Movement and population structure of westslope cutthroat trout *Oncorhynchus clarki lewisi* inhabiting headwaters streams of Montana

Bradley B. Shepard
Montana Department of Fish, Wildlife and Parks
Department of Biology
Montana State University, Bozeman, Montana 59717, USA

Jim Robison-Cox
Department of Mathematical Sciences
Montana State University, Bozeman, Montana 59717, USA

and

Susan C. Ireland and Robert G. White
Montana Cooperative Fishery Research Unit[a]
Department of Biology, Montana State University
Bozeman, Montana 59717, USA

Final Report to:
USDA, Forest Service, Rocky Mountain Research Station
316 East Myrtle Street
Boise, Idaho 83702

Contract: **INT-93845-RJVA**

August 1998

[a] The Unit is jointly sponsored by Montana State University, Montana Department of Fish, Wildlife, and Parks, and the U.S. National Biological Service.

Executive Summary

Retention of visible implant (VI) tags in westslope cutthroat trout Oncorhynchus clarki lewisi inhabiting 11 isolated headwater tributary drainages in Montana was evaluated during 1993 and 1994. In 1993 2,071 VI tags were implanted in westslope cutthroat trout (100 to 324 mm; FL) and adipose fins were removed as a secondary mark to evaluate tag retention. Of 348 westslope cutthroat trout recaptured during the year they were tagged, 201 (58%) had retained their tags. Of 616 westslope cutthroat trout recaptured the year after tagging, 355 (58%) had retained their tags. Logistic regression analyses indicated that fish length was the most significant variable that positively influenced tag retention. Other significant variables were wetted width and channel gradient of the stream in which fish were tagged, and quality of tag insertion, which was rated at time of tagging. Fish condition did not significantly improve deviance performance of logistic regression models that included fork length and tag insertion quality. Neither slopes nor intercepts of $\log_{10}$length-$\log_{10}$weight regressions were significantly different ($P > 0.10$) for fish which retained versus lost their tags. Fish condition was not significantly different ($P > 0.951$; ANCOVA) between previously tagged and untagged westslope cutthroat trout after accounting for differences between drainages and years. We found no significant differences between slopes ($P > 0.50$) or intercepts ($P > 0.05$) of $\log_{10}$length-$\log_{10}$weight regressions between previously tagged and untagged fish. However, for 11 drainages where comparisons could be made, we found significant differences ($P < 0.05$) between $\log_{10}$length-$\log_{10}$weight regression slopes for previously tagged versus untagged fish in one drainage and for regression intercepts in an additional three drainages. Ninety-four percent of all tags were readable at recapture. A logistic regression model predicted that tag retention would be 75% or higher in westslope cutthroat trout $\geq$ 155 mm (FL) if tag insertion quality was good. In spite of relatively poor tag retention (< 75%) in smaller (< 155 mm) westslope cutthroat trout, VI tags were a valuable tool to assess movements of those fish, which retained their tags.

Movement of resident westslope cutthroat trout was also assessed using VI tags from 1993 to 1995. Little movement over 500 m was observed; however, the proportion of fish moving further than 0.5 km appeared to be correlated to level of physical isolation of that population. Length-frequency histograms of captured westslope cutthroat trout could be used for identifying missing year-classes, especially the year immediately following the emergence of the missing year-class. Our ability to interpret age classes from length-frequency histograms was inconsistent among streams. For some streams we could interpret age classes 1, 2, and sometimes, 3 from histograms, but for some others we could not. We could not discern any age classes beyond age 3 from histograms. We recommend a consistent time of year be used as a standard for collecting length-frequency data for comparative purposes, and suggest late summer for this purpose.

Table of Contents

List of Tables

Introduction

Spatial diversity and dispersal among populations of animals is thought to play an important role in regional or metapopulation persistence. Metapopulation processes have not been clearly demonstrated in interior salmonids and the scale of population structuring is unknown. The general objective of this project was to improve our understanding of the movements of trout at a local level. The two specific objectives were:

1. Describe the movement and population structure of westslope cutthroat trout within an individual stream.
2. Determine whether habitat condition influences dispersal among stream reaches and habitat units.

In this final report we present a paper we published in the North American Journal of Fisheries Management in 1996 (Volume 16: 913-920) that documents what factors influenced the retention of visible implant tags in westslope cutthroat trout as Chapter 1. A companion paper authored by Jim Robison-Cox of Montana State University (Robison-Cox 1998) appears in Appendix A. In Chapter 2 we present summaries of tag recovery data showing movement patterns observed in different stream populations. In Chapter 3 we present length-frequency summaries by drainage by year. The data collected during this study is available in electronic format. The descriptions of these data are found in Appendix B. Two companion reports were prepared. One report details the "Population dynamics and demographics of westslope cutthroat trout Oncorhynchus clarki lewisi inhabiting isolated headwater tributaries of Montana" (Shepard et al. 1998a). The other describes the "Influence of abiotic and biotic factors on abundance of stream-resident westslope cutthroat trout Oncorhynchus clarki lewisi in Montana streams" (Shepard et al. 1998b).

Chapter 1:
Factors influencing retention of visible implant tags in westslope cutthroat trout *Oncorhynchus clarki lewisi* inhabiting headwater streams of Montana

Bradley B. Shepard
Montana Department of Fish, Wildlife and Parks
Department of Biology
Montana State University, Bozeman, Montana 59717, USA

Jim Robison-Cox
Department of Mathematical Sciences
Montana State University, Bozeman, Montana 59717, USA

and

Susan C. Ireland and Robert G. White
Montana Cooperative Fishery Research Unit[a]
Department of Biology, Montana State University
Bozeman, Montana 59717, USA

[a] The Unit is jointly sponsored by Montana State University, Montana Department of Fish, Wildlife, and Parks, and the U.S. National Biological Service.

Abstract

Retention of visible implant (VI) tags in westslope cutthroat trout Oncorhynchus clarki lewisi inhabiting 20 reaches of 11 isolated headwater tributary drainages in Montana was evaluated during 1993 and 1994. In 1993 2,071 VI tags were implanted in westslope cutthroat trout (100 to 324 mm; FL) and adipose fins were removed as a secondary mark to evaluate tag retention. Of 348 westslope cutthroat trout recaptured during the year they were tagged, 201 (58%) had retained their tags. Of 616 westslope cutthroat trout recaptured the year after tagging, 355 (58%) had retained their tags. Logistic regression analyses indicated that fish length was the most significant variable that positively influenced tag retention. Other significant variables were wetted width and channel gradient of the stream in which fish were tagged, and quality of tag insertion, which was rated at time of tagging. Fish condition did not significantly improve deviance performance of logistic regression models that included fork length and tag insertion quality. Neither slopes nor intercepts of $\log_{10}$length-$\log_{10}$weight regressions were significantly different ($P > 0.10$) for fish which retained versus lost their tags. Fish condition was not significantly different ($P > 0.951$; ANCOVA) between previously tagged and untagged westslope cutthroat trout after accounting for differences between drainages and years. We found no significant differences between slopes ($P > 0.50$) or intercepts ($P > 0.05$) of $\log_{10}$length-$\log_{10}$weight regressions between previously tagged and untagged fish. However, for 11 drainages where comparisons could be made, we found significant differences ($P < 0.05$) between $\log_{10}$length-$\log_{10}$weight regression slopes for previously tagged versus untagged fish in one drainage and for regression intercepts in an additional three drainages. Ninety-four percent of all tags were readable at recapture. A logistic regression model predicted that tag retention would be 75% or higher in westslope cutthroat trout $\geq$ 155 mm (FL) if tag insertion quality was good. In spite of relatively poor tag retention (< 75%) in smaller (< 155 mm) westslope cutthroat trout, VI tags were a valuable tool to assess movements of those fish, which retained their tags.

Introduction

Fish researchers and managers mark fish to obtain information on abundance, movements and migration, age and growth, mortality, behavior, exploitation rates, and stocking success (McFarlane et al. 1990). Evaluating retention of marks is important in any mark-recapture study (e.g., Nielsen 1992). Haw et al. (1990) developed an alphanumeric coded visible implant (VI) tag that can be inserted just beneath clear tissue, usually in a post-orbital location, and read upon subsequent recapture. Due to their small size, VI tags can be used to uniquely identify small fish without sacrificing the fish to recover the tag. Initial testing of VI tags by Haw et al. (1990) documented that only one tag was lost from 42 tagged rainbow trout (Oncorhynchus mykiss; 149-172 mm TL; mean 158 mm) held 22 weeks in a hatchery environment.

Visible implant tag retention has been related to fish size (length and/or weight), or age, for Atlantic salmon Salmo salar (Kincaid and Calkins 1992), brook trout Salvelinus fontinalis (Bryan and Ney 1994), and brown trout Salmo trutta (Niva 1995). McMahon et al. (1996) suggested that environmental conditions might also affect tag retention due to observed differences in tag retention between rainbow trout raised in a hatchery versus wild environment. We needed to document the retention of VI tags as part of a study to estimate mortality and movement of small (100-320 mm, FL) westslope cutthroat trout Oncorhynchus clarki lewisi inhabiting headwater streams of Montana. We wanted to determine what factors influenced tag loss and to test if VI tags adversely affected the condition of tagged fish.

Study Area

Visible implant tag retention was assessed in westslope cutthroat trout from 20 reaches within 11 tributary drainages of the upper Missouri River and two tributary drainages of the upper Clark Fork River, Montana (Figure 1). These streams were characterized by low-flow wetted widths of 1.5 to 5.8 m, water conductivities of 72 to 661 umhos, elevations of 1,320 to 2,570 m, and gradients of 3 to 11% (Table 1). Westslope cutthroat trout in sampled populations exhibited little evidence of introgression with either rainbow trout or Yellowstone cutthroat trout Oncorhynchus clarki bouveri using external morphometric characteristics and/or electrophoretic testing (Salmon and Trout Genetics Laboratory, University of Montana, Missoula, Montana, unpublished data).

Methods

Fish were captured using a Smith-Root BP-15 backpack electrofisher set at 40 mHz pulse with a pulse width of 1 msec. Voltages were set from 400 to 700 volts. These settings were used to maximize capture efficiency while simultaneously minimizing risk of injuring fish (W. Fredenberg, U.S. Fish and Wildlife Service, personal communication). All captured fish were anesthetized with MS-222, measured to the nearest millimeter (FL), and weighed to the nearest gram. Condition factors (weight*10^5/length^3) were calculated for individual fish (Anderson and Gutreuter 1983).

