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AGE DETERMINATION, GROWTH, FECUNDITY, AGE AT SEXUAL MATURITY, AND LONGEVITY FOR ISOLATED, HEADWATER POPULATIONS OF WESTSLOPE CUTTHROAT TROUT

by

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ABSTRACT

This study examined the validity and precision of scales as aging structures as well as fecundity, age at sexual maturity, and longevity for headwater populations of westslope cutthroat trout (Oncorhynchus clarki lewisi). This information will be used by the U.S. Forest Service Intermountain Research Station biologists to model extinction risk associated with small population size. Evidence for the validity of otoliths as aging structures for westslope cutthroat trout was provided through comparison with a length-frequency histogram from West Fork Cottonwood Creek, MT. Ages assigned from otoliths agreed with ages assigned from the length-frequency histogram. Ages interpreted from otoliths were significantly higher than ages interpreted from scales for 424 paired age structure samples ($\chi^2 = 295.5$, $p < 0.001$). I developed a model using >6 circuli to the first annulus as a predictor of a missing first year annulus. The model improved age structure agreement from 24% to 66%. This model will allow biologists to use scales as aging structures with increased accuracy up to the age of sexual maturity. Beyond the age of sexual maturity, when growth rates slow, it becomes difficult to interpret annuli near the edge of scales. This reduces the reliability of ages interpreted from the scales of older individuals. Fecundity was estimated from three study populations and appears highly variable. I produced a linear regression model to predict fecundity (E) at fork length (FL): $E = -515.5 + 4.5(FL)$ ($r^2 = 0.52$, $p < 0.01$). I recommend applying this model to headwater populations of westslope cutthroat trout from the upper Missouri River drainage. Males from study populations began to sexually mature at age 2 with all sampled males sexually mature by age 4. Some females (26%) from study populations were sexually mature at age 3, with most (93%) mature by age 5. Logistic regression indicated that length is more important in determining sexual maturity than age and this is supported by statistical differences in mean lengths at age for sexually immature and sexually mature trout. Males matured between 110 and 160 mm and females matured between 150 and 180 mm. The maximum age estimated, based on ages interpreted from 475 otoliths from fish in 29 streams, was 8 years.

INTRODUCTION

Westslope cutthroat trout Oncorhynchus clarki lewisi have undergone a major reduction in their distribution and abundance attributed to habitat loss due to land use practices, introduction of non-native fish species, and over exploitation (Liknes and Graham 1988; Behnke 1992). Liknes and Graham (1988) estimated that genetically pure populations of westslope cutthroat trout occupied only 2.5% of their historic range in Montana by 1988. Rieman et al. (1993) suggested that isolation of salmonid populations due to habitat fragmentation increases deterministic, stochastic, and genetic risks of extinction. Populations of westslope cutthroat trout in Montana, and throughout their historic range, have become increasingly fragmented in recent years with many of the remaining genetically pure populations relegated to headwater areas. Headwater habitats may provide a refugia from anthropogenic disturbance and allow native fishes to maintain local adaptations and competitive advantages over non-native species in relatively undisturbed habitats.

Since headwater populations usually provide little recreational opportunity, likely due to slow growth rates and remoteness, little is known about these populations. Fish managers must assess extinction risks and develop conservation and recovery strategies if this sub-species is to survive and persist in the wild. Information on age and growth, as well as means and variances of basic population parameters including age at sexual maturity, fecundity, and longevity are necessary to model extinction risks. This study was conducted to provide this information.

Scales are commonly used to age many species of fish and are often preferred because their removal and examination does not require sacrificing the fish. Major problems associated with using scales to estimate the ages of salmonids are that a first year annulus does not always form (Lentsch and Griffith 1987) and annuli may become crowded or indistinguishable as fish growth slows (Johnson 1976). Scales may also be partially resorbed as individuals age and mature, as was documented in chinook salmon Oncorhynchus tshawytscha (Chilton and Bilton 1986). Further, scales may become damaged or lost and regenerated scales will not accurately reflect an individual fish's age or growth.

