely numbered anchor T-bar tag, marked by complete excision of their adipose fin, measured for length, sampled for scales, and released. All recaptured fish were inspected for missing fins, tag scars, and tag numbers, measured for length, sampled for scales, and released. In 1991 and 1992, sampling was conducted in littoral areas with depths ≤14 m, and in 1993 and 1994 sampling was extended across the entire lake surface without regard to depth. Sampling was advanced to earlier dates each year as researchers discovered that catch rates were substantially greater earlier in the year. The duration of sampling ranged from 50 to 78 days per year, and the mean dates of sampling were July 16 (1991), June 5 (1992), May 11 (1993), and May 5 (1994).

In previous studies, Lincoln/Petersen and/or Darroch closed-population (CP) models (Seber

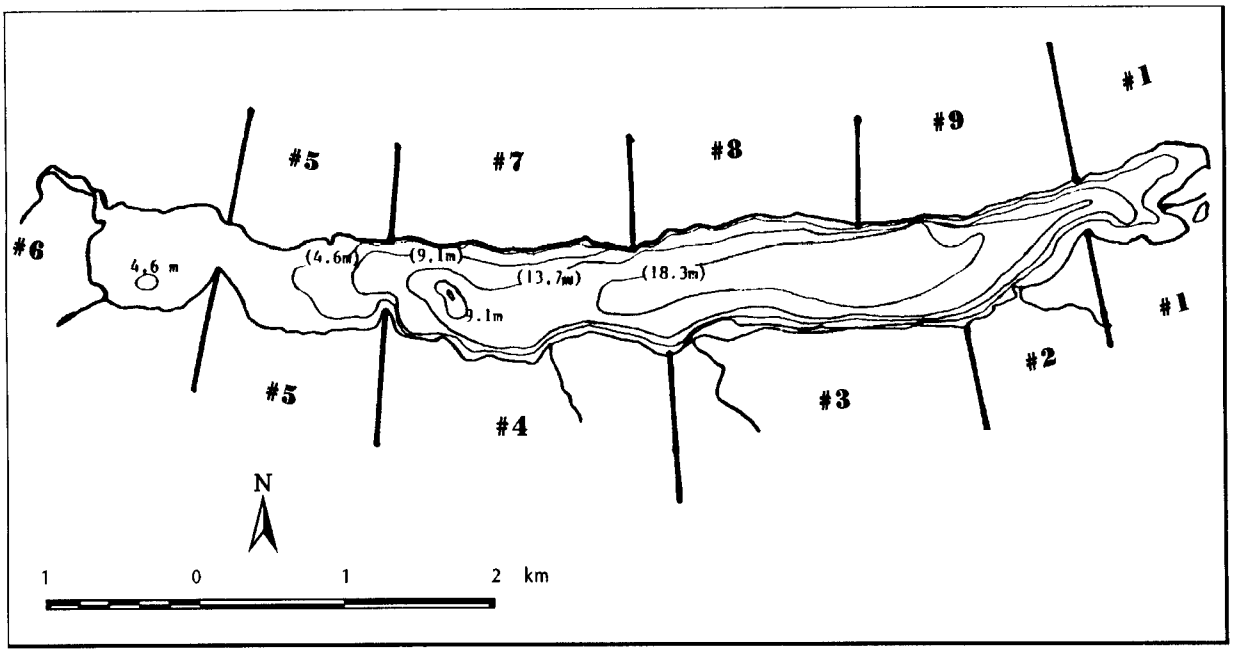

Figure 1.–Bathymetric map of Florence Lake on Admiralty Island, Southeast Alaska, showing location of the nine sampling areas in 1991–1994.

1982:59,431) were used to estimate abundance. The estimator of choice depended on whether capture probabilities varied significantly by area (ends or middle) of the lake. Annual data for these CP analyses (excluding weir samples) were pooled to yield "marking" and "recapture" events separated by 6, 29, 7, and 10 days from 1991 to 1994, respectively. Hypothesis that fish of different sizes were captured with equal probability was tested, and in 1991 and 1992 the population was stratified into two size classes (above or below about 210 mm FL) to reduce bias in the estimation procedure. Abundance estimates for 1991 to 1994 were 8,924 (SE = 1,052), 10,586 (SE = 1,536), 8,382 (SE = 818), and 10,787 (SE = 674), for fish ≥180 mm fork length (Jones et al. 1992; Harding and Jones 1993, 1994; Harding 1995).

The primary objective of the analysis reported below was to estimate annual survival rates for the population of cutthroat trout in Florence Lake from mark-recapture data collected from 1991 through 1994. Jolly-Seber (JS) and log-linear models (LLMs) for open populations were applied to data pooled by sampling year to create a 4-event experiment, and to data segregated by sampling trip to create a 16-event experiment. However, abundance estimates from the JS experiments contrasted poorly with results from previously concluded CP models based on the same data (Jones et al. 1992; Harding and Jones 1993, 1994; Harding 1995). The comparison revealed striking differences that we investigated with additional analyses sensitive to the underlying assumptions of the JS and CP experiments. The results provide important insights into past and future sampling programs for cutthroat trout in Southeast Alaska.

METHODS

Compiling Data

We compiled capture histories for individual cutthroat trout ≥180 mm FL sampled from 1991 through 1994 in four independent CP experiments into two Jolly-Seber (JS) experiments: a 4-event version and a 16-event version. In the 4-event version, each year's CP experiment represents one sampling event. Data for this analysis included the small number of fish collected at weirs (1992–1994) and during the early-season sampling trip in

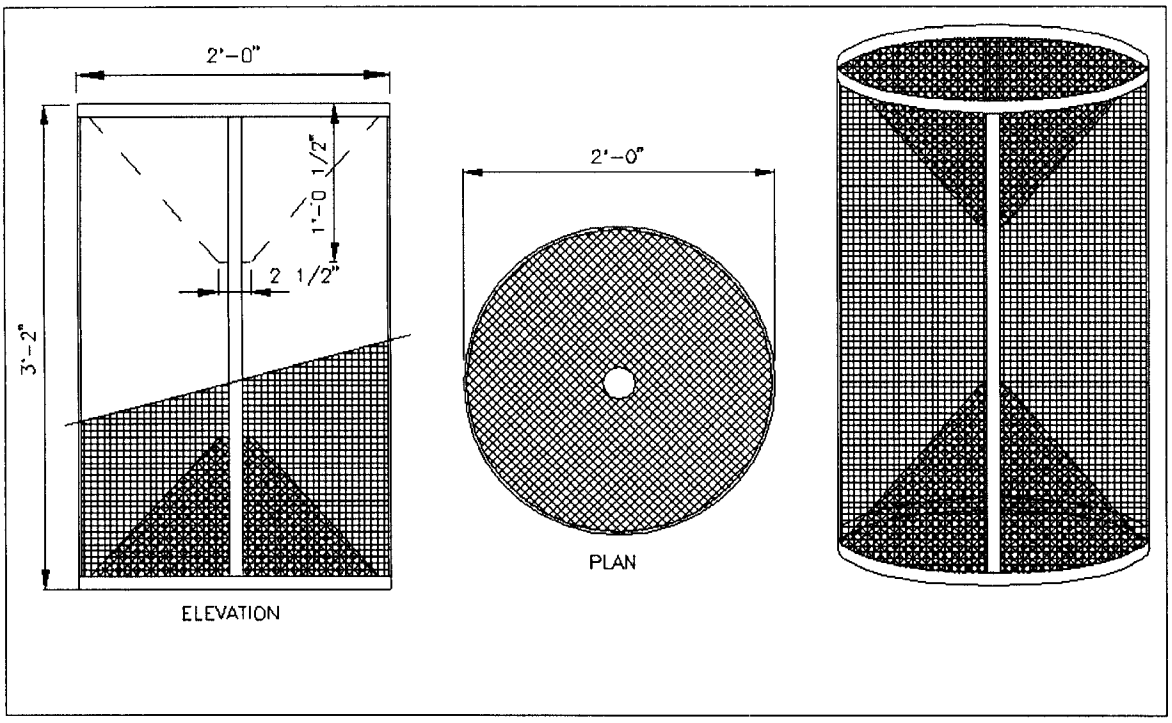

Figure 2.–Design of trap used at Florence Lake.