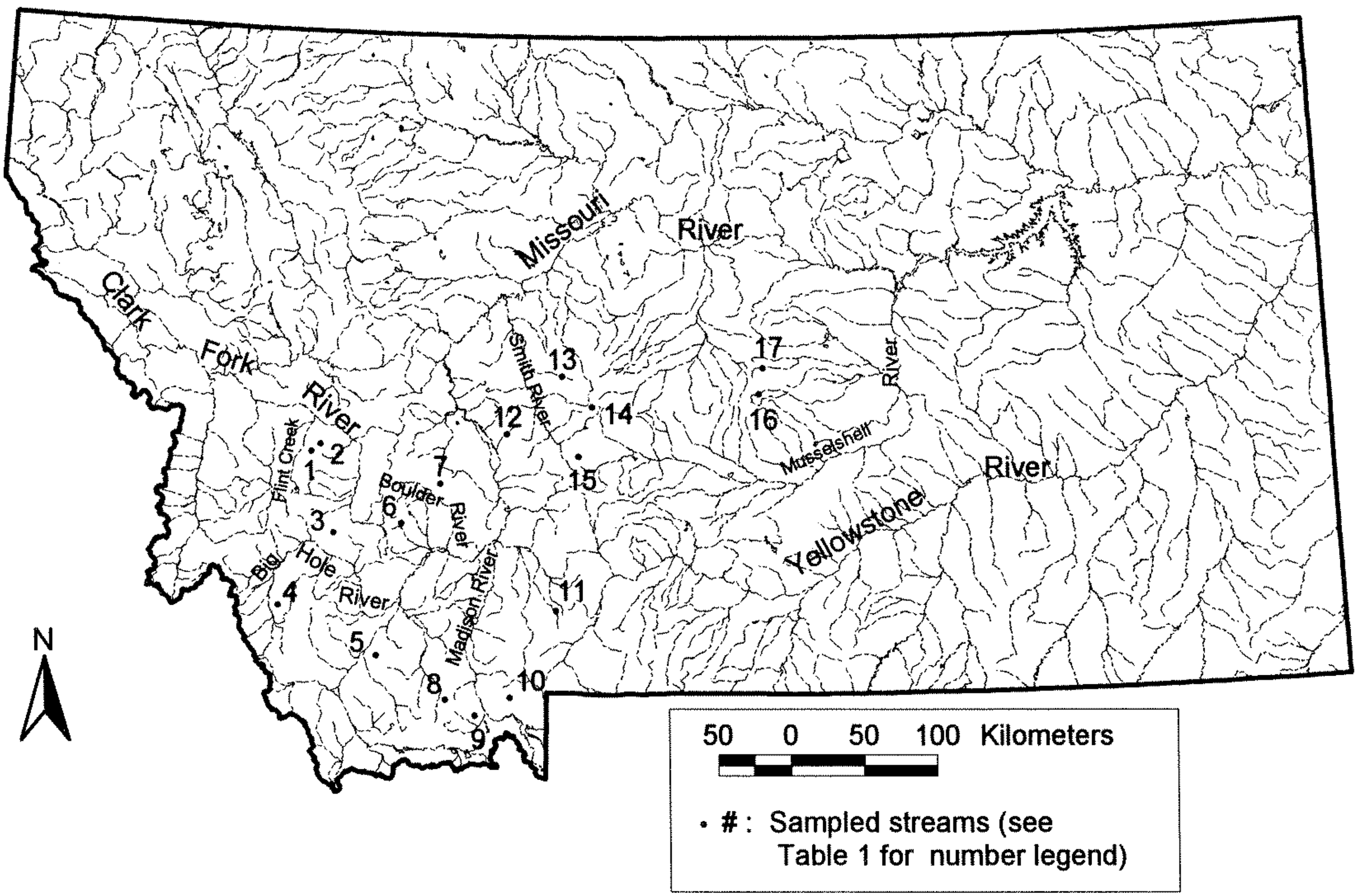

Figure 1. Map of Montana showing sample locations (dots) where tag retention, movement, and size structure of westslope cutthroat trout was assessed. Numbers next to locations correspond to numbers in parentheses by stream names in Table 1. Only sites 1, 2, 3, 6, 8, 10, 12, 14, 15, 16, and 17 were used for assessing tag retention in 1993 and 1994.

Table 1. Physical features of streams (numbers in parentheses are map locations shown in Figure 1) where densities of westslope cutthroat trout were estimated from 1992 to 1995. Mean temperatures, conductivities, and pH's are averages for several point estimates taken during field sampling. . "Model sample size" refers to number of fish tagged in each reach (see "Methods" for further explanation).

Stream (map number)	Rosgen[a] Type	Mean temperature (F)	Mean Conductivity (μmhos)	pH	Mean wetted width (m)	Length with cutthroat (km)	Lower elevation (m)	Upper elevation (m)	Mean channel gradient (%)	Number of tags out	Model sample size
Cabin (10)	C3	57.2	329	8.8	6.6	2.9	2170	2304	4.6	-[c]	-
M Fork Cabin	B3	53.0	203	8.7	3.3	7.0	2300	2600	4.2	-	-
Unnamed Trib	B3	46.6	268	8.7	1.6	1.0	2540	2560	2.4	-	-
Collar Gulch (17)	B2	46.2	174	8.3	2.0	2.7	1450	1550	3.6	232	134
Cottonwood (Smith)(15)	B1	46.0	130	8.9	2.5	0.6	1830	1850	4.0	89	88
East Fork Cottonwood	A3	48.8	144	8.8	1.5	3.0	1850	2190	11.4	25	0
West Fork Cottonwood	A3	47.9	126	8.1	2.5	2.8	1850	2110	9.1	333	124
Douglas (1)	A2	41.5	245	8.9	3.0	1.1	1570	1630	5.5	81	26
N. Fork Douglas (1)	B2	47.1	252	8.5	1.5	3.1	1650	1790	4.7	152	39
Geyser (8)	A3	48.2	380	8.6	1.6	1.6	2460	2570	6.6	305	79
Half Moon (16)	A2	49.9	344	8.7	3.0	7.3	1710	2010	4.2	11	0
Halfway (6)	B3	49.2	72	8.8	1.7	7.8	1830	2290	5.9	193	73
Jerry (3)	A3	43.7	156	8.7	5.8	2.8	2050	2220	3.0	95	28

Table 1. (Continued).

Stream (map number)	Rosgen[a] Type	Mean temperature (F)	Mean Conductivity (μmhos)	pH	Mean wetted width (m)	Length with cutthroat (km)	Lower elevation (m)	Upper elevation (m)	Mean channel gradient (%)	Number of tags out	Model sample size
Lick (11)	A3	51.1	262	8.4	2.3	2.0	1950	2020	6.1	-	-
Mcvey (4)	B3	42.9	64	9.3	1.5	2.3	1860	1940	3.4	-	-
Muskrat (7)	A2	46.0	NA[b]	NA[b]	3.6	2.2	1570	1700	5.6	-	-
N. Fork Deadman (14)	A3	43.3	235	8.6	1.7	2.5	1960	2130	6.8	5	0
N. Fork Gold (2)	B3	44.3	166	8.5	1.9	4.2	1880	2010	3.2	102	16
Soap Creek(10)	A3	46.7	72	8.5	2.5	3.9	1910	2170	6.6	166	58
Stone Creek (5)											
Left Fork	A3	50.0	296	8.0	2.1	3.5	1920	2150	6.6	-	-
Middle Fork	B4	51.0	336	8.0	1.4	1.2	1920	1970	4.6	-	-
Tenderfoot (13)	A3	44.0	116	8.6		8.1	1730	3000	4.5	-	-
White's Gulch (12)	B3	47.5	661	8.2	1.5	4.6	1320	1470	3.3	38	29

[a] Rosgen channel types based on Rosgen (1994).
[b] Data "Not Available".
[c] Tag retention study not done in these streams..

All westslope cutthroat trout from 120 mm to the largest fish captured (324 mm) and a few between 100 and 120 mm were tagged with individually-coded alpha-numeric VI tags as described by Haw et al. (1990) and Kincaid and Calkins (1992)(Figure 2). A minimum fish length of 150 mm (TL) is recommended by the manufacturer to obtain reasonable tag retention (P. Bergman, Northwest Marine Technology, personal communication); however, we were interested in obtaining information on movements and retention of tags for smaller fish. We implanted 2,071 rectangular, plastic-laminate tags (2.5 mm x 1.0 mm x 0.1 mm thick) with a white code on a black background in 1993. Most fish were tagged behind the left eye where tags were injected into the clear post-orbital adipose tissue with a Northwest Marine Technology tagging syringe. A few fish were tagged behind the right eye when tag insertion was poor behind the left eye. Each person who tagged fish had extensive experience applying VI tags (at least 1,000 tags) prior to this study. Adipose fins were excised from all tagged fish to assess tag retention. Prior to excision, no westslope cutthroat trout were missing their adipose fin in any of our sampled streams.

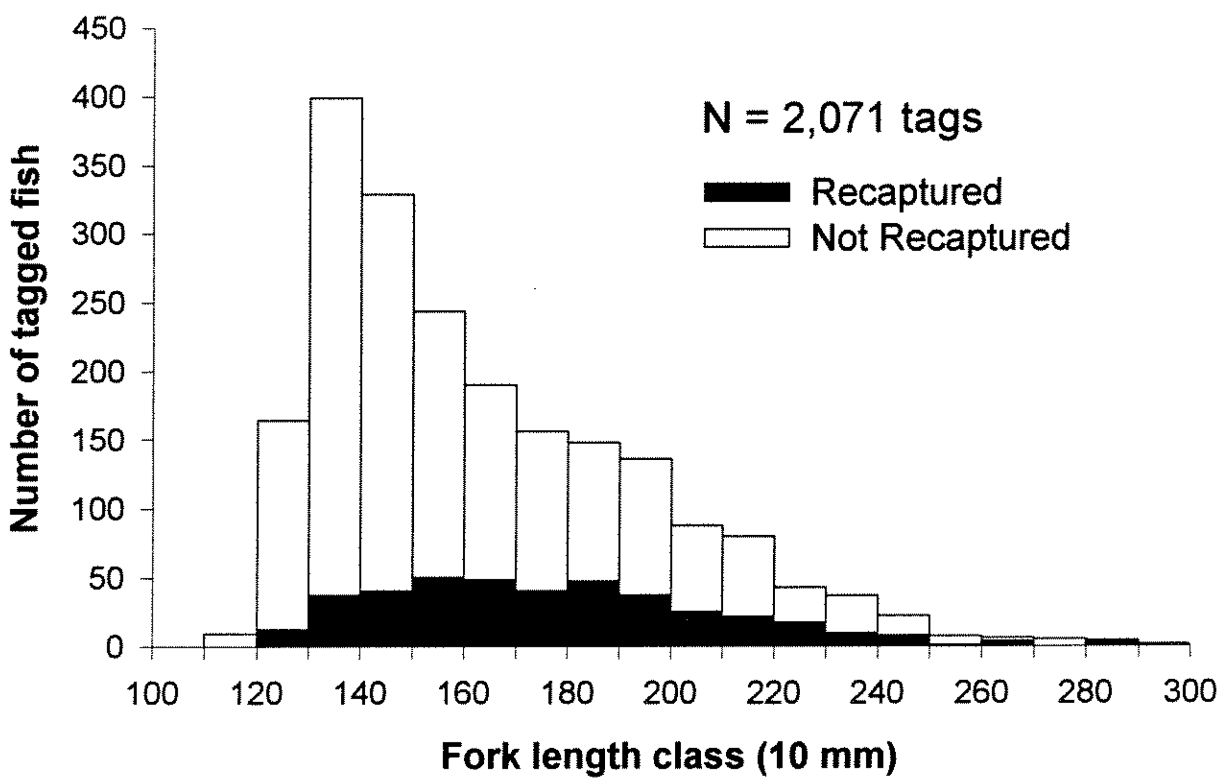

Figure 2. Size distribution of westslope cutthroat trout tagged with visible implant tags in 1993 and of those recaptured with tags during 1993 and 1994.

We rated tagging quality using three classes: 1) good - tag properly inserted without tearing any adipose tissue and easily read; 2) fair - some adipose tissue torn or tag inserted too deep for easy reading; or 3) poor - large rip in adipose tissue or tag inserted so deeply that it was extremely difficult to read or could not be read. Of the 2,071 tags implanted, 1,421 (69%) were classed as "good" insertions, 494 (24%) as "fair", and 34 (1%) as "poor", while 122 (6%) were not classed. Following tagging, fish were allowed to fully recover from the effects of the anesthetic in a perforated bucket prior to being released into calm water areas in the stream.

Recoveries of tagged fish were made from 1 to 406 d after tagging. We followed the protocol of Geoghegan et al. (1990) for quality control and assurance of tag data with the following modifications. When a fish with a clipped adipose fin was recaptured, an attempt was made to find and read the VI tag by inspecting post-orbital tissue behind each eye. If two separate people could not see a VI tag it was recorded as lost. Those fish that had lost their original VI tag were re-tagged, if possible. We were unable to re-tag eight adipose clipped fish in 1993 and 35 in 1994.

Upon recapture, the tag's code was recorded when possible. If a tag was difficult to read, a second person read the tag in an attempt to reduce observer error. Tag readability was classified as unreadable, difficult to read (there was a question on one or more of the letters or numbers), or readable. All retained tags were considered as tag recaptures, regardless of readability. Tag retention at recapture was estimated within the year tagged and the year following tagging by dividing the number of recaptured westslope cutthroat trout with tags by the number recaptured with adipose fin clips.