Lentsch and Griffith (1987) documented the absence of a first year annulus in 21 of 24 populations of cutthroat trout and cutthroat-rainbow trout hybrids O. clarki * O. Mykiss. Fraley et al. (1981) and Shepard et al. (1984) reported that 30% to 61% of westslope cutthroat in the upper Flathead basin of Montana did not form a first year annulus. Some researchers (Laakso and Cope 1956; Jensen and Johnsen 1982; Shepard et al. 1984; Lentsch and Griffith 1987) have suggested that the number of circuli prior to the first discernible annulus on a scale can be used to determine if the first annulus is missing. This number varies between populations and must be determined empirically.

Accepting scales as a valid aging structure for headwater populations of westslope cutthroat trout without first determining the accuracy and precision of this method could result in inaccurate estimates of age. Inaccurate estimates of age could lead to errors in the calculation of growth, recruitment, and mortality rates, which are important in guiding management actions.

In addition to scales, fin rays are another potentially non-lethal aging structure. Fin rays have been validated for aging brown trout Salmo trutta (Burnett 1969; Shirvell 1980), and lake whitefish Coregonus clupeaformis (Mills and Beamish 1980). I wanted to determine if they could be used to accurately age westslope cutthroat trout inhabiting small headwater streams.

Otoliths have been used to age various salmonid species including chinook salmon (Neilson and Green 1983), sockeye salmon Oncorhynchus nerka (Marshall and Parker 1982), steelhead trout Oncorhynchus mykiss (Campana 1983), and brook trout Salvelinus fontinalis (Hall 1991). It has been demonstrated that scale growth slows at maturity while otoliths continue to grow in relation to length for lake trout, Salvelinus namaycush (Simard and Magnin 1972). Simkiss (1972) demonstrated that bones and otoliths in many fishes have priority over scales in calcium deposition and, in some instances, calcium may be resorbed from scales. The major concern over the use of otoliths as an aging structure is that the fish must be sacrificed.

To assess extinction risk, biologists need some estimate of the reproductive potential of individual populations. Modeling fecundity at length holds promise. The few studies that have documented fecundity for westslope cutthroat trout report egg numbers ranging from 183 to 2025 per female (Averett 1962; Johnson 1963; Smith et al. 1983). Rieman and Apperson (1989) fit a fecundity versus length regression based on documented fecundity. However, few smaller (only 25 % $<$ 275 mm) mature females, typically encountered in headwater populations, were sampled. The validity of a fecundity versus length relationship for populations containing small females is uncertain.

Information on age and length at sexual maturity is also necessary to estimate reproductive potential. In river and lake systems westslope cutthroat trout reach sexual maturity between ages 3 and 5 (Brown 1971; Liknes and Graham 1988; Behnke 1992). Because headwater populations of westslope cutthroat trout grow slower than those in mainstem rivers and lakes, they may mature at older ages.

Longevity estimates make it possible to predict the long term reproductive potential of individuals and populations. Longevity of westslope cutthroat trout is not well documented, particularly for headwater populations. Using scales, Johnson (1963) and Lukens (1978) estimated maximum ages of 6 years compared to 7 years reported by Shepard et al. (1984). Fraley (Montana Department of Fish, Wildlife and Parks, personal communication) documented a 13-year-old westslope cutthroat trout from the South Fork Flathead River drainage.

Specific objectives of my study were to:

1) Validate ages interpreted from scales through recapture of visible implant tagged fish and comparisons of paired age structure samples.
2) Determine growth rates for isolated headwater populations.
3) Compare the relative precision of ages interpreted from scales and otoliths between experienced readers.
4) Examine the use of fin rays for aging small westslope cutthroat trout.
5) Determine fecundity, age at sexual maturity, and longevity for headwater populations.

STUDY AREA

Nineteen headwater streams were selected for this study. Fifteen of the selected study streams were in the upper Missouri River drainage and four were part of the Clark Fork River drainage (Figure 1).

Streams selected for study represented typical headwater habitats in Montana. Study stream elevations ranged from 1470 m at White's Gulch to 2290 m at Halfway Creek (Table 1). Mean channel gradients ranged from 3.2% for North Fork Gold Creek to 6.6% for Soap Creek. Productivity in most streams was low, as indicated by water conductivity's ranging from 57 μmhos in East Fork Cottonwood Creek to 649 μmhos in White's Gulch.