1992. Cutthroat trout captured several times in a given year were treated as being caught only once. In the 16-event version, each sampling trip was treated as an event. Samples collected only occasionally with fyke nets and weirs (1992–1994) and during the early-season sampling trip in 1992 were excluded from this analysis. Again, fish repeatedly recaptured within a sampling event were considered as being captured but once for analysis. Information on timing of spawning collected from weirs (1992–1994) and during the early-season sampling trip in 1992 was used in the analysis.

Fork length measurements of all cutthroat trout captured were kept in the data to permit stratification based on fish size. Extensive error checking was performed to identify suspect records, insure accurate capture history records, and to eliminate data recording and entry errors. Incorrectly recorded length measurements were the most common error found, but frequently, this can be corrected with information from field notes or by comparing lengths when recaptured. In a very few instances, suspect records (tag numbers) were removed from the analysis or simple probability arguments were used to assign a missing length when a better method was unavailable.

Model and Assumptions

The main objective of this research led to selection of the "full" Jolly-Seber model, which provides k-2 survival rate estimates and k-2 abundance estimates (k = number of sampling events). The JS model requires the following assumptions (Seber 1982:196,223; Pollock et al. 1990:18,24):

- all fish in the population at the time of the ith sample have the same probability of capture; or
- marked and unmarked fish mix completely between sampling events; and
- all marked fish in the population immediately after the ith sample have the same the probability of surviving until the $(i + 1)$th sample; and
- fish do not temporarily leave the population (or become uncatchable) then return at a later time; and

- marks are not lost or overlooked; and
- sampling is instantaneous with animals being released immediately;

and uses the following statistics:

n_i = number of fish caught in sample *i*;

m_i = number of marked fish caught in sample *i*;

R_i = number returned to the population alive with marks from sample *i*;

r_i = number caught in sample *i* which are recaptured later; and

z_i = number not caught in sample *i* which were previously captured and are recaptured later.

The JS and Lincoln-Petersen abundance estimators both assume that the proportion of marked fish in the sample is representative of that in the population. An intuitive basis for the JS model is found in the following formulas relating marked and unmarked contingents of the population (Seber 1982:200; Pollock et al. 1990:20). The number of marked fish M_i immediately before the *i*th sample is estimated as

$$\hat{M}_i = m_i + \frac{R_i z_i}{r_i}, \quad i = 2,...,k-1 \qquad (1)$$

The total population size N_i immediately before the *i*th sample is estimated as

$$\hat{N}_i = \frac{n_i \hat{M}_i}{m_i}, \quad i = 2,...,k-1 \qquad (2)$$

The survival rate between the *i*th and $(i+1)$th sampling event ϕ_i is estimated as

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}, \quad i = 2,...,k-2 \qquad (3)$$

where $\hat{\phi}_1 = \hat{M}_2 / R_1$. The probability of capture p_i during the *i*th sampling event is estimated as

$$\hat{p}_i = \frac{m_i}{\hat{M}_i} = \frac{n_i}{\hat{N}_i}, \quad i = 2,...,k-1 \qquad (4)$$

Recruitment B_i between the *i*th and $(i+1)$th sample that survives to the $(i+1)$th sample is estimated as

$$\hat{B}_i = \hat{N}_{i+1} - \hat{\phi}_i(\hat{N}_i - n_i + R_i), \quad i = 2,...,k-2 \qquad (5)$$

Of primary interest in this analysis were the survival and abundance estimates, both of which depend on $\hat{M}$, the estimated number of marked fish in the population. The survival rate estimator $\hat{\phi}_i$ is formed as the ratio of $\hat{M}$ before sample $i+1$ and after sample *i*. This estimator is somewhat robust to unequal catchability induced by differences in *individual animal* behavior or sampling techniques (Carothers 1973), but applies to marked fish only.

Thus the assumption of an equal survival rate for all fish marked and unmarked is necessary for making inferences about the population as a whole. Capture history matrices for the analyses were constructed using computer code written in the SAS language (SAS 1990). POPAN-PC (Arnason et al. 1992) was used to fit JS and log-linear models (LLMs) to capture histories and to calculate likelihood ratio GOF statistics. Program JOLLY (Pollock et al. 1990) was used to obtain contingency table GOF statistics, and RECAP (Buckland 1980) to obtain confidence intervals and constrained estimates of model parameters in special situations as noted in the text.

TESTING MODEL ASSUMPTIONS

Detecting Heterogeneous Capture and Survival Probabilities

Two contingency table chi-square tests developed by Pollock et al. (1985) were used to evaluate goodness-of-fit (GOF) for both versions of JS experiments. As implemented in our analysis (see below), both tests have similar abilities to detect heterogeneous capture probabilities (Pollock et al. 1990:24). The first portion of the two-component test (Figure 3) is equivalent to the Robson (1969) test for short-term mortality. Note that the nomenclature "short-term" refers to less than a *one-year* period in the 4-event version of the experiment and less than a few days for most instances in the 16-event version. Pollock et al. (1990:24) report the second test component (Figure 4) to be the better of the two at

	First captured before sample *i*	First captured in sample *i*
Captured in sample *i* and recaptured later	*	*
Captured in sample *i* and not recaptured later	*	*

Figure 3.–Diagram of contingency table for the first component of the goodness-of-fit test. There are k-2 such tables in each test.

	First captured before $i-1$ and not captured in $i-1$	First captured before $i-1$, and captured in $i-1$	First captured in $i-1$
Captured in sample *i*	*	*	*
Captured after *i* but not in *i*	*	*	*

Figure 4.–Diagram of the second component of the goodness-of-fit test. There are k-3 such tables in each test.

detecting heterogeneous survival probabilities among marked groups (newly marked and previously marked). A summation of the chi-squares from each component forms an omnibus test for violations of the first three assumptions listed above. Note that there are certain violations of these three assumptions these tests cannot detect; e.g., permanent trap response and permanent lowering of survival rate due to handling and marking (Pollock et al. 1985, 1990:24).

Detecting Heterogeneity in Capture Probabilities Related to Size

Capture probabilities were found to vary by fish size at Florence Lake during two of four CP experiments (1991 and 1992; Jones et al. 1992; Harding and Jones 1993). In our reworking of the CP experiments, data were stratified into size groups and estimates of abundance were compared. If the estimates were significantly different, we would assume the result from the stratified analysis to be more accurate.

Because stratification confounds estimates of survival and recruitment for all but the largest size class, and can lead to declines in precision as within-strata sample sizes decline, we adopted a likelihood ratio goodness-of-fit statistic obtained by fitting LLMs to the mark-recapture data (Cormack 1989). The objective of this fitting procedure was to find cutpoints between size groups (large and small) which maximized total P-value from test statistics given a minimum P-value of 0.10 across strata. If this criterion could not be met, we increased the number of strata and repeated the GOF procedure.

Assumptions behind the LLMs are the same as those for the JS model described above. By modeling the log expected value of the count of animals with each capture history as a linear combination of GLIM (generalized linear model) parameters, LLMs can be fit through numerical maximization of a joint likelihood. This allows the straightforward calculation of a single likelihood ratio goodness-of-fit statistic, which we used to compare various length-stratification schemes, and

also for comparison to the GOF statistics obtained with the contingency table analysis.

Detecting Heterogeneity in Survival Probabilities Related to Size/Age

Because estimated ages of cutthroat trout sampled were not available for this analysis, we used size as a surrogate. Survival rates over time were estimated for size groups based on fish size *at the time of the initial marking.* If estimated survival rates varied significantly by size group, simulation could easily be conducted to investigate the relative magnitudes of biases on parameter estimates. Size groups for the analysis were adopted from results of the length-based testing described above.

The analysis was implemented by building an ($N \times 4$) capture history matrix for each size group of interest, where N represents the number of distinct fish marked during the four-year experiment. Capture histories of fish within a given size group first marked and released in 1991 were grouped without regard to size in 1992–1994 to produce an ($S \times 4$) matrix ($S < N$) with each row vector of the form (1xxx), where 1 signifies a capture and x is either 1 or 0 (not captured). Note that each succeeding capture represents existence over an annual increment.