McMahon et al. (1996) and P. Bergman (Northwest Marine Technology, personal communication) indicated that different stocks inhabiting different environments might retain VI tags differentially. To assess potential effects of different stream environments on tag retention using easily measured variables, wetted stream widths and reach gradients were estimated. Wetted stream widths were measured and averaged to the nearest 0.1 m for each reach. Reach gradients were estimated to the nearest percent using 1:24,000 U.S. Geological Survey contour maps. Reaches were sub-divided based on distribution of westslope cutthroat trout and changes in channel gradient (Table 1). Tag retention was coded as 0 for missing or 1 for present so that logistic regression (Hosmer and Lemeshow 1989) could be used to model the probability of tag retention. We used weighted logistic regression where a weighting variable was assigned to each tagged fish based on our estimated probability that the fish was subsequently recaptured. A weighting variable of 1 was assigned to each fish subsequently recaptured with a tag. Because fin clips did not uniquely identify each fish, length at tagging was unknown for fish that had lost their tags.

To estimate length at tagging for recaptured fish that had lost their tags; we first estimated daily growth by tributary drainage based on tag-recaptured fish and an assumed growth season of May 15 to September 30. We then estimated the 95% prediction interval for length at tagging by back-calculating from length at recapture using daily growth estimates for each tributary drainage and time-at-large for each recaptured fish which had lost its tag. Regression weightings were assigned to all tagged fish that were not subsequently recaptured with a retained tag by assessing the probability that they were recaptured with a lost tag. We did that by examining 95% prediction intervals for estimated length at tagging of fish recaptured with lost tags during the next sampling event. We attempted to match the recaptured fish known to have lost tags with the fish that were tagged and not recaptured. For this matching we assumed fish did not move more than 200 m between tagging and first recapture, which was true for more than 95% of the tag-recaptured fish.

For example, if a fish was recaptured without a tag we could estimate that its length at tagging was between 165 to 185 mm (95% prediction interval) using the growth regression. All fish (n) of unknown fate (ie., not recaptured with a tag) tagged within 200 m of the recapture location with a recorded length at tagging within the predicted 165-185 mm length interval were assigned weightings according to the formula: Weighting = 1/n. If three fish fit the criteria, then each was given a weighting factor of 0.33. We followed this procedure for each adipose marked fish recaptured without a tag and weightings accumulated to a maximum of one for each fish tagged.

For weighted logistic regression we had a sample size of 770 fish (see Table 1 for sample size by reach). We were unable to weigh 58 fish, consequently for models that tested effects of fish condition, and our sample size was 712, which included 359 fish recaptured with tags and 353 fish of unknown fate. The effective degrees of freedom were 501. We did not rate tag insertion quality for 59 fish, consequently models which tested effects of tag insertion quality had a sample size of 711 with 500 effective degrees of freedom. Explanatory variables explored were fork length at tagging (FL), condition factor (C), tag rating (R), reach gradient (G), wetted width (W), and drainage as a class variable (LOC). Variables were added to the model one at a time and tested to determine if they added significantly to the model by comparing the two models under a Chi-square distribution with the appropriate degrees of freedom (Hosmer and Lemeshow 1989).

We tested for differences in length-weight relationships between those fish which lost tags and those fish which retained tags; and between fish which had, to those that had not, been previously tagged by comparing $\log_{10}$length-$\log_{10}$weight regressions (Anderson and Gutreuter 1983). If regression slopes were found to not be significantly different, we tested for differences in elevations (intercepts) according to methods described by Zar (1974). We also tested for influences of tagging on fish condition by comparing condition factors between previously tagged and untagged cutthroat trout $\geq$ 110 mm using ANCOVA and by comparing $\log_{10}$length to $\log_{10}$weight regression slopes and intercepts. Using ANCOVA we tested for effects of VI tagging on condition after accounting for effects of tributary drainage (13 drainages tested) and year of capture (within year tagged or 1 year post-tagging) on 4,960 observations. Statistical tests were made using the SAS Windows program (version 6.03; SAS Institute 1994) and Splus (version 3.1; Statistical Sciences 1993) with significance levels set to 0.05.

Results

We recaptured 348 previously tagged (clipped adipose fin) westslope cutthroat trout during the year they were marked. Of these, 201 (58%) had retained their tag. Of the 616 previously tagged westslope cutthroat trout recaptured the year after tagging, 355 (58%) had retained their tag. We observed a sigmoid relationship between tag retention and fish length at time of recapture (Figure 3).

Weighted logistic regression analyses indicated that fish length was the most significant variable which influenced tag retention (N=712; deviance improvement of 42.5 over intercept only model; P<0.001). Fish condition did not significantly improve the deviance performance of the length model (N=712; deviance improvement of 0.2 over intercept and length model; P=0.69).

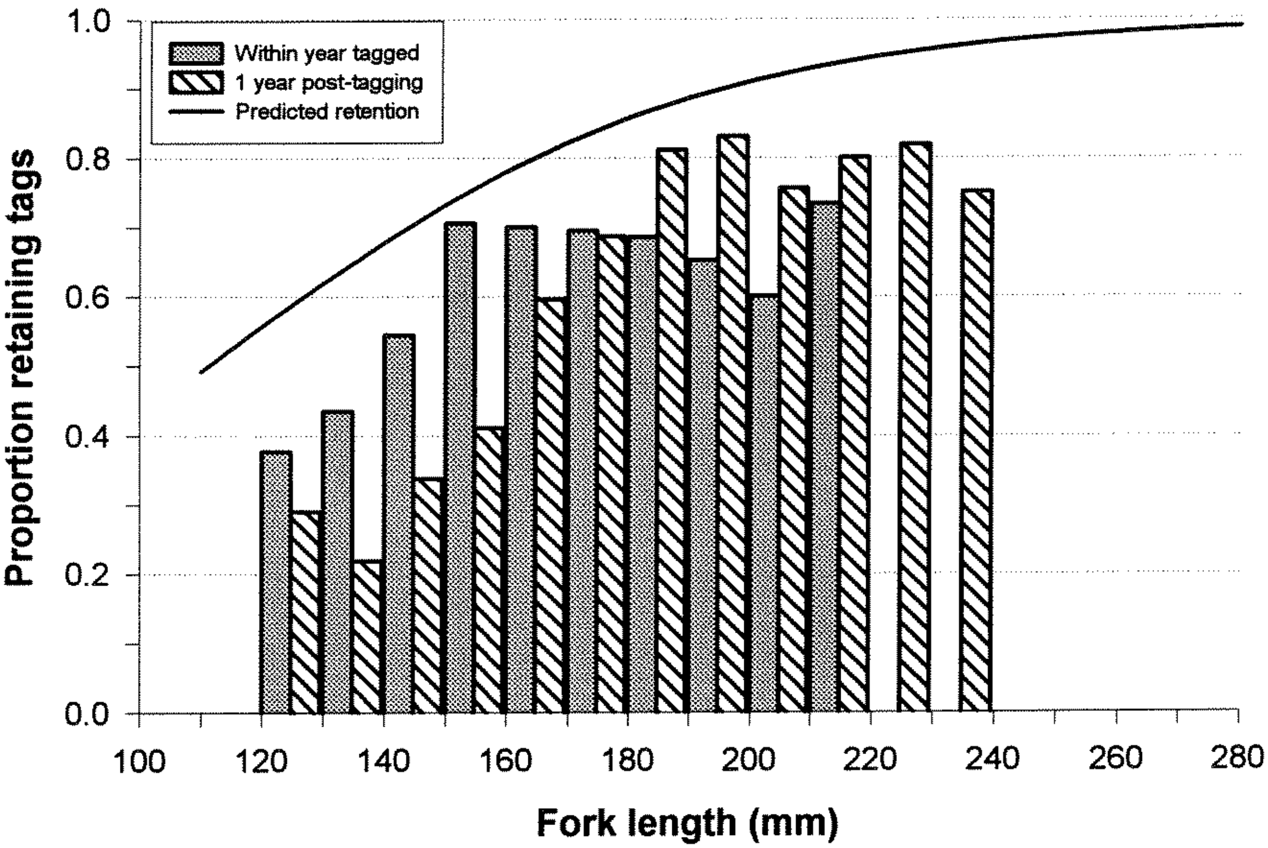

Figure 3. Proportional size distributions at recapture for westslope cutthroat trout that retained visible implant tags within the year of tagging (shaded bars) and 1 year after tagging (crosshatched bars), and the predicted retention of visible implant tags based on length at tagging (solid line).

Because condition factor did not add significantly to the model, we added the 58 fish that did not have weight measurements back into the sample. We then tested effects of tagging quality rating (R), so we removed the 59 fish for which tagging quality had not been rated from the sample. Fish length was still the most significant variable influencing tag retention ($P < 0.001$; Table 2). Tag rating, wetted stream width, and reach gradient significantly improved the model. Tag retention improved as fish length increased, as tag insertions improved, and as streams became narrower and of lower gradient. The model which used tributary drainage as a class variable was not significantly better than the model which used reach estimates of wetted width and channel gradient, suggesting that drainage effects were not as important as reach effects. There was not a significant difference ($P > 0.10$) in slopes or intercepts of $\log_{10}$length-$\log_{10}$weight regressions between those recaptured fish which had retained versus lost their tags.

After accounting for differences between drainages and year ($P < 0.01$; ANOVA), fish condition was not significantly different (ANCOVA; $P > 0.95$) between previously tagged and untagged westslope cutthroat trout. There was also not a significant difference in slopes ($P > 0.50$) or intercepts ($P > 0.05$) of $\log_{10}$length-$\log_{10}$weight regressions between fish which had previously been tagged and newly captured fish $\geq$ 110 mm across all drainages. However, when the 11 drainages which had adequate sample sizes were run individually, significant ($P < 0.05$) differences were found between $\log_{10}$length-$\log_{10}$weight regression slopes for previously tagged versus untagged fish in one of the drainages and between regression intercepts in an additional three drainages.

Ninety-five percent of all tags were easily readable at recapture (526 of 556) with 96% (193 of 201) readable at recapture within the year tagged and 94% (333 of 355) readable a year after tagging. Only one (< 1%) recaptured tag was unreadable within the same year as it was implanted, while three tags (1%) were unreadable one winter after tagging. Tags were unreadable either because they had been inserted too deeply into opaque tissue or because adipose tissue had clouded over the tags. We subsequently found that unreadable tags could be read if they were recoverable using the syringe.

Discussion

While the proportion of recovered westslope cutthroat trout which retained VI tags within the year tagged (58%; N=348) or the year following tagging (58%; N=616) was consistent, our estimated tag retention was lower than most previous studies of VI tag retention. These results can be partially explained by the small lengths at which we tagged the majority of our fish (1,145, or 55%, were <150 mm; FL). Using logistic regression we predicted tag retention (P_r) based on fork length (FL) and "good" tagging quality at time of tagging (Figure 3):

$$P_r=[e^{(-2.894+0.026*FL)}]/[1+e^{(-2.894+0.026*FL)}].$$

Table 2. Results of weighted logistic regression analyses to assess the probability of retention of visible implant tags in westslope cutthroat trout showing the improvement in model deviance the last entered explanatory variable provided. Explanatory variables are fork length at tagging (FL), tag insertion quality rating (R), wetted stream width (W), stream channel gradient as a percentage (G), and drainage (LOC). Explanatory variable coefficients and their associated standard errors (in parentheses) are shown for each model in variable order starting with the intercept, where the last explanatory variable added significantly to the model. Model run only for tagging data where tag insertions were rated.

Covariate(s)	df	Deviance improvement	P	Deviance	Coefficients (SE)
Intercept	499	598.5			
FL	498	551.1	47.4	<0.0001	-2.888(0.612) + 0.025(0.004)*FL
FL+R	496	544.0	7.1	0.029	0.026(0.004)*FL - 2.894(0.615), when tag rating "Good" - 3.406(0.676), when tag rating "Fair" - 5.212(1.494), when tag rating "Poor"
FL+R+W	495	512.8	31.2	<0.001	0.029(0.004)*FL - 1.873(0.659) , when tag rating "Good" - 2.348(0.722), when tag rating "Fair" - 4.056(1.403), when tag rating "Poor"
FL+R+W+G	494	496.4	16.4	<0.001	0.027(0.004)*FL + 0.611(0.908), when tag rating "Good" + 0.181(0.963), when tag rating "Fair" - 1.706(1.512), when tag rating "Poor" - 1.069(0.163)*W - 0.291(0.074)*G
FL+R+LOC	483	482.5	13.9	0.382	

Note that lengths for "within year tagged" and "1 year post-tagging" are lengths at recapture, while lengths for the prediction equation are lengths at tagging.