Fish species composition in most study streams consisted solely of genetically pure westslope cutthroat trout. Seven study streams also supported populations of brook trout *Salvelinus fontinalis* and two study streams supported populations of rainbow trout x westslope cutthroat trout hybrids (Table 2).

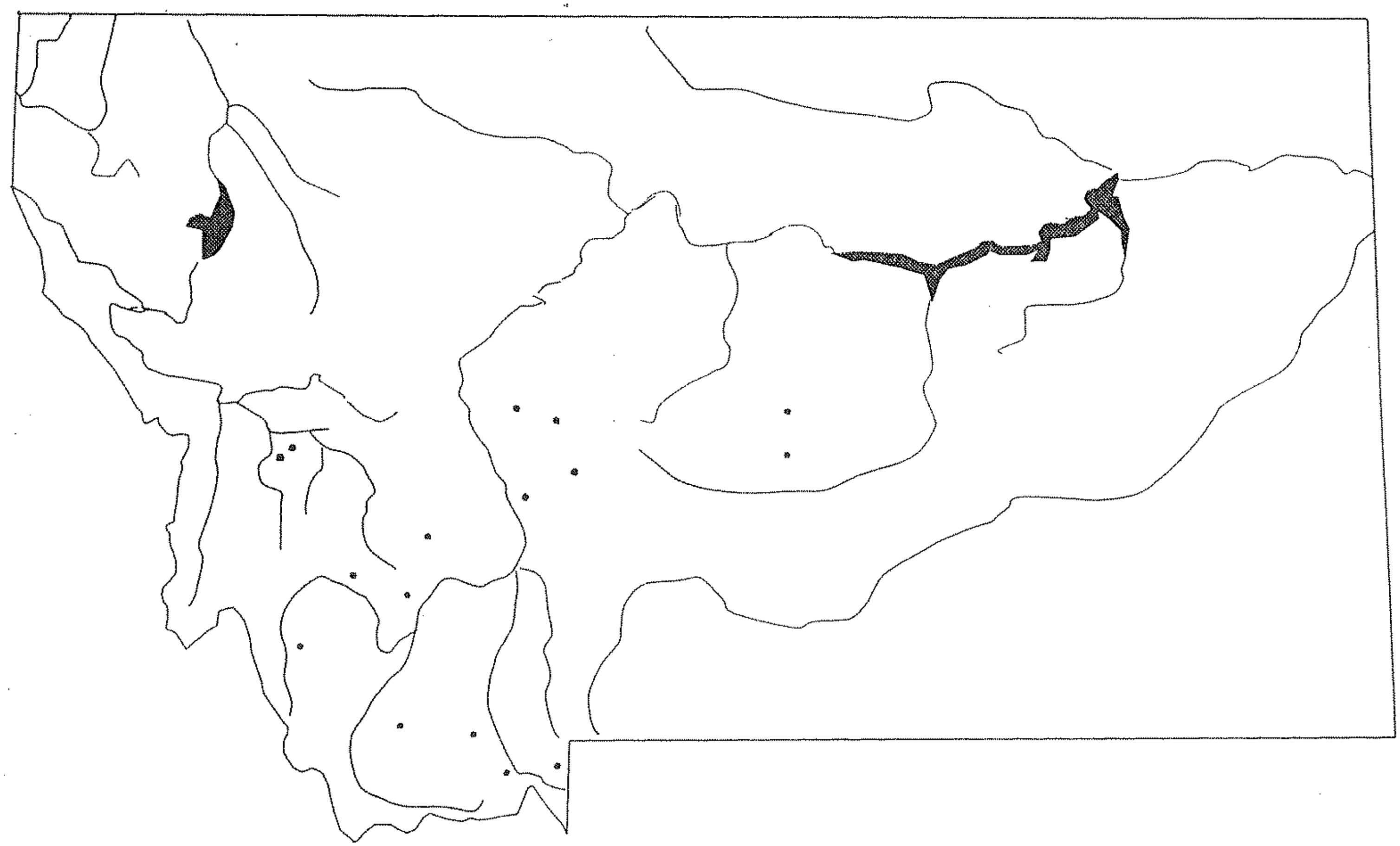

Figure 1. Distribution of headwater streams selected for study.

Table 1. Physical characteristics of headwater streams selected for study.