Next, each fish identified in the former analysis was removed from the data, and capture histories of fish within the same size group first marked and released in 1992 were grouped without regard to size in 1993–1994 to produce an ($T \times 4$) matrix ($T < N$) with each row vector of the form (01xx). Additional repetition of the procedure yielded matrices with row vectors of the form (001x) and (0001). Concatenation of the matrices yielded a complete size/age-based capture history matrix for fish of one size group at the time of marking.

Repetition of the entire procedure above yielded complete capture-history matrices for each size group at the time of marking. As size and age at the time of marking are related, comparing the k-2 survival estimates produced in each analysis provides a test of the assumption that survival is not dependent on age or size group in the analysis.

Detecting Effects Related to Handling

Our data for Florence Lake cutthroat trout were collected during four 10-day sampling trips each summer, and many fish were caught two or more times during the same summer. We were concerned that stress from repeated trapping and handling could lower survival rates and cause a violation of the assumption of homogeneous survival rates. To investigate this concern, the entire capture history for each fish caught more than once in a year was deleted from the data, then the model for the 4-event version refit to the remaining data. If estimates were significantly different after deleting the multiple captures, a failure of the experimental assumptions would be indicated.

Effects of Tag Loss

All newly captured fish in this experiment were doubly marked so that fish that had lost their primary (dart) tags could still be identified. Since the original tagging date for fish with lost tags could not be determined, only estimates of the *maximum* annual rate of tag loss were possible. Tag loss for each summer was thus estimated by dividing the number of captured fish having only a missing adipose fin by the total number of fish recaptured from previous years that carried both marks. This provided a "worst-case" estimate, since newly tagged fish were excluded from the denominator. True annual rates of tag loss thus were surely lower than the estimates.

Instantaneous Sampling

Estimates of survival rate and surviving recruitment from the 16-event version of the JS experiment were contrasted with like statistics from the 4-event version. If sampling had been instantaneous relative to the dynamics of the population, there would be no appreciable mortality or recruitment within sampling each year in the 16-event experiment.

RESULTS

Estimates

Estimated abundance from both versions of the JS experiment (Table 1) was about 24–64% lower than comparable CP estimates for 1991 and 1992, and 63% lower to 6% higher in 1993 and 1994 (Figure 5). Estimated abundance from the 16-event version was relatively stable within 1991 and 1992, but dropped precipitously during sampling in 1993 and 1994. Estimates of survival rates and surviving recruitment (Figure 6; Table 1)

Table 1.–Estimates from the 4-event and 16-event versions of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake. Statistics in parentheses are from fitting log-linear models (LLM) to capture histories.

Year(event)	$\hat{N}$	SE($\hat{N}$)	$\hat{\phi}$	SE($\hat{\phi}$)	$\hat{p}$	SE($\hat{p}$)	$\hat{B}$	SE($\hat{B}$)
4-EVENT VERSION:[a]								
1991 (1)			0.5151 (0.516)	0.0257				
1992 (2)	5,481[b] (5,496)	294			0.4456	0.0248		
			0.3964 (0.399)	0.0244			3,457 (3,843)	257
1993 (3)	5,629[b] (5,674)	342			0.4786	0.0298		
1994 (4)								
16-EVENT VERSION:[c]								
1991 (1)			0.96	0.05				
1991 (2)	4,730	408	0.83	0.05	0.152	0.0149	484	352
1991 (3)	4,418	377	0.85	0.06	0.161	0.0148	611	309
1991 (4)	4,344	373	0.82	0.06	0.125	0.0118	2,012	386
1992 (5)	5,570	460	0.85	0.06	0.161	0.0135	1,378	431
1992 (6)	6,118	500	0.79	0.06	0.117	0.0104	1,129	443
1992 (7)	5,937	586	1.00	0.04	0.095	0.0099	2,132	900
1992 (8)	8,069	955	0.71	0.06	0.031	0.0044	2,054	645
1993 (9)	7,745	359	0.65	0.04	0.149	0.0078	0	1
1993 (10)	5,025	280	0.71	0.05	0.167	0.0106	0	1
1993 (11)	3,567	235	0.91	0.06	0.203	0.0153	0	72
1993 (12)	3,230	230	1.00	0.01	0.163	0.0127	8,425	594
1994 (13)	11,655	703	0.83	0.08	0.069	0.0045	0	96
1994 (14)	9,657	829	0.42	0.05	0.092	0.0083	0	0
1994 (15)	4,066	435			0.181	0.0200		
1994 (16)								

[a] Bias adjusted estimates (Seber 1992:204) from POPAN-PC (Arnason et al. 1992).

[b] 95% 'minimum length' bootstrap confidence intervals for the 4-event abundance estimates are: (5027, 6198) for 1992 and (5121, 6389) for 1993.

[c] Estimates of ϕ and p constrained to >0 and ≤ 1.0, $B > 0$ from RECAP (Buckland 1980).

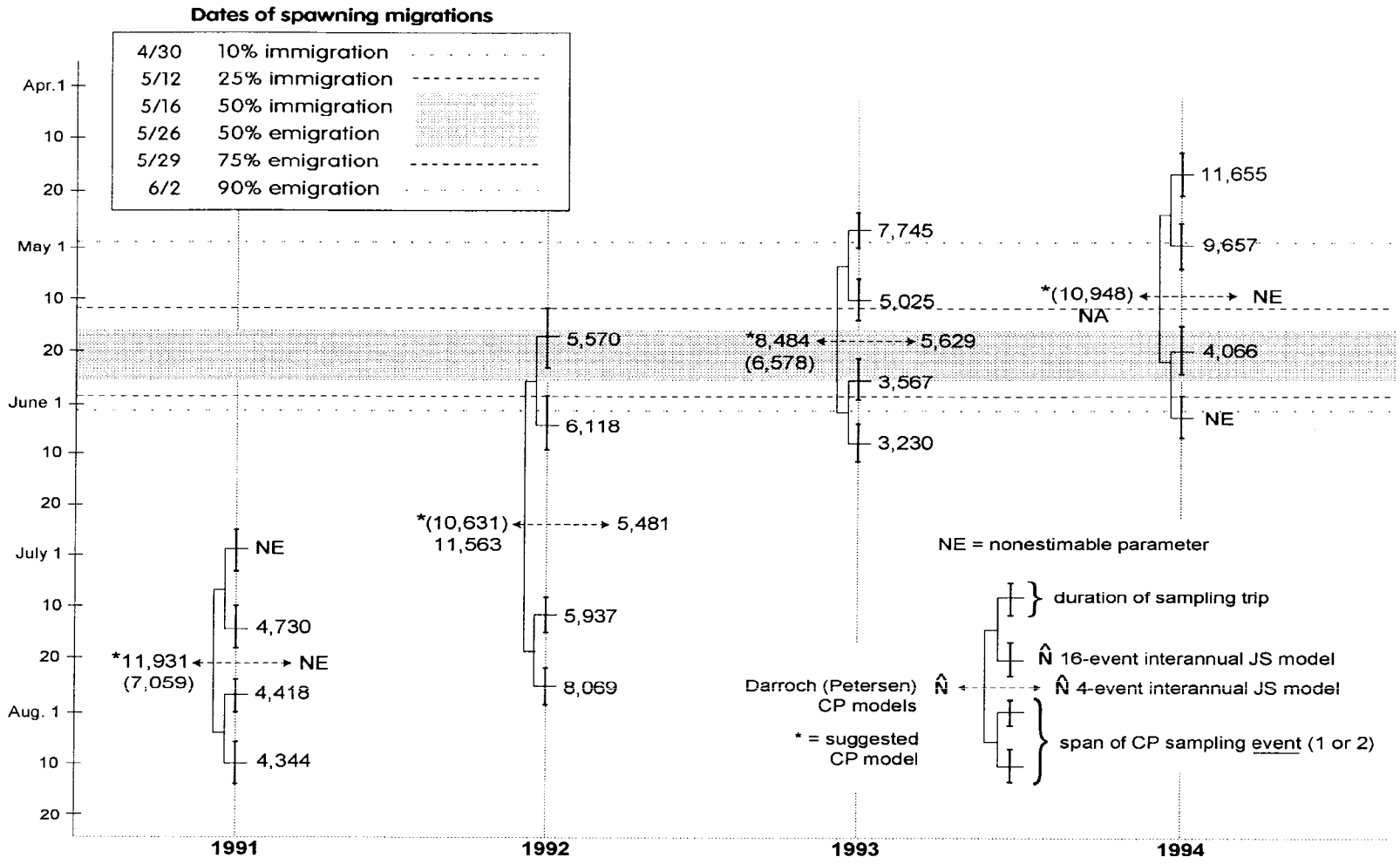

Figure 5.–Abundance estimates for 1991–1994 under three experimental designs. Horizontal lines crossing the diagram during May denote the estimated timing of spawning migrations into three creeks, based on data in Harding (1995). The four vertical bars over each year on the abscissa denote the span of individual sampling trips. Jolly-Seber (JS) estimates of abundance for each trip are shown at the right of each bar (the 16-event version); annual estimates (from the 4-event version) are to the right of the dashed arrow. Estimates based on CP models are to the left of the bars with the "best" (unbiased) on top and noted with a star. Petersen estimates are in parentheses, Darroch estimates are not. Estimates for CP experiments were recomputed using data summaries compiled for the 16-event JS analysis, and thus differ slightly from those in Harding and Jones (1993, 1994).