Our predicted retention rates were consistent with observed retention rates of 94% for 200-307 mm (FL) hatchery raised sea-run cutthroat trout O. clarki released into the Cowlitz River, Washington (Blankenship and Tipping 1993) and 82% retention estimated for rainbow trout 140-240 mm (TL)(Mourning et al. 1994). However, our observed retention rates were slightly higher than the 50% retention observed in brook trout 130-160 mm (TL) and slightly lower than the 100% retention observed for brook trout 200 mm and longer in the wild (Bryan and Ney 1994). Our predicted and observed tag retention rates indicated that the manufacturer's recommended minimum tagging length of 150 mm (TL) would result in at least a 73% retention rate for fish this length and longer. For retention rates over 90% the minimum size at tagging for westslope cutthroat trout would have to increase to about 195 mm.

Quality of tag insertion (tag rating) was significantly related to retention. This result was not unexpected because we assumed that "good" tag insertions resulted in better tag retention. This result emphasizes the need to have experienced personnel do the tagging.

Tag retention varied by drainage, but most drainage variation appeared to be explained by estimates of wetted width and channel gradient made in each reach. These variables are relatively easy to estimate. We are uncertain of the mechanism by which these two variables affect tag retention. We speculate that since higher channel gradients indicate faster water velocities, tag retention might be related to water velocity. Niva (1995) reported that VI tag retention was related to immediate post-tagging handling, with a higher proportion of fish dropped into the water losing tags than fish gently placed into the water. Release of VI tagged fish into high or highly variable velocities might cause similar tag loss. Differences in tag retention rates may also be related to differences between species or environments (McMahon et al. 1996; P. Bergman, Northwest Marine Technology, personal communication). We recommend further research to determine if, and why, different environments, or different fish stocks, lead to different tag retention rates.

We expected fish in better condition to retain tags at higher rates since we initially believed that adipose tissue at tag insertion sites was a form of fatty, or excess, tissue. However, fish condition did not significantly improve deviance performance in the logistic regression model nor were $\log_{10}$length-$\log_{10}$weight regression slopes or elevations significantly different between recaptured fish that retained versus lost tags. Our inability to find a significant relationship between fish condition and tag retention led us to question or original assumption that post-orbital adipose tissue is fatty, or excess, tissue. We have subsequently discovered that the post-orbital, clear tissue at tag insertion sites is primarily a stroma (matrix) of extremely fine, microfibrils of collagen, a form of connective tissue. This tissue contains a few fibrocytes (which form and maintain the collagen), blood vessels, and sinuses (J. Morrison, Fish and Wildlife Service, personal communication).

We found no significant difference ($P > 0.95$; ANCOVA) in fish condition between previously tagged and untagged westslope cutthroat trout in our study. This finding is consistent with findings of Bryan and Ney (1994) who found no significant differences ($P > 0.2$) between condition factors of VI tagged and untagged brook trout in the wild. We also found no significant differences between $\log_{10}$length-$\log_{10}$weight regression slopes ($P > 0.50$) and regression elevations ($P > 0.05$) for previously tagged versus untagged fish. However, we did observe significant differences ($P < 0.05$) in either slopes, or elevations for non-significant slope differences, for four of 11 drainages tested. We are uncertain if those differences in fish condition we observed were caused by tagging effects or factors associated with electrofishing and handling. Since we do not have good evidence that VI tags affected condition of tagged fish, our evidence suggests that VI tags do not affect growth or, inferentially, survival. We recommend that studies be conducted to further test potential effects of VI tags on growth and survival of tagged fish.

Since we used adipose clips as a secondary mark, our efforts to find VI tags on recaptured fin-clipped trout were probably more thorough than if no secondary mark had been used. Since Coombs et al. (1990) found little (0.2%) adipose fin regeneration, or effect of fin removal on growth or survival on Atlantic salmon 3 months following fin clipping, we believe that this mark identified all tagged fish without affecting their growth or survival. Use of this secondary mark might have led to a slight positive bias in our assessment of tag retention.

We conclude that VI tags provide a valuable means to individually mark small fish that typically make up headwater populations. However, investigators must recognize that a relatively high rate of tag loss (> 25%) may occur in fish under 150 mm because tag retention is strongly and positively related to fish length. In spite of the relatively low tag retention rates in these smaller fish, we obtained valuable information on movements for fish that retained their tags. Tag insertion quality positively influenced tag retention and should be considered and documented in any tagging study.

When using VI tags we recommend: 1) personnel inserting the tags must be experienced (Niva 1995) and records should be kept of tag insertion quality; 2) tagging and tag recovery protocols must be established and followed (Geoghegan et al. 1990); 3) if it is necessary to use different tag colors, select colors which contrast sharply to enhance ability to recognize colors upon recapture (Niva 1995); and 4) tag retention should be evaluated (Vreeland 1990; McFarlane et al. 1990; Nielsen 1992). We developed a predictive equation to estimate tag retention by length at tagging for westslope cutthroat trout 100 to 300 mm (FL) and suggest that future investigators could adopt this protocol to evaluate tag retention.

Chapter 2:
Movement of resident westslope cutthroat trout inhabiting isolated headwater streams of Montana

Bradley B. Shepard
Montana Department of Fish, Wildlife and Parks
Department of Biology
Montana State University, Bozeman, Montana 59717, USA

and

Susan C. Ireland and Robert G. White
Montana Cooperative Fisheries Research Unit[a]
Department of Biology, Montana State University
Bozeman, Montana 59717, USA

[a] The Unit is jointly sponsored by Montana State University, Montana Department of Fish, Wildlife, and Parks, and the U.S. National Biological Service.

Introduction

Home range has been defined as "the area over which the animal normally travels" (Hayne 1949; Gerking 1953). Home range differs from territory in that territories are usually relatively smaller areas that are actively defended (Noble 1939; Nice 1941; Gerking 1953), while home ranges are usually larger areas that are not defended. Brook trout (Shetter 1937), brown trout (Schuck 1943), cutthroat trout (Miller 1957), Atlantic salmon (Saunders and Gee 1964), and other species (Gerking 1959) have been reported to remain in a relatively restricted home range during some or all of their life phases. Gerking (1953) suggested that for fishes that inhabit streams containing riffle-pool structure "each pool can be considered as a more or less isolated unit containing a natural population of its own". Gerking (1953) further hypothesized that "the fish population of a small stream may be thought of as a series of discrete, natural units rather than as a single, homogeneous, freely-mixing group". Allen's (1951) study of brown trout in the Horokiwi Stream of New Zealand and Miller's (1957) study of cutthroat trout in a small Colorado stream support these views. Gerking (1953) made it clear that while restricted home ranges may exist for most individuals, some individuals may not remain within restricted home areas. He emphasized that stray fish were very important for potentially occupying territories left vacant and spreading the species over the geographic limits of its tolerance.

Rieman and McIntyre (1993) discussed the role of movement and dispersal in population structuring of bull trout. We investigated the scale of movement that occurred in populations of westslope cutthroat trout that inhabited headwater portions of tributary streams. Since most of these populations were isolated, we also investigated the relationship between the level of isolation and the amount of movement we documented for each population.

Study Area

Movement of westslope cutthroat trout was assessed in 13 tributary drainages of the upper Missouri River and two tributary drainages of the upper Clark Fork River, Montana (Figure 1). Streams in these tributary drainages were characterized by low-flow wetted widths of 1.4 to 6.6 m, water conductivities of 64 to 661 umhos, elevations of 1320 to 3000 m, and gradients of 3 to 11% (Table 1). Cutthroat trout in sampled populations exhibited little evidence of introgression with either rainbow trout Oncorhynchus mykiss or Yellowstone cutthroat trout Oncorhynchus clarki bouveri using external morphometric characteristics and/or electrophoretic testing (Salmon and Trout Genetics Laboratory, University of Montana, Missoula, Montana, unpublished data).

Methods

Fish were captured using a generator powered Smith-Root BP-15 backpack electrofisher ™ (product names are for clarification of methods and do not represent product endorsement). We used frequencies under 40 Hz at pulse widths of at least 1 msec and voltages between 100 to 700 volts to maximize the number of fish captured, while minimizing injury to the fish caused by the shock (W. Fredenberg, Fish and Wildlife Service, personal communication). All captured fish were measured to the nearest mm (FL) and weighed to the nearest gram using either a Ohaus LS2000 or C505 battery powered scale. Most Oncorhynchus spp. over 120 mm were tagged with individually numbered visible implant (VI) tags (available from Northwest Marine Technology, Shaw Island, Washington) using a syringe (Haw et al. 1990; Kincaid and Calkins 1992). Some cutthroat over 120 mm were not tagged because either: 1) their post-orbital adipose tissue was so fragile a VI tag would not stay in place; or 2) they were worked after dark tags could not be read; or 3) when the tagging syringe froze solid during late fall sampling.

We measured the length of stream channels from a fixed point (usually the stream's mouth) on 1:24,000 USGS maps with a map wheel to establish reference points for each sample section. Reference distances were assigned to the middle of each sample section and these stream kilometer distances were used to compute movement distances. We verified our map measurements by measuring stream lengths in the field using a hip chain over at least a 1.5 km distance in three streams. Map measurements were within 0.1 km of field measurements. Lengths of sample sections were generally 50 to 150 m in length. We believe our estimates of movement were accurate to about 100 m.

Gowen et al. (1994) and Gowen and Fausch (1996) cautioned that traditional methods for assessing movement may lead to erroneous conclusions and made some suggestions regarding study design to document movement. Movement was assessed from recaptures of VI tags. VI tags were implanted in Oncorhynchus spp. captured during all sampling events from 1992 through 1994. Recoveries of tags occurred from 1993 through 1995. Most sampling occurred during the summer period from late-June through mid-September. However, from late-September through early November of 1993 and from May through June of 1994 we re-sampled all permanent sample sections as well as sections adjacent to all sample sections in an effort to recover previously marked fish and to tag fish over a larger proportion of the stream. Shepard et al. (1996; Chapter 1 this report) evaluated factors affecting retention of visible implant tags in westslope cutthroat trout. They found tag retention to be strongly related to fish length at tagging and retention rates averaged slightly over 50%.

Movement of recaptured tags were plotted as histograms showing both the direction of movement and absolute value of distance moved for those drainages where at least 20 recapture events had occurred. In addition, Spearman rank correlation coefficients were computed between the proportion of recapture events within a drainage where a fish had moved at least 0.5 km and the rated level that the habitats supporting that fish population were isolated by some type of barrier to fish movement upstream (Table 3).

Table 3. Ranks assigned to levels of isolation for westslope cutthroat trout populations where movement was evaluated from 1993 to 1995.

Rank	Isolating mechanism
0	No known isolation.
1	Isolated from downstream habitats due to recent (anthropgenic – culverts, dams, etc.) causes.
2	Isolated from downstream habitats during all times except during extreme high stream flow events due to natural intermittent portions.
3	Isolated from downstream habitats due to a geologic barrier such as waterfall.

Results

We sampled relatively high proportions of the habitat occupied by westslope cutthroat trout in sample drainages (Table 4). For most streams we sampled at least 10% of the occupied habitat during at least one sampling occasion and for some streams sampling occurred over more than 50% of occupied habitats during at least one sampling event.

A large proportion (580 of 841 recaptures; 70%) of tag recaptured fish had remained within the sample section in which they had been tagged or last recaptured (Figure 4). We observed some slight differences in the numbers of fish that had moved between stream drainages (Figure 5). The proportion of tag recaptured fish that had moved over 0.5 km was significantly and inversely correlated to the ranked level of isolation (Spearman correlation coefficient = -0.621; $P<0.05$).

Table 4. Length (km) of habitat occupied by westslope cutthroat trout and length (%) of occupied habitats sampled by season and year (Su93 = Summer 1993, Fa93 = Fall 1993, Sp93 = Spring 1993, Su94 = Summer 1995, and Su95 = Summer 1995) by stream.