Stream	Rosgen type	Temp (C) [a]	Conduct (μmhos)[a]	pH	Wetted width (m)	Length with WCT (km)	Low elev (m)	Upper elev (m)	Channel gradient (%)
Collar Gulch	B2	6.4	206	8.3	2.5	2.7	1450	1550	3.6
Cottonwood (Ruby drainage)	A3	8.3			2.2	5.8	2260	2540	4.8
Geyser	A3	6.8	447	8.6	1.6	1.6	2460	2570	6.7
Cottonwood (Smith drainage)	B1	8.6	131	8.4	3.6	0.6	1830	1850	4.1
E. Fk.	A3	9.5	57	8.1	1.4	3.0	1850	2190	6.4
W. Fk.	A3	11.8	126	8.2	2.1	2.8	1850	2110	6.4
Douglas	A2	5.3	245	8.9	3.1	1.1	1570	1630	5.5
N. Fk.	B2	7.1	253	8.7	1.5	3.1	1650	1790	4.7
Half Moon	A2	12.4	333	8.7	3.0	7.3	1710	2010	4.2
Halfway	A3	5.3	78	8.4	1.1	7.8	1830	2290	5.9
Jerry	A3	7.8	160	8.9	1.7	2.8	2100	2220	4.4
Delano	A3	4.6	180	8.7	1.2	1.9	2120	2260	7.1
Mcvey	B3	5.5	78	8.7	1.4	2.3	1860	1940	3.4
Muskrat	A2	7.8			3.6	2.2	1570	1700	5.5
N. Fk. Deadman	A3	6.3	254	8.6	1.7	2.5	1960	2130	6.8
N. Fk. Gold	B3	7.0	174	8.8	2.3	4.2	1880	2010	3.2
Soap	A3	6.3	81	8.2	2.5	3.9	1910	2170	6.6
Tenderfoot	A2	10.4	119	8.6	3.1	8.1	1730	2100	4.5
White's Gulch	B3	11.7	649	8.2	1.5	4.6	1320	1470	3.3

[a] Mean of point samples over time

Table 2. Fish species composition for headwater streams selected for study.

Stream	Species composition [a]
Collar Gulch	WCT
Cottonwood (Ruby drainage)	WCT, RBT, WCT x RBT
Geyser	WCT
Cottonwood (Smith drainage)	WCT
E. Fk.	WCT
W. Fk.	WCT
Douglas	WCT
N. Fk.	WCT
Half Moon	WCT
Halfway	WCT
Jerry	WCT, BT
Delano	WCT, BT
Mcvey	WCT, BT
Muskrat	WCT, BT
N. Fk. Deadman	WCT, BT
N. Fk. Gold	WCT
Soap	WCT
Tenderfoot	WCT, RBT, WCT x RBT, BT, SC
White's Gulch	WCT, BT

[a] BT brook trout
RBT rainbow trout
SC sculpin
WCT westslope cutthroat trout

METHODS

Age Determination

Fish were captured using a Smith-Root backpack electrofisher model 15-B. Low frequency DC current was utilized to minimize injury to the fish. Frequencies and voltages employed varied with stream temperature and conductivity, but generally voltages ranged from 200 to 800 volts and frequencies were always under 50 Hz. Captured fish were weighed to the nearest gram and fork lengths measured in millimeters. All fish 120 mm and longer were marked using visible implant tags (Haw et al. 1990).

During the 1993 field season, May through September, scale samples were taken from a minimum of 10 fish per 10 mm length group from each stream when possible. Scales were removed from the left side of the body just above the lateral line at the anterior end of the caudal peduncle, the location of the earliest scale formation on westslope cutthroat trout (Averett 1962). During the 1994 field season sampling was repeated. Scale samples were removed from the right side of the body on all recaptured visible implant tagged fish to validate annulus formation and determine empirical growth rates.

I compared ages assigned from a length-frequency histogram with ages interpreted from otoliths for West Fork Cottonwood Creek to determine the validity of otoliths as aging structures for westslope cutthroat trout. West Fork Cottonwood Creek was used because it provided an easily interpretable length-frequency histogram where other study streams did not.