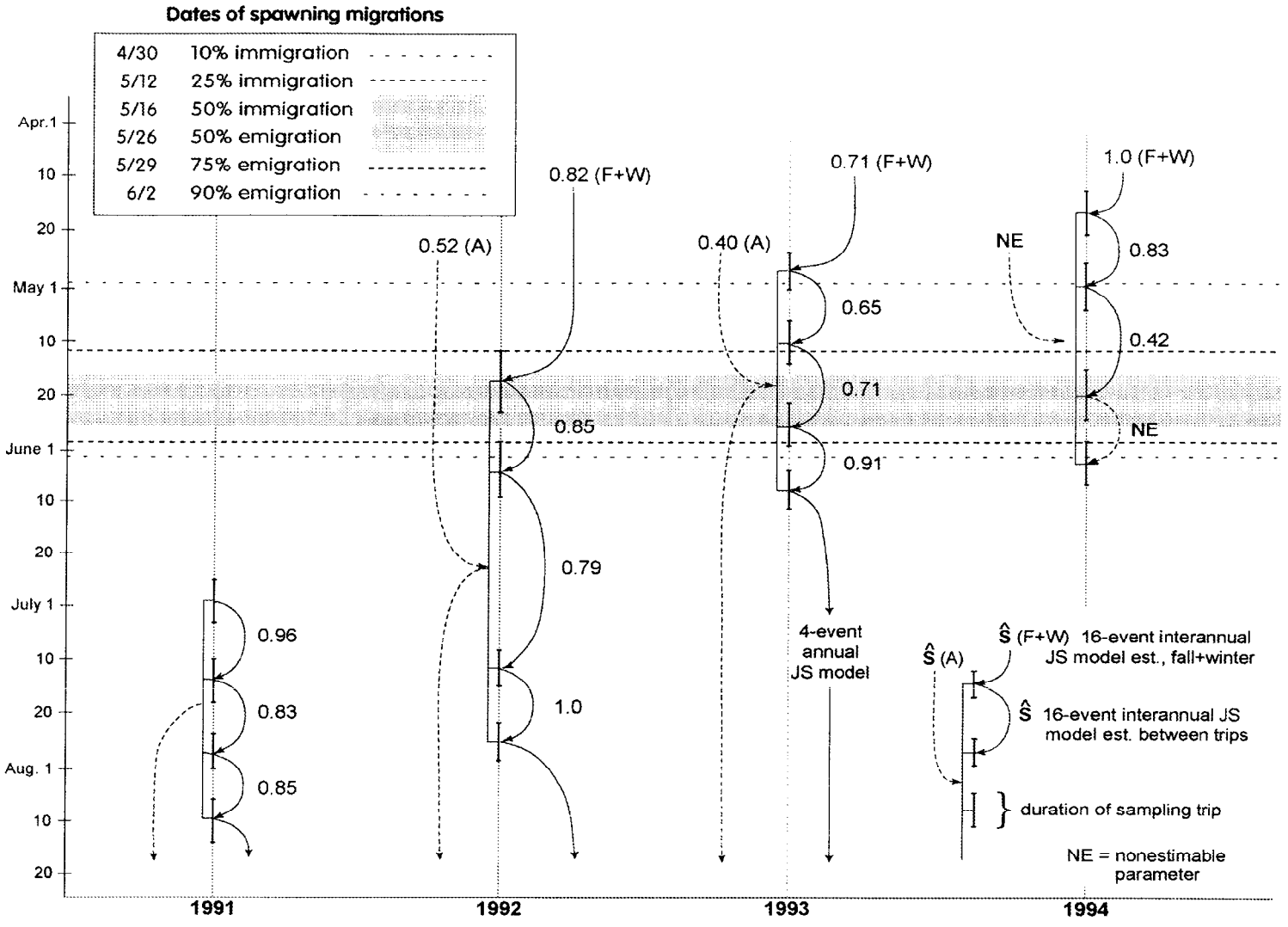

Figure 6.–Estimated survival rates from 1991–1994 under two experimental designs. Horizontal lines crossing the diagram during May denote the estimated timing of spawning migrations into three creeks, based on data in Harding (1995). The four vertical bars over each year on the abscissa denote the span of individual sampling trips. Jolly-Seber (JS) estimates of survival rates between trips are shown just right of each bar (the 16-event version); annual estimates (from the 4-event version) are to the left, denoted by an (A). Estimates for overwinter (Fall+Winter) survival rates are denoted F+W.

from the 16-event version implied unusually high turnover in the population during sampling in 1991 and 1992. Recruitment between the 2nd and 4th sampling events in 1991 was estimated at 1,095 (= 484 + 611) over at most 32 days; estimated survival rate over that period was 0.71 (= 0.83 • 0.85). Statistics for 1992 (events 5–6, 6–7, and 7–8) are recruitment 4,639 (= 1378 + 1129 + 2132) and survival rate 0.67 (= 0.85 • 0.79 • 1.00) for the 78 days containing the sampling that year. In contrast, similar estimates in 1993 and 1994 indicated high loss to the population with no balancing recruitment. Estimated survival rates during sampling are 0.42 (= 0.65 • 0.71 • 0.91) in 1993 and 0.35 (= 0.83 • 0.42) in 1995, while no recruitment was detected at all (Table 1). Considering these statistics from the 16-event version, sampling over several weeks to collect data for a single annual sampling event was hardly instantaneous sampling. Estimates from fitting LLMs to capture histories are almost exactly the same as estimates obtained through more traditional methods (Table 1).

Heterogeneity in Survival and Capture Probabilities

The overall GOF statistics (Tables 2 and 3) suggest there was some heterogeneity in survival and/or capture rates of cutthroat trout, but not a meaningful amount. Component 1 may be regarded as a test of H_O: newly tagged fish were recaptured at the same rate as previously tagged fish. This null hypothesis was rejected in the 4-event version for 1992 (Table 4, Panel A); fish tagged in 1991 were recaptured more often (0.26 estimated probability) than expected while fish tagged in 1992 were recaptured less often (0.21). Examination of the individual chi-squares in this test shows cell 1,1 contributes most to the overall statistic, i.e. recaptures in 1993 or 1994 of fish caught in both 1991 and 1992 were higher than expected (139 vs. 118, $\chi^2 = 3.9$). Recaptures of fish first tagged in 1992 (cell 1,2) were lower than expected (400 vs. 421, $\chi^2 = 1.1$). In contrast, the null hypothesis was not rejected for 1993 (Table 4, Panel B) when estimated probabilities of recapture are 0.17 and 0.14 for previously and newly marked fish released that year.

Component 2 of the GOF test also yields a significant result ($\chi^2 = 6.97$, df = 2, P = 0.03, Table 5). Again, the majority of the test statistic was generated by one cell (2,2), which had the lowest count and expected value, but was responsible ($\chi^2 = 4.59$) for about 2/3 of the total. This cell (2,2) contains the count of fish caught in 1994, which were also caught in both 1991 and 1992, not unlike the contents of the "deviant" cell (1,1) in the previous test. Overall, the power of these GOF tests is generally high due to large sample sizes. Given that deviations in the two "deviant" cells are small (9–21 fish, 10–16%), the practical significance of these test results for the 4-event version appears small relative to the magnitude of differences observed in the CP and JS abundance estimates. The GOF tests on the 16-event version produced an irregular pattern of results with the null hypothesis (equal rates of recapture) rejected ($\alpha = 0.05$) in 11 of 14 instances for component 1 and 6 of 13 instances for component 2 (Table 3).