Drainage	Stream	Occupied	Length sampled (% of occupied)				
			Su 93	Fa 93	Sp 94	Su 94	Su 95
Collar Creek (Box Elder Creek)	Collar	2.70	2.09 (77)	0.53 (20)	0.54 (20)	0.64 (24)	0.47 (17)
Cottonwood (Ruby River)	Geyser	1.65	0.71 (43)	0.89 (54)	0.50 (30)	0.40 (24)	1.16 (70)
	Cottonwood	5.80	0.12 (2)	0.11 (2)	0.11 (2)	0.43 (7)	-
Cottonwood (Smith River)	Main Cottonwood	0.60	0.07 (12)	0.14 (23)	0.13 (22)	0.16 (27)	0.14 (23)
	E Fk Cottonwood	3.30	0.18 (5)	0.12 (4)	0.03 (1)	0.35 (11)	0.12 (4)
	W Fk Cottonwood	4.25	0.42 (10)	0.09 (2)	0.32 (8)	0.71 (17)	0.22 (5)
Douglas (Flint Creek)	N Fk Douglas	3.10	1.00 (32)	1.53 (49)	0.47 (15)	0.48 (15)	0.64 (21)
	Main Douglas	1.10	0.27 (25)	0.46 (42)	0.18 (16)	0.08 (7)	-
Gold (Clark Fork)	N Fk Gold	4.20	0.32 (8)	0.77 (18)	0.32 (8)	0.34 (8)	0.34 (8)
Halfmoon (Flatwillow Creek)	Halfmoon	7.30	0.35 (5)	-	-	0.70 (10)	0.67 (9)
Halfway (Jefferson River)	Halfway	9.60	0.61 (6)	0.95 (10)	0.56 (6)	0.74 (8)	0.20 (2)
Jerry (Big Hole River)	Delano	1.90	0.23 (12)	0.84 (44)	0.34 (18)	0.22 (12)	0.28 (15)
	Jerry	5.80	0.36 (6)	0.34 (6)	0.27 (5)	0.25 (4)	0.20 (3)
	Flume	1.00	0.03 (3)	0.05 (5)	-	-	-
McVey (Big Hole River)	McVey	3.30	2.36 (72)	0.75 (23)	1.14 (35)	0.48 (15)	0.45 (14)
Soap (W Fk Madison R)	Soap	3.90	0.40 (10)	0.95 (24)	0.27 (7)	0.40 (10)	0.42 (11)
Tenderfoot (Smith River)	Tenderfoot	8.1	0.76 (9)	0.76 (9)	-	0.97 (12)	0.85 (10)
White's (Missouri River)	White's	4.60	2.96 (64)	1.14 (25)	0.13 (3)	1.06 (23)	2.48 (54)

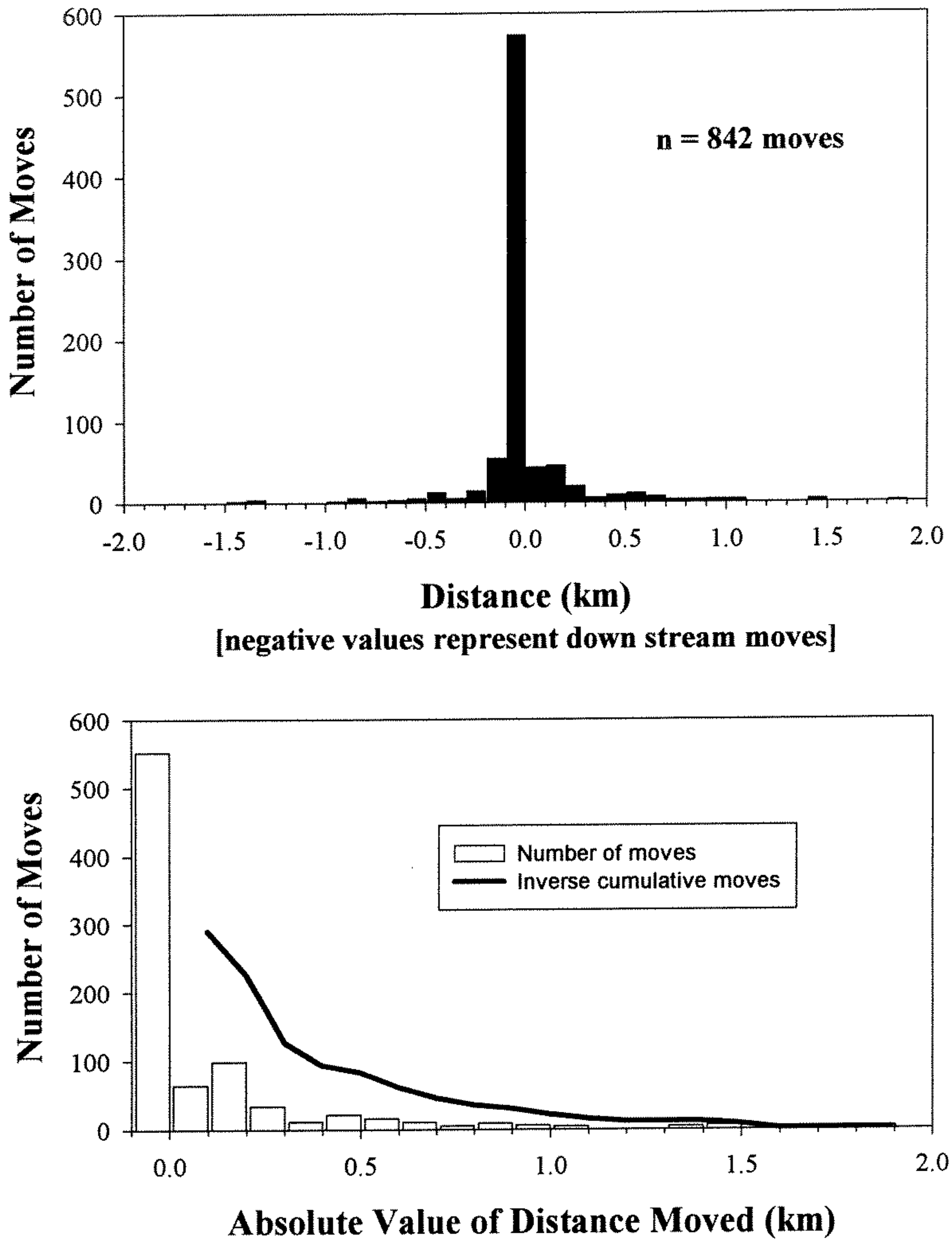

Figure 4. Distance that tagged and recaptured westslope cutthroat trout had moved upstream or downstream (upper graph) and the absolute value of the distance moved (lower graph) in 14 tributary drainages from 1993 to 1995.

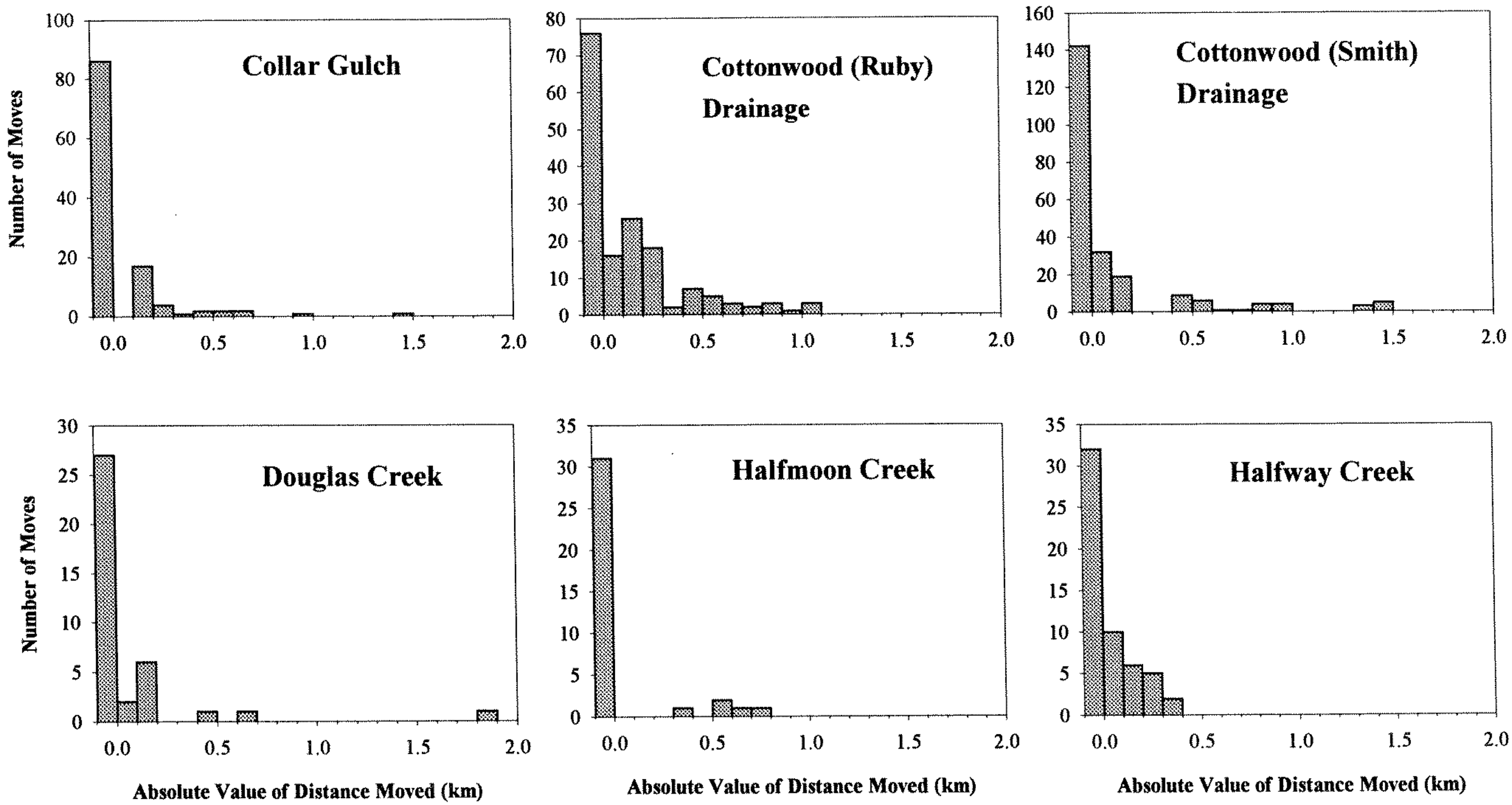

Figure 5. Absolute value of the distance that tagged and recaptured westslope cutthroat trout had moved in the Collar, Cottonwood (Smith), Cottonwood (Ruby), and Douglas, Halfmoon, and Halfway drainages during the period 1993 to 1995.