Residuals from fitting the LLM (Table 6) clearly show that capture histories for multiple recaptures yielded the largest deviations from expected values. For instance, the 107 fish caught in the 3 consecutive years 1991–1993 exceeded the expected value (86) and produced the largest standardized residual (2.21). The count of 10 fish caught in 1991, 1992, and 1994 was lower than the 17 predicted by the model and led to the largest negative standardized residual (–1.60), similar to the result from the "deviant" cell (2,2) in the component 2 GOF test above. When the three captures are consecutive, observed counts exceed the expected values, but if a year passes between two of the captures, observed counts are lower than expected. Similarly, the count of fish captured in all four years exceeded expectation.

Heterogeneity in Capture Probabilities by Size

Unequal catchability of cutthroat trout of different sizes does not appear to be an important factor in this experiment. Two-level stratification was rejected by our likelihood-based fitting criterion (Table 7). For example, stratification of the capture data at 210 mm FL provided good fit for

Table 2.–Summary of GOF tests to the model used in the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake.

		Test statistic	Degrees of freedom	P-value
Component 1	1992	6.423	1	0.0113
	1993	1.747	1	0.1863
Component 2	1993	6.973	2	0.031
Overall		15.143	4	0.004

fish <210 mm FL (P = 0.706), but poor fit for fish ≥210 mm FL (P = 0.045). Splitting the population at 210 or 230 mm FL were the best options, but each scheme left one size class with GOF P-value <0.06. Testing of three-level stratification (Table 8) showed that cutpoints at 210 and 235 mm FL provided the "best" fit of the model to the data. Total abundance from summing estimates of the three-level stratified analysis (5,191 and 4,665; Tables 9 and 10) was not significantly different from the unstratified JS analysis (5,481 and 5,629; see Tables 1 and 3) for 1992 and 1993. The survival rate estimate for fish ≥235 mm FL was similar to the estimate from the unstratified JS analysis for 1991 (0.50 vs. 0.52) and only slightly lower for 1992 (0.34 vs. 0.40).

HETEROGENEITY IN SURVIVAL PROBABILITIES BY SIZE/AGE

There is little evidence for age or size-specific mortality rates for cutthroat trout in our experiments (Table 11). Estimated survival rates from 1991 to 1992 were 0.49 and 0.51 for the smallest (180–209 mm FL) and largest (≥235 mm FL) size groups, respectively, with the estimated rate for the mid-sized group (210–234 mm FL) marginally higher (0.57). Estimated survival rates from 1992 to 1993 ranged from 0.43 to 0.37. The average (1991–1992, 1992–1993) annual survival

Table 3.–Summary of GOF tests to the model used in the 16-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake.

		Component 1		Component 2	
Year	Period	Test statistic	P-value	Test statistic	P-value
1991	2	7.78	0.0053		
"	3	25.86	<0.0001	9.98	0.0068
"	4	11.30	0.0008	28.30	<0.0001
1992	5	47.85	<0.0001	5.91	0.052
"	6	2.46	0.117	74.46	<0.0001
"	7	8.01	0.0047	13.24	0.0013
"	8	0.34	0.562	0.0766	0.9624
1993	9	20.24	<0.0001	1.903	0.3863
"	10	4.21	0.040	0.3541	0.8377
"	11	7.34	0.0067	5.237	0.0729
"	12	1.90	0.169	32.47	<0.0001
1994	13	5.98	0.0145	1.33	0.515
"	14	4.57	0.0326	13.88	0.0010
"	15	9.44	0.0021	2.45	0.294

Table 4.–Breakdown for 1992 and 1993 of statistics for component 1 of the GOF tests to the model used in the 4-event version of the JS experiment on cutthroat trout in Florence Lake. (p = probability of capture for each group of tagged fish).

PANEL A: TEST FOR 1992	First captured in 1991	First captured in 1992
Captured in 1992 and recaptured later	139.00	400.00
Expected value	117.55	421.45
Captured in 1992 and not recaptured later	394.00	1,511.00
Expected value	415.45	1,489.55
χ^2 = 6.42, 1 df, P = 0.011 $\hat{p} \rightarrow$	0.26	0.21
PANEL B: TEST FOR 1993	**First captured before 1993**	**First captured in 1993**
Captured in 1993 and recaptured later	94.00	304.00
Expected value	84.07	313.93
Captured in 1993 and not recaptured later	470.00	1,802.00
Expected value	479.93	1,792.07
χ^2 = 1.75, 1 df, P = 0.186 $\hat{p} \rightarrow$	0.17	0.14

Table 5.–Breakdown for 1993 of statistics for component 2 of the GOF tests to the model used in the 4-event version of the JS experiment on cutthroat trout in Florence Lake. (p = probability of capture for each group of tagged fish).

	Captured in 1991, not in 1992	Captured in 1991 and 1992	First captured in 1992
Captured in 1993	122.00	129.00	339.00
Expected value	126.43	119.55	344.02
Captured in 1994, not in 1993	25.00	10.00	61.00
Expected value	20.57	19.45	55.98
χ^2 = 6.97, 2 df, P = 0.031 $\hat{p} \rightarrow$	0.17	0.07	0.15

rates for fish 180-209 mm FL (0.46, SE = 0.02), 210-234 mm FL (0.49, SE = 0.03), and fish ≥235 mm FL (0.44, SE = 0.03) are not significantly different. Although the omnibus test for heterogeneity in survival and capture rates showed statistically significant differences for models describing large fish (α = 0.05 in Table 11), these differences are too slight to explain differences between statistics from the CP and JS experiments.

EFFECT OF HANDLING

Deleting fish captured more than once a year from the data reduced the number of fish in the analysis by 18.8% (from 8,607 to 6,993) but yielded only minor changes in the estimates (Table 12). Estimated abundance from the 4-event version increased from 5,481 to 6,145 for 1992, but other estimates are very close to those from the full data set; agreement between

Table 6.–Residuals from the fitting the log-linear model (LLM) to capture histories for the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake.

Capture history	Count	Expected value	Residual	Standardized residual
1111	22	14.96	7.04	1.82
1110	107	86.44	20.56	2.21
0111	56	53.43	2.57	0.35
1101	10	16.50	-6.50	-1.60
1011	16	18.65	-2.65	-0.61
0011	304	310.97	-6.97	-0.39
1100	396	417.11	-21.11	-1.03
0110	283	308.75	-25.75	-1.47
1010	106	107.78	-1.78	-0.17
1001	25	20.57	4.43	0.98
0101	61	58.93	2.07	0.27
0100	1,511	1,489.89	21.11	0.55
0010	1,804	1,797.04	6.97	0.16
1000	1,649	1,649.00	0.00	0.00
0001	2,257	2,257.00	0.00	0.00

log-linear and JS estimates is also very good. Once again, no overlap of confidence intervals with CP abundance estimates was achieved (Table 13). The most notable change was a dramatic improvement in GOF test statistics, where P-values increased from 0.004 to 0.203 for the JS model and from 0.015 to 0.5 for the LLM.

In general, the deletion of multiple recaptures within years decreased the magnitude of "noisy" residuals from the full analysis and produced a lesser effect on residuals from fish caught only once or twice during the experiment (Table 14). The largest effect was on fish caught in all four years, although substantial reductions in counts and in the magnitude of standardized residuals also occurred for fish caught in three of the four years. For instance, the count of fish caught in 1991, 1992, and 1993 decreased from 107 to 39, which lowered the log-linear residual from 2.21 to 0.99.

Table 7.–Results of likelihood ratio tests from log-linear models to test two-level length-stratification in the 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake. The goal was to maximize total stratum P-value while keeping minimum within-stratum P-value >0.10. Asterisks indicate the "best" fit by this criteria.