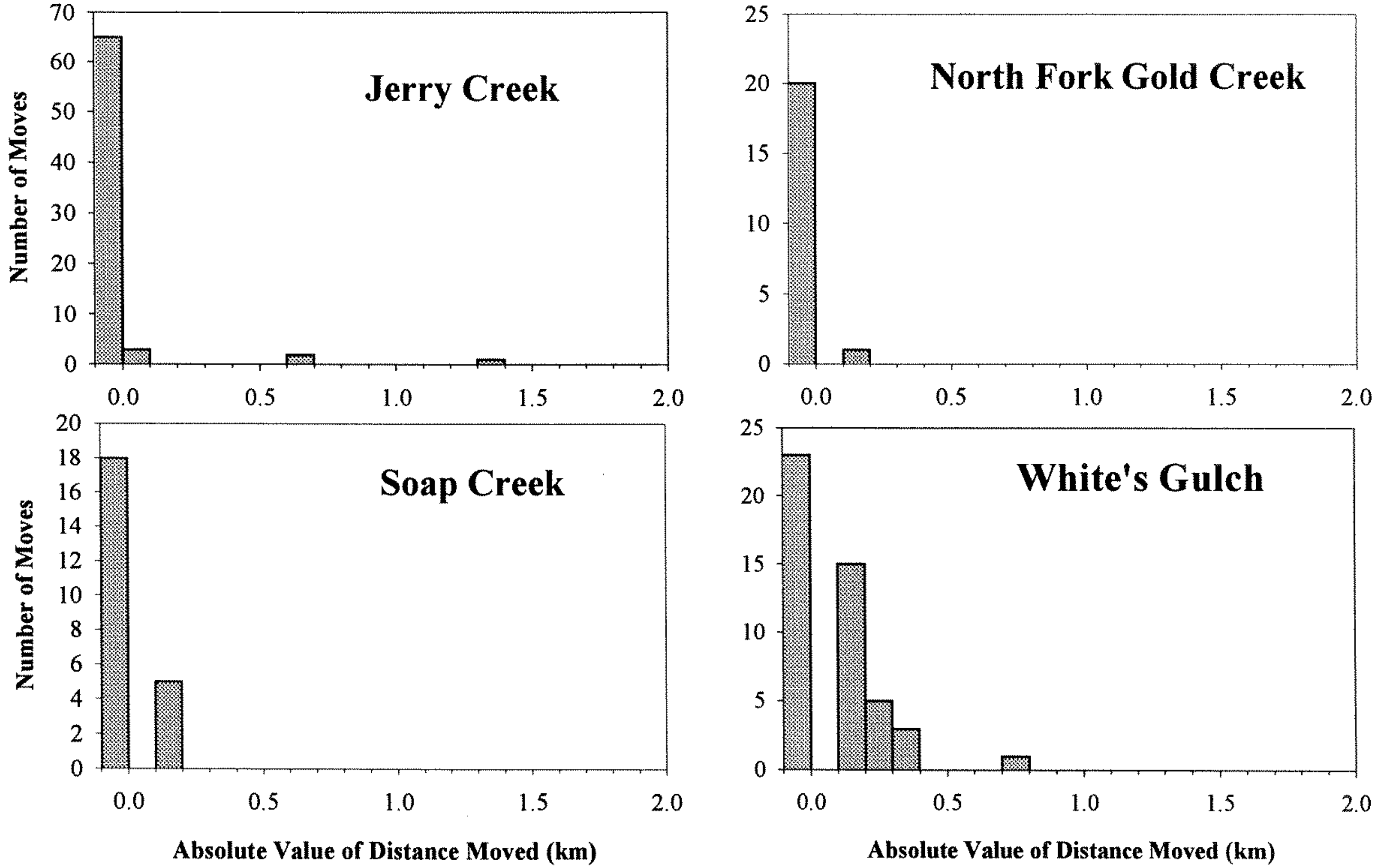

Figure 6. Absolute value of the distance that tagged and recaptured westslope cutthroat trout had moved in the Jerry, North Fork Gold, Soap, and White's drainages during the period 1993 to 1995.

Discussion

We sampled relatively large proportions of occupied habitats (Table 4). This extensive sampling should have reduced movement bias associated with small sample size. Our recapture information suggests that relatively little movement is occurring in these resident westslope cutthroat trout populations, but that a few individuals may be moving relatively long distances. Since we did not set downstream traps at the lower boundaries of population distributions nor sample much below the known distribution of westslope cutthroat trout, fish that moved downstream out of the habitats that supported the majority of the population would not have been sampled. We documented that a few large fish moved downstream into segments of stream channels in both Collar and Cottonwood (Smith drainage) creeks that only carried stream flow during high flow events. We also documented that large fish occupying a sample section in Halfway Creek apparently left that section and moved out of the headwater reaches because we did not recapture these larger fish after tagging them. This sample section was located below an old mining settling pond and large fish appeared to move down out of this pond and then were unable to move back up into the pond. The proportion of documented movements 0.5 km or longer was correlated with the level of isolation experienced by the fish population.

Chapter 3:
Length frequencies of westslope cutthroat trout resident of headwater streams in Montana

Bradley B. Shepard and Robert G. White
Montana Cooperative Fishery Research Unit[a]
Biology Department
Montana State University
Bozeman, Montana 59717-0001

[a] The Unit is jointly sponsored by Montana State University, Montana Department of Fish, Wildlife, and Parks, and the U.S. National Biological Service.

Introduction

This chapter presents summarized length-frequency data for westslope cutthroat trout sampled from 1993 through 1995 in headwater streams of Montana (Figure 1). Fork lengths were measured to the nearest millimeter. Sampling was done primarily during the summer, from June 20 through September 15. Additional sampling was done during fall 1993 from September 22 through November 4, and during spring 1994 from May 24 to June 16.

Results and Discussion

The length-frequency histogram for all westslope cutthroat trout sampled from all sites during the summer season showed two nodes that could possibly be used for separating age classes (Figure 7). A node appeared from 60 to 90 mm that probably indicated age 1 fish and another slight node existed between 100 to 140 that might indicate age 2 fish. Age 0 fish were generally under 50 mm and in most streams age 0 fish had not emerged from the streambed until late summer or early fall. In addition, age 0 fish were not always captured because they slipped through dip nets due to their extremely small size and were so fragile that we chose not to capture, hold, and work them during most sampling events.

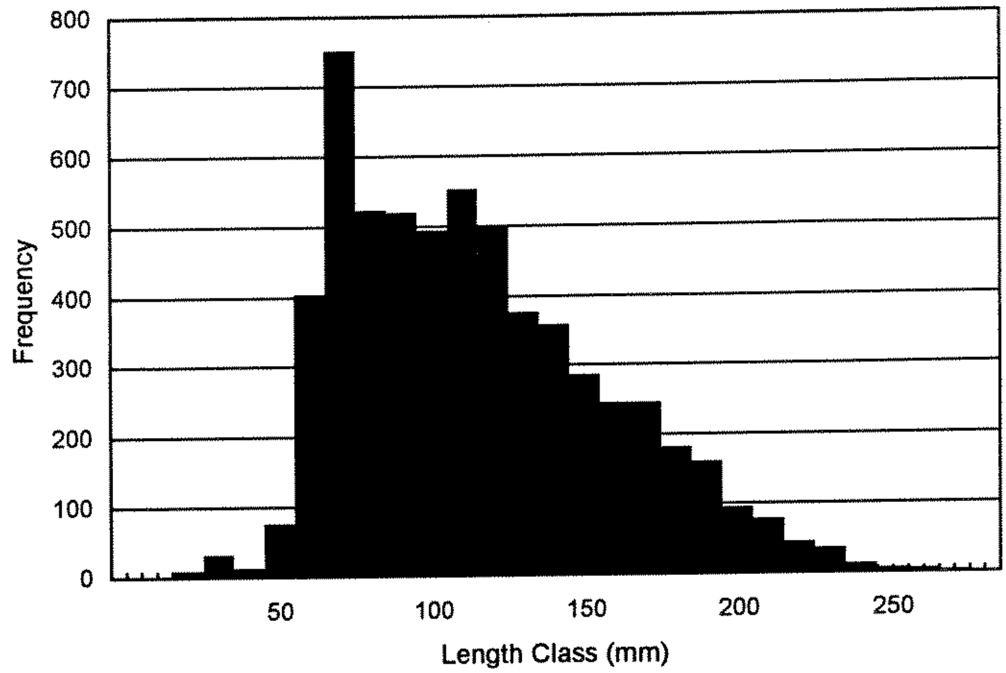

Figure 7. Length-frequency histogram for the summer season (June 20 to September 15) combined for all years (1993 through 1995) and for all streams.

Length-frequency histograms were constructed for individual streams where at least 100 westslope cutthroat trout had been sampled during at least one of the three years (Figures 8 to 10). These length-frequency histograms showed relatively clear nodes for age 1 and 2 fish for some streams. Age 3 fish could also sometimes be identified using these histograms for a few streams. The histogram for the West Fork of Cottonwood Creek shows relatively strong nodes for ages 1, 2, and 3 (Figure 10). However, ages were not easily interpreted from all the histograms.

For some streams the histograms showed that a year class had been severely depressed. For instance, it appeared that very few age 1 fish (60 to 90 mm) were present in Collar Creek during 1993 (the 1992 year-class). This missing year-class was also obvious in 1994 (low numbers of fish between 100 and 140 mm) and 1995 (low numbers between 140 and 160 mm; Figure 8). Delano, Geyser, Soap, and West Fork Cottonwood creeks also appeared to have weak 1992 year-classes; however, Soap Creek was the only stream where this poor year-class could be easily seen in histograms from subsequent years (Figures 8 and 10). Conversely, the remaining streams seemed to have supported a good 1992 year-class based on 1993 histograms.

We suspect that growth that occurred throughout the summer months may have made the interpretation of ages from summer length-frequency histograms difficult. We had hoped that histograms for fish collected during the fall and spring might have been easier to interpret, but we did not find that to be the case (Figures 11 and 12). We also concur with Downs' (1995) suggestion that different fish inhabiting different microhabitats within a single stream

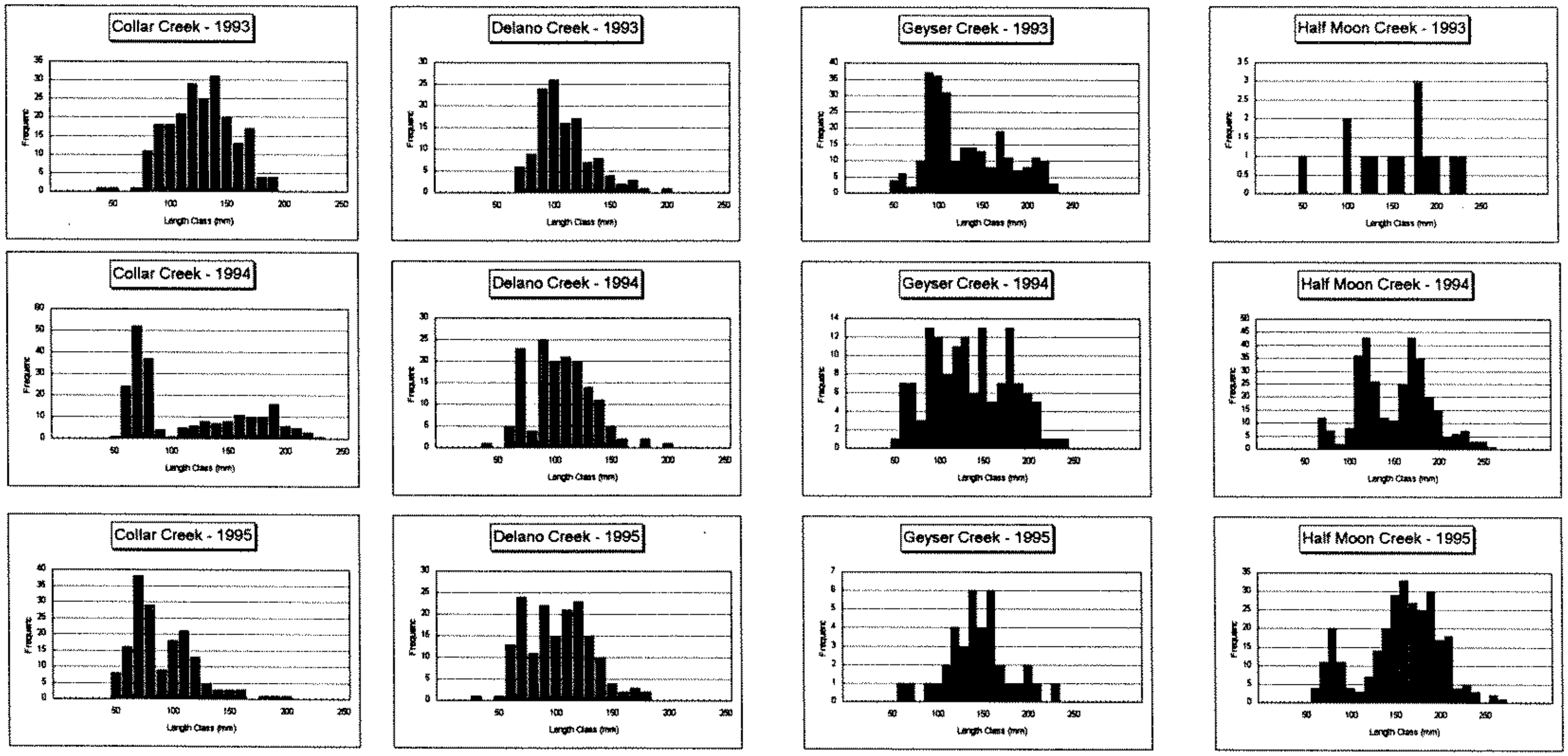

Figure 8. Length-frequency histograms for westslope cutthroat trout sampled from Collar, Delano, Geyser, and Halfmoon creeks during the summers of 1993 through 1995.