FL (mm)	*n*	P-value	Total stratum P-value	Minimum stratum P-value
< 200	2,779	0.645		
≥ 200	5,995	0.012	0.657	0.012
< 205	3,470	0.824		
≥ 205	5,337	0.009	0.833	0.009
< 210	4,111	0.706		
≥ 210	4,864	0.045	0.751	0.045
< 215	4,737	0.747		
≥ 215	4,084	0.012	0.759	0.012
< 220	5,285	0.877		
≥ 220	3,672	0.006	0.877	0.006
< 225	5,780	0.491		
≥ 225	3,149	0.031	0.522	0.031
< 230	6,185	0.501		
≥ 230	2,710	0.066	0.567*	0.066*
< 235	6,567	0.058		
≥ 235	2,295	0.197	0.255	0.058
< 240	6,840	0.013		
≥ 240	1,989	0.462	0.475	0.013
< 245	7,154	0.006		
≥ 245	1,641	0.704	0.710	0.006

TAG LOSS

Because tag loss was estimated at less than 7.5% in all years under the worst-case scenario described above, we discounted tag loss as a significant problem. Although a CP estimate of abundance would be biased high as a result of undetected tag loss, Arnason and Mills (1981) show that tag loss does not affect JS abundance estimates if the probability of loss is the same for each member of the tagged population.

Table 8.–Results of likelihood ratio testing of three-level stratification by size in 4-event version of the JS experiment from 1991–1994 on cutthroat trout in Florence Lake. Asterisks indicate "best" fit.

FL (mm)	*n*	P-value	Sum of P-values	Minimum P-value
< 200	2,779	0.645		
200–234	4,188	0.062	0.904	0.062
≥ 235	2,295	0.197		
< 205	3,470	0.824		
205–234	3,510	0.011	1.032	0.011
≥ 235	2,295	0.197		
< 210	4,111	0.706		
210–234	2,857	0.304	1.207*	0.197*
≥ 235	2,295	0.197		
< 210	4,111	0.706		
210–239	3,154	0.041	1.209	0.041
≥ 240	1,989	0.462		
< 215	4,737	0.747		
215–234	2,199	0.113	1.057	0.113
≥ 235	2,295	0.197		
< 215	4,737	0.747		
215–239	2,502	0.006	1.215	0.006
≥ 240	1,989	0.462		
< 220	5,285	0.871		
220–239	1,925	0.002	1.335	0.002
≥ 240	1,989	0.462		

DISCUSSION

The discrepancies between CP and JS estimates arise largely as a result of where we sampled in 1991 and 1992, and when we sampled in 1993 and 1994. During 1991 and 1992, we sampled depths ≤14 m, leaving about a third to half the lake unsampled. Any fish in deeper waters would have a relatively low chance of being caught. Because fish were routinely captured in waters to 30 m in 1993 and 1994, and at other lakes in Southeast Alaska, indications are that fish were present in the unsampled area in 1991 and 1992. These statistics are far too dramatic to be caused by the progress of natural and fishing mortality and by growth recruitment. More likely their drama comes from some partial, random mixing of fish across the boundary between sampled and unsampled areas. This is just the behavior that has been detected in other lakes for the genetically similar species, rainbow trout *O. mykiss* (Havens et al. 1992:10,31). Under these conditions:

- abundance estimates for 1991 and 1992 from the 16-event and 4-event versions of the JS experiment would be accurate, but only for fish residing in the sampled areas;

Table 9.–Estimates of cutthroat trout abundance, survival rate, surviving recruitment, and probability of capture from Jolly-Seber and log-linear models, 1991–1994 study at Florence Lake: data stratified by fork length (millimeters). P-values for GOF tests in each stratum were (JS model) 0.574, 0.120, and 0.128; and (log-linear model) 0.706, 0.304, and 0.197.

Length stratum	Year	Jolly-Seber estimates				Log-linear estimates		
		$\hat{N}$	$\hat{\phi}$	$\hat{B}$	$\hat{p}$ [a]	$\hat{N}$	$\hat{\phi}$	$\hat{B}$
180–209	1991		0.2343				0.2351	
	1992	1,900	0.2018	1,700	0.5217	1,923	0.2027	1,718
	1993	2,083			0.6222	2,107		
210–234	1991		0.4098				0.4122	
	1992	1,751	0.1923	931	0.4067	1,775	0.1938	1,026
	1993	1,346			0.6397	1,370		
≥235	1991		0.5028				0.5050	
	1992	1,540	0.3367	761	0.4966	1,552	0.3437	768
	1993	1,236			0.4472	1,301		

[a] Capture probability calculated as $n_i / \hat{N}_i$.

Table 10.–Estimated cutthroat trout abundance and survival rates at Florence Lake, 1991–1994, and associated analytical standard errors SE_A, bootstrap standard errors SE_B, and bootstrap confidence intervals (CI) for the 4-event JS experiment, optimally stratified by fork length in millimeters.

Length stratum	$\hat{N}_{1992}$	SE_A	SE_B	95% CI[a]
180–209	1,900	287	301	(1,309, 2,458)
210–234	1,751	270	313	(1,273, 2,556)
≥235	1,540	142	139	(1,208, 1,756)
Sum ≥180	5,191	419	456	(3,790, 6,770)[b]
Length stratum	$\hat{N}_{1993}$	SE_A	SE_B	95% CI
180–209	2,083	339	355	(1,511, 2,811)
210–234	1,346	257	268	(959, 2,011)
≥235	1,236	176	173	(877, 1,525)
Sum ≥180	4,665	460	477	(3,347, 6,347)
Length stratum	$\hat{\phi}_{1991}$	SE_A	SE_B	95% CI
180-209	0.2343	0.0353	0.0380	(0.1755, 0.3201)
210–234	0.4098	0.0599	0.0630	(0.2999, 0.5564)
≥235	0.5028	0.0450	0.0415	(0.4248, 0.5896)
Length stratum	$\hat{\phi}_{1992}$	SE_A	SE_B	95% CI
180-209	0.2018	0.0341	0.0344	(0.1349, 0.2677)
210–234	0.1923	0.0388	0.0376	(0.1274, 0.2806)
≥235	0.3367	0.0479	0.0481	(0.2154, 0.4084)

[a] "Minimum length" bootstrap confidence intervals from RECAP.

[b] CI from summing lower and upper bounds of the strata "minimum length" bootstrap confidence intervals.

- estimates of "survival" rates and recruitment in 1991 and 1992 would be compromised (confounded) with movements within the lake; and
- abundance estimates for 1991 and 1992 from the CP experiment would also be germane to the sampled areas; however, they would be biased high as noted below.

Note that bias in a CP estimate from simultaneous recruitment and "mortality" is recruitment divided by the "survival" rate. For 1992, that estimated bias would be 6,924 fish (= 4,639/0.67) and is of sufficient size to explain the discrepancy between the JS abundance estimate for all 1992 (5,481) and the CP estimate (11,563). The same comparison for 1991 falls short because there is no estimate for surviving recruitment between the first two events of the 16-event version.

Sampling in the later years (1993 and 1994) was spread out to cover the lake, but timing was advanced to straddle the spawning season. The dramatic declines in estimated abundance in the later years of the 16-event version of the JS experiment (7,745 to 3,230 in 1993 and 11,655 to 4,066 in 1994), along with the dramatically low "survival" rates 0.42 (= 0.65 • 0.71 • 0.91) in 1993 and 0.35 (= 0.83 • 0.42) in 1994 clearly suggest that fish were leaving the lake to spawn in streams where they were no longer subject to capture. The lack of surviving recruitment in 1993

Table 11.–Estimates of cutthroat trout abundance and survival rates and goodness-of-fit (GOF) statistics for the 4-event version of the JS experiment at Florence Lake, 1991–1994: data stratified by size of fish at the time of the initial marking. Note the similarity to an analysis of cohorts over time based on age.

		Estimates				GOF statistics		
Stratum	Year	$\hat{N}$	SE($\hat{N}$)	$\hat{\phi}$	SE($\hat{\phi}$)	Test component	GOF test year	P-values
180–209	1991			0.4915	0.0399	1	1992	0.2451
	1992	2486	226	0.4397	0.0354	1	1993	0.1577
	1993	2930	242			2	1993	0.1542
	—	—	—	—	—	Overall		0.1314
210–234	1991			0.5735	0.0552	1	1992	0.0427
	1992	1690	184	0.4017	0.0497	1	1993	0.1753
	1993	1614	195			2	1993	0.3206
	—	—	—	—	—	Overall		0.0838
≥235	1991			0.5095	0.0448	1	1992	0.0140
	1992	1464	133	0.3715	0.0565	1	1993	0.8226
	1993	1125	170			2	1993	0.0936
	—	—	—	—	—	Overall		0.0286

Table 12.–Estimates for the 4-event version JS experiment from 1991–1994 on cutthroat trout in Florence Lake, fitted to analytical and log-linear models after multiple recaptures within a year were deleted. Overall GOF for JS model, P = 0.203; GOF for log-linear model, P = 0.500.