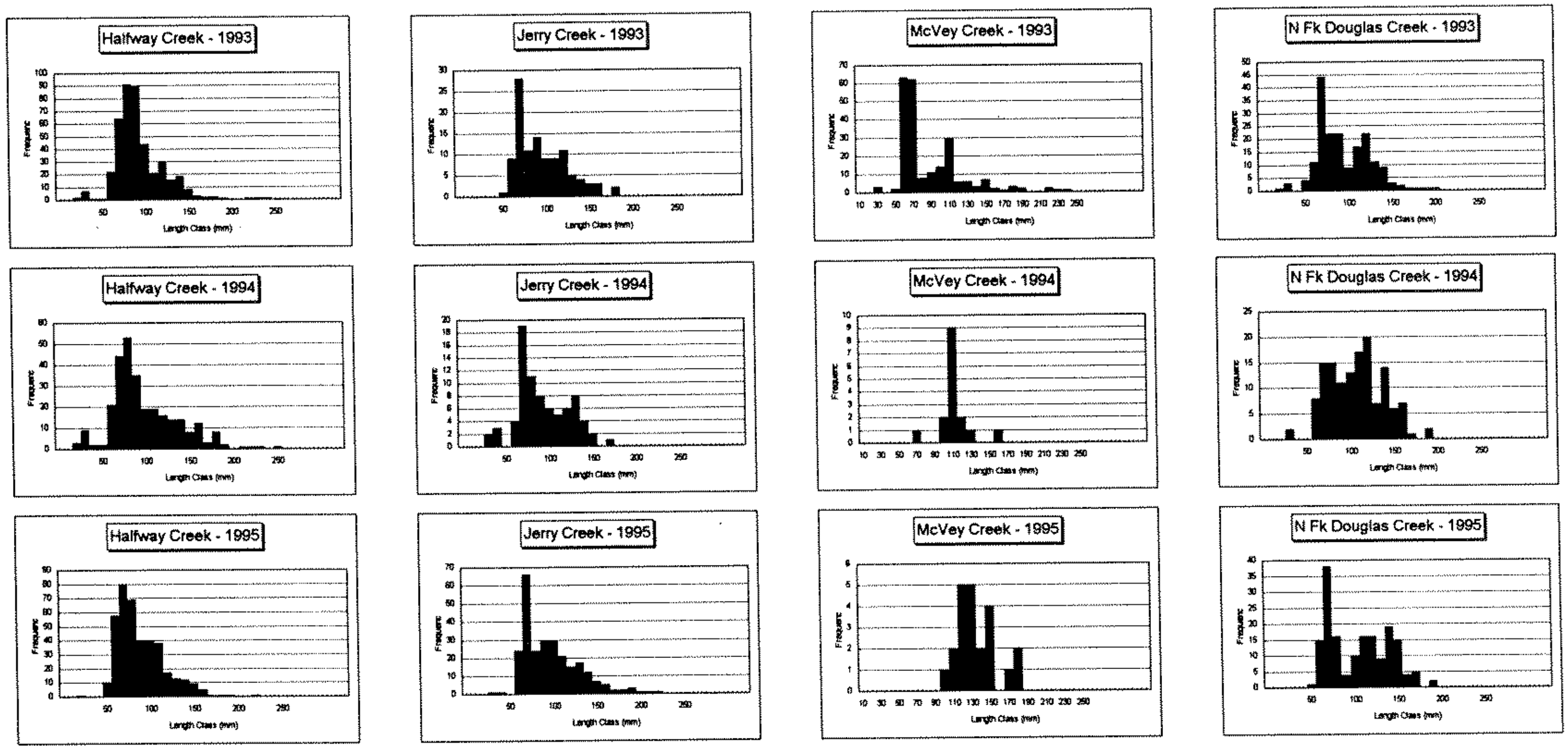

Figure 9. Length-frequency histograms for westslope cutthroat trout sampled from Halfway, Jerry, McVey and North Fork Douglas creeks during the summers of 1993 through 1995.

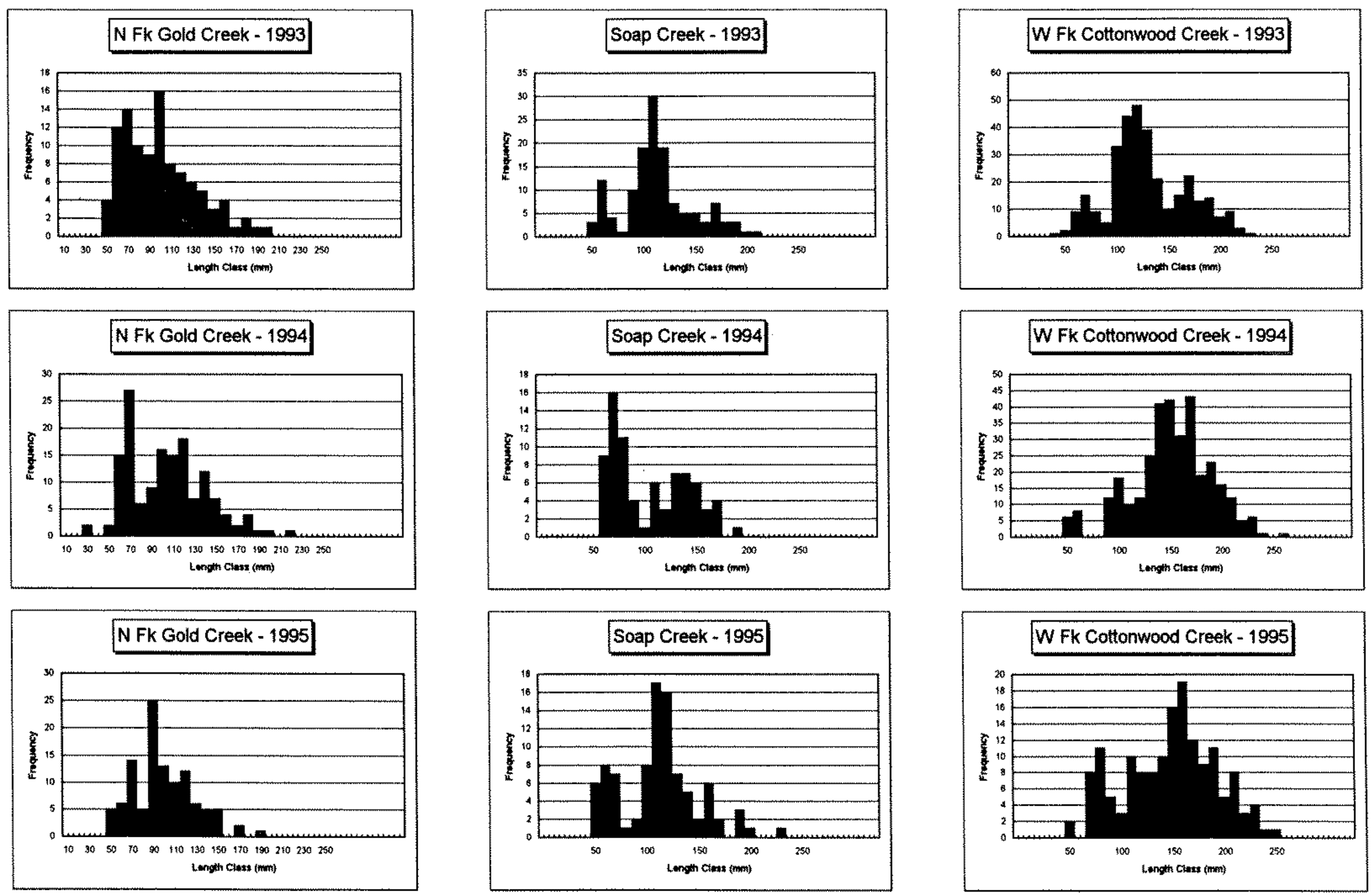

Figure 10. Length-frequency histograms for westslope cutthroat trout sampled from North Fork Gold, Soap, and West Fork Cottonwood creeks during the summers of 1993 through 1995.

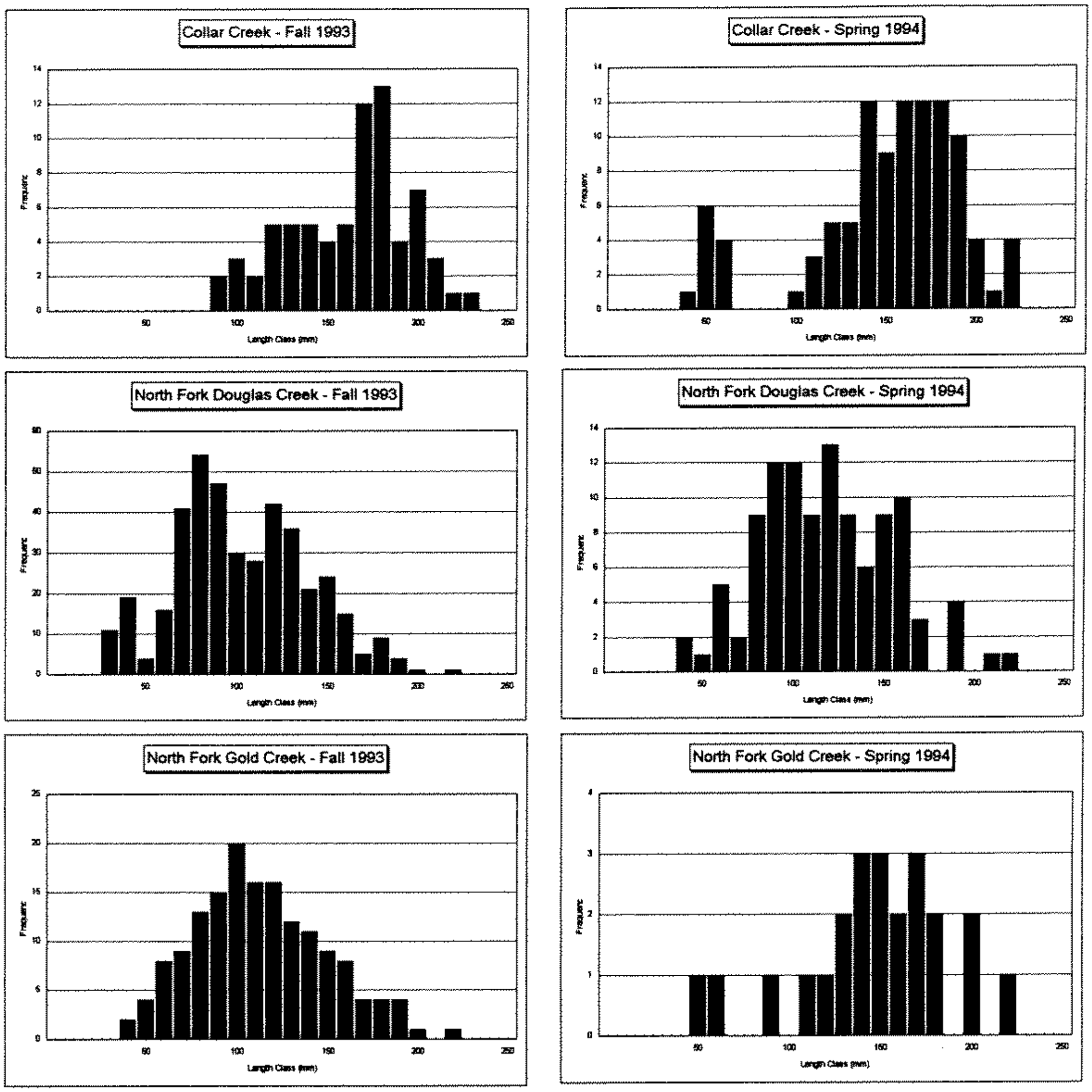

Figure 11. Length-frequency histograms for westslope cutthroat trout sampled from Collar, North Fork Douglas, and North Fork Gold creek, during the fall of 1993 and spring of 1994.