	Analytical estimates				Log-linear estimates		
Year	$\hat{N}$	$\hat{\phi}$	$\hat{B}$	$\hat{p}$	$\hat{N}$	$\hat{\phi}$	$\hat{B}$
1991		0.4978				0.4989	
1992	6,145	0.3907	3,224	0.3110	6,178	0.3940	3,255
1993	5,625			0.3546	5,689		

Table 13.–Standard errors and confidence intervals of the Jolly-Seber abundance and survival estimates for Florence Lake cutthroat trout, derived from the data after multiple recaptures within a year were deleted.

	Estimate	SE[a]	SE[b]	95% C.I.[a]	95% C.I.[b]
$\hat{N}_{1992}$	6,145	531	537	(5,103, 7,186)	(5,160, 7,143)
$\hat{N}_{1993}$	5,625	531	533	(4,584, 6,667)	(4,701, 6,722)
$\hat{\phi}_{1991}$	0.4978	0.0381	0.0386	(0.4231, 0.5725)	(0.4299, 0.5778)
$\hat{\phi}_{1992}$	0.3909	0.0364	0.0351	(0.3196, 0.4622)	(0.3258, 0.4611)

[a] Analytic error estimates and confidence intervals.

[b] Bootstrap error estimates and confidence intervals.

Table 14.–Comparison of standardized residuals from log-linear models of cutthroat trout capture histories at Florence Lake in the 4-event version of the 1991–1994 JS experiment between the full (original) analysis and the analysis after all fish captured more than once within a year were deleted.

Capture history	Original count	Deleted count	Decrease (%)	Original std. resid.	Deleted std. resid.
1111	22	5	77.3	1.82	0.57
1110	107	39	63.6	2.21	0.99
0111	56	28	50.0	0.35	0.89
1101	10	4	60.0	-1.60	-1.19
1011	16	10	37.5	-0.61	0.46
0011	304	165	45.7	-0.39	-0.52
1100	396	221	44.1	-1.03	-0.24
0110	283	195	31.1	-1.47	-0.58
1010	106	70	34.0	-0.17	-0.50
1001	25	19	24.0	0.98	0.74
0101	61	44	27.9	0.27	0.03
0100	1,511	1,375	9.0	0.55	0.10
0010	1,804	1,483	17.8	0.16	0.18
1000	1,649	1,375	16.6	0.00	0.00
0001	2,257	1,960	13.2	0.00	0.00

and 1994, save for the exceptionally large 8,425 fish between years, is in stark contrast to estimates for earlier years when only part of the lake was sampled. The exception of 8,425 fish represents the spawning population returning to the lake in late 1993 after sampling that year had ended, plus some *bona fide* growth recruitment. By sampling across the spawning season:

- abundance estimates for 1993 and 1994 from the 16-event and 4-event versions of the JS experiment would be accurate, but only for fish subject to being sampled (most likely those fish remaining in the lake);
- estimates of survival rates and recruitment in 1993 and 1994 would be compromised (confounded) with movements between the lake and tributaries and by any transient changes in behavior associated with spawning that would reduce the probability of capture (an exception exists for estimates from fall 1992 to spring 1993, as noted below); and
- abundance estimates for 1994 and maybe 1993 from the CP experiment would be accurate and germane to all fish above the minimum size (180 mm FL) in the population.

Note the similarity between estimated abundance for the first event in the JS experiment in 1994 (11,655) and the CP estimate for that year (10,948). Both estimates are accurate. Sampling that year was spread out uniformly across the lake. Early sampling that year (11–20 April and perhaps 26 April–5 May) occurred prior to the spawning season, when all fish in the population were still in the lake to be sampled. The equal-probability condition was met for both experiments at a time when all fish were present. As noted in Seber (1982:71), removal of fish from the population for any reason will not bias estimated abundance, so long as the removal is a random process. Most likely this occurred as both marked and unmarked fish left the lake later to spawn. Under these conditions, the abundance estimate for the CP experiment is germane to a combination of the first two sampling events. There is similarity between estimates in 1993, as well; however, the later start of sampling that year (first event 25 April–4 May)

may have been too late to catch all the population in the lake. Of available survival statistics, the survival (0.71) and recruitment (2,054) estimates for fall 1992 to spring 1993 are accurate since the entire lake was sampled in 1993, if all fish were available for sampling during the first sampling trip of 1993. Note, however, that these estimates are not annual statistics, because significant recruitment and mortality (related to spawning, for example) probably occurred between the May and August sampling trips in 1992.

The shift to earlier sampling in the later years also explains the unusual frequency of multiple captures that triggered significance in the GOF tests in the JS experiment. Fish marked in 1991 were subject to capture in 1992 when sampling occurred after the spawning season. In contrast, fish marked in 1992 and 1993 were exposed to recapture only during sampling that straddled spawning seasons. Considering that most marked cutthroat trout were not exposed to capture during much of 1993 and 1994, little wonder that the probability of recapturing fish marked in 1991 was higher overall, setting up the relatively high frequency of multiple captures. This situation also explains the residuals seen in the log-linear models of capture histories. Because so many fish marked in 1991 were recaptured in 1992, not being recaptured that year would lower the frequency of capture histories involving these fish. Expectations being averages, these lower frequencies would be below expectation. Trap happiness would be an alternative explanation for this phenomenon; however, that explanation is not supported by ancillary results gathered in 1996 at McKinney Lake, where sampling was conducted with two types of gear, including the same traps fished in 1994 at Florence Lake (Harding et al. *In prep*).

The slightly lower probability of capturing newly marked vs. previously marked was consistent throughout the experiment, even though this difference would not have explained the trends seen in the abundance and survival statistics. Possible explanations are:

- Tag loss in the short term;
- Higher mortality rates in smaller fish; or
- Tag-induced mortality that occurred just after release.

The low rate of tag loss in general argues against quick tag loss as a major cause for the discrepancy between recapture rates. Considering that related species such as Yellowstone cutthroat and sea-run cutthroat trout experience high rates of mortality associated with spawning (Sumner 1962; Gresswell et al. 1994) and that length limits in the fishery target larger fish, a higher mortality rate for younger fish is also an unlikely cause. Tag-induced mortality is the most likely explanation, so long as that mortality is realized shortly after a newly tagged fish has been released. Unfortunately, the spatial and temporal patterns in sampling over the four years blur conclusions that may be drawn on this matter.

Slight problems in tag-induced mortality as evidenced in our study can be solved by using an innocuous mark or by basing calculations on previously marked cutthroat trout. In the first solution, there is no tag-induced mortality. Unfortunately, innocuous marks are usually batch marks that do not carry enough information for more complicated experiments, such as JS experiments. If tagging-induced mortality is rapid and occurs well before the next sampling event, recapture and subsequent release of previously marked fish should be unaffected. However, estimates from only previously marked fish would (potentially) be far less precise, as well as less biased. JS experiments would also have to be stretched to four events to obtain the first unbiased estimates of abundance and survival.

RECOMMENDATIONS

After four years of sampling, some procedures can be recommended to provide accurate, efficient estimates of annual abundance, survival rates, and surviving recruitment for lacustrine populations of cutthroat trout. There is more than one way to design an experiment; however, one rule is common to all designs: ***fishing effort during each sampling event must be spread uniformly across the lake regardless of the design used.*** The specific options are:

THE SPAWNING SEASON STRADDLE

A two-event CP experiment can produce accurate abundance estimates of lacustrine cutthroat trout by sampling as soon as possible after ice-out (first event) and then later during or shortly after the spawning season (second event). *The first event should be scheduled well ahead of the spawning season.* Experience at Florence Lake is that there will be no growth recruitment to the population at that time, making the abundance estimate germane to the first event. Delaying the second sampling event into summer runs the risk of growth recruitment biasing the estimate. Efficient sampling (high catch rates) is the advantage to straddling the season. Experience has been that catch rates will be high, and cool water and air temperatures in spring reduce stress on captives. Marking should be restricted to innocuous procedures, like shallow excisions or punched holes on finned rays. A JS experiment could also straddle the season; however, all statistics except early abundance would be useless. Size-selective sampling may be indicated during the second sampling event under this method, because fish not spawning during event 2 are likely to be smaller than those spawning. This result would be ignored in the analysis, and only fish captured during the first sampling event would be used to estimate age/length composition. Obviously, though, this option requires confidence that gear is not size-selective.