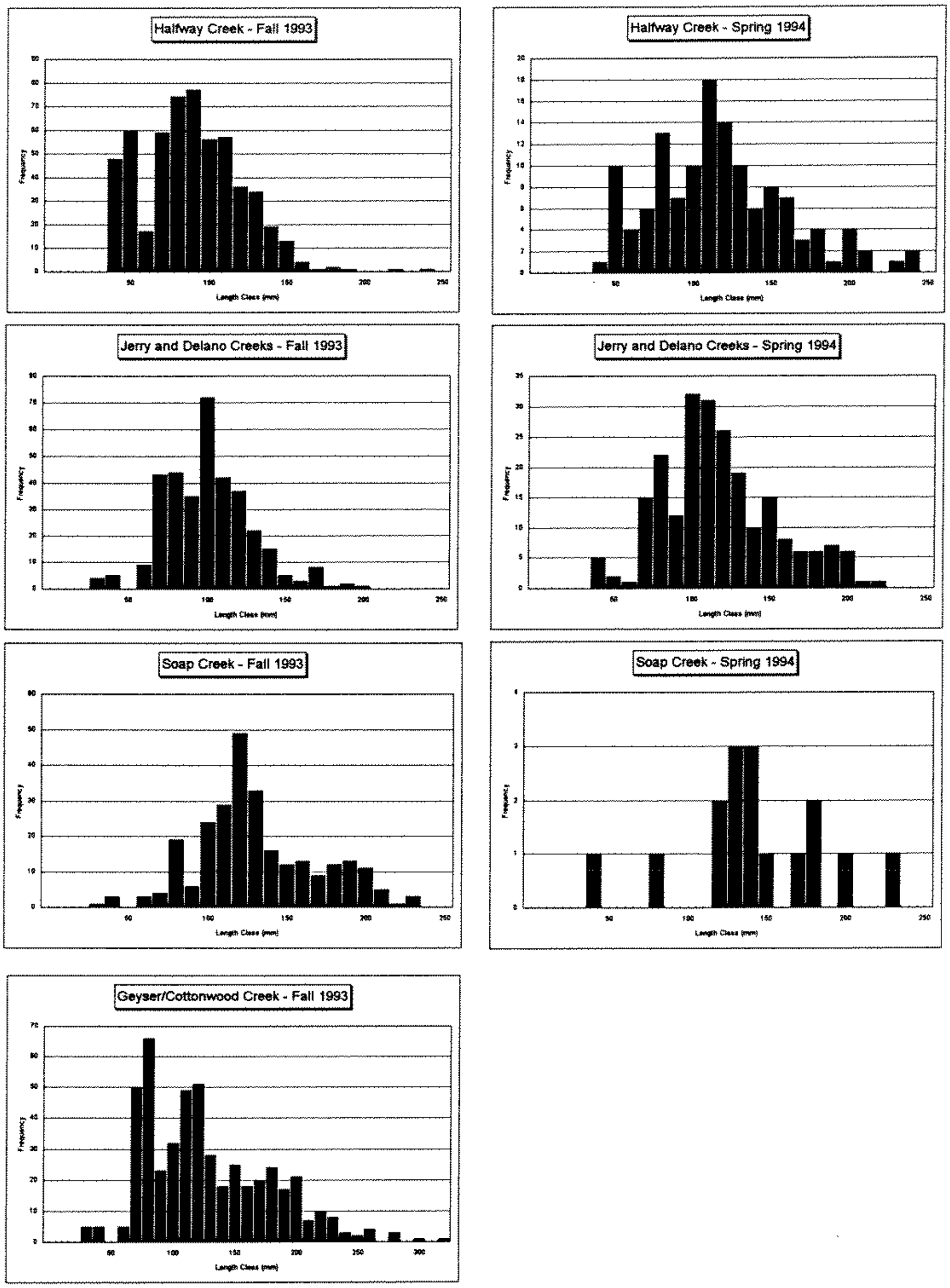

Figure 12. Length-frequency histograms for westslope cutthroat trout sampled from Halfway, Jerry/Delano, Soap, and Geyser/Cottonwood creeks during the fall of 1993 and spring of 1994.

may exhibit different growth rates. If true, this mechanism would also make it more difficult to interpret ages using length-frequency histograms.

In conclusion, length-frequency histograms could not be easily used for assigning ages and assessing relative year-class strengths across all sampled streams. We believe that length-frequency histograms could be used for determining that a year-class was nearly absent, especially if the missing year-class was age 1 at the time length-frequency sampling was done. We recommend that any length-frequency sampling done to compare among streams or years be done at similar times of year and suggest using either early or late summer as a preferred sampling time. We further recommend that a minimum of 100 fish be measured from each stream at each sampling period to construct length-frequency histograms for size structure analyses. These fish should be collected over the length of habitat occupied by the population to ensure that all age classes that are present are sampled.

Acknowledgements

This research was supported by funds provided by the U.S. Department of Agriculture, Forest Service, Rocky Mountain (formerly Intermountain) Research Station; U.S. Department of Agriculture, Forest Service, Region One; Montana Department of Fish, Wildlife and Parks; Montana Cooperative Fishery Research Unit; Montana State University; and the U.S. Department of Interior, Bureau of Land Management's Headwaters and Judith Resource Areas. C. Downs, D. Nixdorf, J. Pravochek, and D. Fuller assisted with field data collection. Montana Department of Fish, Wildlife and Parks fisheries biologists provided data and R. Spoon, D. Oswald, and J. Brammer and their staffs assisted with field work. Forest Service personnel on the Beaverhead, Deerlodge, Helena, and Lewis and Clark Forests and Bureau of Land Management personnel from the Judith and Headwaters Resource Areas of the Bureau of Land Management provided data and field support. D. Dunlap, B. Peresinni, and D. Webb assisted with data analysis for Chapter 1. L. Ahlm, P. Bergman, L. Blankenship, S. Martin, T. McMahon, B. Rieman, and A. Zale reviewed earlier drafts of Chapter 1 and provided valuable comments.

References

Allen, K.R. 1951. The Horokiwi Stream. A study of a trout population. New Zealand Marine Department of Fisheries Bulletin 10:1-231.

Anderson, R.O., and S.J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283-300 in L.A. Nielsen, and D.L. Johnson, editors. Fisheries Techniques, American Fisheries Society, Bethesda, Maryland.

Blankenship, H.L., and J.M. Tipping. 1993. Evaluation of visible implant and sequentially coded wire tags in sea-run cutthroat trout. North American Journal of Fisheries Management 13:391-394.

Bryan, R.D., and J.J. Ney. 1994. Visible implant tag retention by and effects on condition of a stream population of brook trout. North American Journal of Fisheries Management 14:216-219.

Coombs, K.A., J.K. Bailey, C.M. Herbinger, and G.W. Friars. 1990. Evaluation of various external marking techniques for Atlantic salmon. American Fisheries Society Symposium 7:142-146.

Downs, C.C. 1995. Age determination, growth, fecundity, age at sexual maturity, and longevity for isolated, headwater populations of westslope cutthroat trout. Master's thesis. Montana State University, Bozeman, Montana.

Geoghegan, P., M.T. Mattson, D.J. Dunning, and Q.E. Ross. 1990. Improved data in a tagging program through quality assurance and quality control. American Fisheries Society Symposium 7:714-719.

Gerking, S. D. 1953. Evidence for the concepts of home range and territory in stream fishes. Ecology 34:347-365.

Gerking, S.D. 1959. The restricted movement of fish popuations. Biology Review 34:221-242.

Gowan, C. and K. D. Fausch. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Canadian Journal of Fisheries and Aquatic Sciences 53:1370-1381.

Gowan, C., M. K. Young, and K. D. Fausch. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626-2637.

Haw, F., P.K. Bergman, R.D. Fralick, R.M. Buckley, and H.L. Blankenship. 1990. Visible implanted fish tag. American Fisheries Society Symposium 7:311-315.

Hayne, D.W. 1949. Calculation of size of home range. Journal of Mammology 30:1-18.

Hosmer, D.W. and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York.

Kincaid, H.L., and G.T. Calkins. 1992. Retention of visible implant tags in lake trout and Atlantic salmon. Progressive Fish-Culturist 54:163-170.

McFarlane, G.A., R.S. Wydoski, and E.D. Prince. 1990. Historical review of the development of external tags and marks. American Fisheries Society Symposium 7:9-29.

McMahon, T.E., S.R. Dalbey, S.C. Ireland, J.P. Magee, and P.A. Byroth. 1996. Field evaluation of visible implant tag retention in brook trout, cutthroat trout, rainbow trout, and arctic grayling. North American Journal of Fisheries Management 16:.921-925

Miller, R.B. 1957. Permanence and size of home territory in stream-dwelling resident trout. Journal of the Fisheries Research Board of Canada 14:687-691.

Mourning, T.E., K.D. Fausch, and C. Gowan. 1994. Comparison of visible implant tags and Floy anchor tags on hatchery rainbow trout. North American Journal of Fisheries Management 14:636-642.

Nice, M.M. 1941. The role of territory in bird life. American Midlands Naturualist 26:441-487.

Nielsen, L.A. 1992. Methods of marking fish and shellfish. American Fisheries Society Special Publication 23, Bethesda, Maryland.

Niva, T. 1995. Retention of visible implant tags by juvenile brown trout, Salmo trutta. Journal of Fish Biology 46:997-1002.

Noble, G.K. 1939. The role of dominance in the life of birds. Auk 56:253-273.

Rieman, B. E. and J. D. McIntyre. 1993. Demographic and Habitat Requirements for Conservation of Bull Trout. General Technical Report INT-302, USDA Forest Service, Intermountain Research Station, Boise, Idaho.

Robison-Cox, J.R. 1998. A record linkage approach to imputation of missing data: analyzing tag retention in a tag-recapture experiment. Journal of Agriculture, Biological, and Environmental Statistics 3:48-61.

Rosgen, D.L. 1994. A classification of natural rivers. Catena 22:169-199.

SAS Institute. 1994. SAS User's Manual Update for Release 6.10. SAS Institute Inc., Cary, North Carolina.

Saunders, R.L., and J.H. Gee. 1964. Movement of young Atlantic salmon in a small stream. Journal of the Fisheries Research Board of Canada 21:27-36.

Schuck, H.A. 1943. Survival, population density, growth, and movement of wild brown trout in Crystal Creek. Transactions of the American Fisheries Society 73:209-230.

Shepard, B.B., J. Robison-Cox, S.C. Ireland, and R.G. White. 1996. Factors influencing retention of visible implant tags by westslope cutthroat trout inhabiting headwater streams of Montana. North American Journal of Fisheries Management 16:913-920.

Shepard, B.B., S.C. Ireland, C.C. Downs, and R.G. White. 1998a. Population dynamics and demographics of westslope cutthroat trout Oncorhynchus clarki lewisi inhabiting isolated headwater tributaries of Montana. Final Report under contract INT-RJVA-92682 (Part 2) to the USDA Forest Service, Rocky Mountain Research Station, Boise, Idaho by the Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, Montana.

Shepard, B.B., M. Taper, and R.G. White. 1998b. Influence of abiotic and biotic factors on abundance of stream-resident westslope cutthroat trout Oncorhynchus clarki lewisi in Montana streams. Final Report under contract INT-RJVA-92682 to the U.S.D.A. Forest Service, Rocky Mountain Research Station, Boise, Idaho by the Montana Cooperative Fishery Research Unit, Montana State University, Bozeman, Montana.

Shetter, D.H. 1937. Migration, growth rate, and population density of brook trout in the North Branch of the Au Sable River, Michigan. Transactions of the American Fisheries Society 66:203-210.

Statistical Sciences. 1993. Splus. Seattle, Washington.

Vreeland, 1990. Random-sampling design to estimate hatchery contributions to fisheries. American Fisheries Society Symposium 7:691-707.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.