THE SUMMER STRATEGY

A two-event CP experiment can also produce accurate abundance estimates if sampling is restricted to a short span of time in the summer well after the spawning season. However, if spawning fish suffer significant mortality during or just after spawning, this strategy would not reflect that fact. The sampling schedule in 1991 at Florence Lake is typical of this strategy (so long as fishing effort is spread evenly over the lake). Sampling events should be close enough together to keep mortalities and recruitment between events to negligible levels (unlike the long duration of the experiment in 1992). Relative to straddling the spawning season, sampling during the summer is inefficient. Catch rates are low, and warm water and air temperatures increase stress on captives. Again, marking should be restricted to innocuous procedures; our evidence is that dart tags cause some, but detectable, mortality of marked cutthroat trout.

THE SPRING STRETCH

A multiple-event JS experiment with a single event each spring for at least three years would produce accurate estimates of abundance and annual survival rates. Sampling must be completed well before the spawning season begins (the time when the first fish stop feeding in preparation for migration to natal streams). Sampling would be efficient for the same reasons given above for the spawning season straddle: high catch rates and cool temperatures. Individually numbered tags would be used, and if they are dart tags, statistics may be biased. Unbiased estimates could be obtained by tabulating capture histories based on only recaptured fish, but precision of estimates would suffer greatly. If the increased imprecision from the solution is greater than the bias from the problem, living with the bias might be a better choice. Four or more consecutive years of sampling would also produce estimates of surviving recruitment.

A multiple-event JS experiment with annual events in the summer probably would not work well. Individually numbered tags would be used, and if tagging-induced mortalities result, there would be little chance of recovery. Catch rates would keep the marked population low, and warm temperatures would probably exacerbate the tagging-induced mortality.

ACKNOWLEDGMENTS

This research resulted from the contributions of many people. J. Douglas Jones supervised overall aspects of the operations at Florence Lake from the inception of the project in 1988. Ken and Karen Koolmo, Kurt Kondzela, Brad Gruening, and Robert Harley worked tirelessly to improve our sampling techniques and obtain the large samples. Mark Laker (USFS) participated in several sampling experiments with us in SE Alaska and provided suggestions on sampling and analysis.

LITERATURE CITED

Arnason, A. N., D. W. Miller, and C. Lapkowski. 1992. POPAN-PC. Installation and users manual for running POPAN-3 on IBM microcomputers under DOS or Windows 3. Charles Babbage Research Centre, Manitoba, Canada.

Arnason, A. N. and K. H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Science 38:1077–1095.

Buckland, S. T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. Biometrics 36:419–435.

Carothers, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29:79–100.

Cormack, R. M. 1989. Loglinear models for capture-recapture. Biometrics 45:395–413.

Gresswell, R. E., W. J. Liss, and G. L. Larson. 1994. Life-history organization of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 51(Suppl. 1):298–309.

Harding, R. D. 1995. Abundance and length composition of cutthroat trout in Florence, Turner, and Young Lakes, Southeast Alaska, 1994. Alaska Department of Fish and Game, Fishery Data Series No. 95-43, Anchorage.

Harding, R. D. and J. D. Jones. 1993. Cutthroat trout studies at Florence Lake, Southeast Alaska, 1992. Alaska Department of Fish and Game, Fishery Data Series No. 93-44, Anchorage.

Harding, R. D. and J. D. Jones. 1994. Abundance of Cutthroat in Florence Lake, Alaska, 1993. Alaska Department of Fish and Game, Fishery Data Series No. 94-35, Anchorage.

Harding, R. D., M. Laker, and R. P. Marshall. *In prep.* Abundance and length, trap avoidance, and short-term spatial movement of cutthroat trout at McKinney Lake, Southeast Alaska, 1996. Alaska Department of Fish and Game.

Havens, A. C., M. Alexandersdottir and S. Sonnichsen. 1992. Evaluation of rainbow trout populations in Big Lake, Alaska, 1991. Alaska Department of Fish and Game, Fishery Data Series No. 92-18, Anchorage.

Jones, J. D., R. P. Marshall, and R. Harding. 1992. Cutthroat trout studies at Florence and Hasselborg lakes, Southeast Alaska, 1991. Alaska Department of Fish and Game, Fishery Data Series No. 92-43, Anchorage.

Jones, J. D. 1993. Southeast Alaska recreational cabin survey, 1992. Alaska Department of Fish and Game, Fishery Data Series No. 93-53, Anchorage.

Jones, J. D. 1994. Harvest surveys at U.S. Forest Service public use cabins in Southeast Alaska, 1993. Alaska Department of Fish and Game, Fishery Data Series No. 94-39, Anchorage.

Jones, J. D. 1995. Southeast Alaska recreational cabin survey, 1994. Alaska Department of Fish and Game, Fishery Data Series No. 95-32, Anchorage.

Pollock, K. H., J. E. Hines and J. D. Nichols. 1985. Goodness-of-fit tests or open capture-recapture models. Biometrics 41:399–410.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical Inference for capture-recapture experiments. Wildlife Monograph No. 107.

Robson, D. S. 1969. Mark-recapture methods of population estimation. Pages 120–140 *in* N. L. Johnson and H. Smith, Jr., editors, New developments in survey sampling. John Wiley and Sons, New York.

SAS Institute Inc. 1990. SAS language: reference, version 6, first edition. SAS Institute Inc., Cary, North Carolina.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillan Publishing, New York.

Sumner, F. H. 1962. Migration of salmonids in Sand Creek, Oregon. Transactions of the American Fisheries Society 82:139–150.

APPENDIX A

Appendix A1.–Statistics for 4-event Jolly-Seber estimates for the Florence Lake data.

Year (event)	n_i	m_i	R_i	r_i	z_i
1991 (1)	2,331	0	2,331	682	0
1992 (2)	2,446	535	2,444	539	147
1993 (3)	2,698	590	2,670	398	96
1994 (4)	2,751	494	2,686	0	0

Appendix A2.–Statistics for 16-event Jolly-Seber estimates for the Florence Lake data.

Year (event)	n_i	m_i	R_i	r_i	z_i
1991 (1)	854	0	853	393	0
1991 (2)	721	125	721	278	268
1991 (3)	709	189	709	256	357
1991 (4)	542	179	541	187	434
1992 (5)	897	237	897	279	384
1992 (6)	715	212	714	201	451
1992 (7)	561	172	561	166	480
1992 (8)	252	69	252	65	577
1993 (9)	1150	218	1147	331	424
1993 (10)	840	286	810	269	469
1993 (11)	723	344	716	227	394
1993 (12)	526	294	526	131	327
1994 (13)	803	122	800	121	336
1994 (14)	888	156	867	126	301
1994 (15)	736	257	717	124	170
1994 (16)	587	294	568	0	0

Appendix A3.–Location of sampling data and file containing this report.

File name	Software	Contents
FL_JS_ALL_16.xls	MS Excel	Data and capture histories for 16-event JS analysis.
FL_JS_91.WK3	Lotus 123	Detailed data for 1991 4-event JS analysis.
FL_JS_92.WK3	Lotus 123	Detailed data for 1992 4-event JS analysis.
FL_JS_93.WK3	Lotus 123	Detailed data for 1993 4-event JS analysis.
FL_JS_94.WK3	Lotus 123	Detailed data for 1994 4-event JS analysis.
FL_JS_AL.WK3	Lotus 123	Data summary for each annual 4-event JS analysis.
91in.xls	MS Excel	Data for 1991 inseason closed population analysis.
94in.xls	MS Excel	Data for 1992 inseason closed population analysis
92in.xls	MS Excel	Data for 1993 inseason closed population analysis
93in.xls	MS Excel	Data for 1994 inseason closed population analysis
Florence2.doc	MS WORD	This report.