Westslope cutthroat trout were not intentionally sacrificed for otoliths during the 1993 field season, but the two sagittal otoliths, a pectoral fin, and a sample of scales were obtained from incidental mortalities after they were weighed and measured. I also utilized westslope cutthroat trout collected for genetic analysis by Montana Department of Fish, Wildlife, and Parks and U.S. Forest Service biologists. This resulted in an additional 148 paired age structure samples from 15 additional headwater streams.

Scale samples were prepared for aging by Wayne Black, Montana Fish, Wildlife, and Parks. Scales were sorted under a 7 to 10 power dissecting microscope, laid out on cellulose acetate sheets, and covered with a stainless steel plate. Samples were then placed in a Carver laboratory press at 450°F and 15000 psi for 1 minute. The scales were then discarded. Scale impressions were interpreted on a microfiche reader at 72 power and ages assigned according to the methods described by Jearld (1983). Number of circuli to the first and second annuli were counted for each scale aged in an attempt to identify and correct for missing first year annuli.

Sagittal otoliths were removed by making an incision perpendicular to the horizontal axis of the fishes body immediately posterior to the eyes and extending downward to the base of the orbit. The brain was exposed by depressing the anterior section of the head. The saggital otoliths were visible just behind and beneath the brain and could be easily removed with a pocket knife in the field. All otoliths collected under field conditions were initially stored together with scales in a scale envelope and later transferred to dry vials. The paired structures from each fish were labeled identically using an alpha numeric combination to facilitate comparisons.

Otoliths were viewed whole. They were immersed in distilled water in a small Pyrex dish, placed on a dark background, then viewed through a compound microscope at 40 power with reflected light. The criteria for assigning ages was similar to that used by Mackay et al. (1990).

Whole pectoral fins were clipped as near to the body as possible and dried in scale envelopes. The trimmed fins were placed between two sheets of 2.54 mm thick PETG plastic. They were slowly heated and compressed under 50 psi to avoid crushing. The plastic containing the fin rays was sectioned as thin as possible (0.5 mm) with a model maker's saw. This technique has been used to section fin rays of northern pike Esox lucius, walleye Stizostediom vitreum, and white sucker Catostomous commersoni (W. Black, Fisheries Laboratory Technician, Montana Fish, Wildlife, and

Parks, personal communication). The samples were cleared with immersion oil and viewed with transmitted light on a binocular stage microscope at 80 to 100 power. A second technique involved embedding the fin rays in paraffin wax and sectioning them to between 5 and 10 microns on a microtome. Transverse cross sections were mounted on glass slides and viewed at 80 to 100 power.

Random subsamples of otoliths and scales were selected and read by another experienced reader. All ages were determined by each reader without *a priori* knowledge about the individual fish (i.e. length or sample location). The "Index of Average Percent Error" (Beamish and Fournier 1981) was calculated to determine which aging technique is more precise. This method is superior to calculating the percent agreement between readers because it accounts for the age of the fish. For example, a 2 year aging discrepancy for a fish which only lives to age 5 is more serious than the same discrepancy for a fish that lives to age 25. Percent agreement does not take this into account.

After aging the paired otolith and scale samples, a Chi-square test was used to test for differences between age estimates. The chi-square test was appropriate because the data can be thought of as a three case multinomial with the expected frequencies for each case greater than five. The three cases are:

case 1: otolith age > scale age

case 2: otolith age = scale age

case 3: otolith age < scale age

If scale age and otolith age are truly equal, then the proportion of cases with otolith age greater than scale age should equal the proportion of cases with otolith age less than scale age, apart from sampling variation.

The otolith-scale pairs were utilized to calculate the percent of fish missing a first year annulus on scales. A model to identify and correct for missing first year annuli on scales was developed using otolith ages as the "true" age. I assumed that a 1 year discrepancy between the age interpreted from an otolith and the age determined from a paired scale for fish age 3 and younger was the result of a failure to form a first year annulus on the scale. As fish grow older, other factors may contribute to the lack of formation of discernible annuli on scales. The average number of circuli to the first year annulus was expected to vary with individual stream conditions, thus using single circuli criteria to indicate a missing first year annulus across many streams may not be valid. I also examined the ratio of the number of circuli before the first annulus to the number of circuli to the second annulus to determine if this ratio would better incorporate growth differences between streams.

I used linear regression to build and test models for identifying and correcting for a missing first year annulus on scales. Models incorporated varying numbers of circuli to the first annulus (5 to 7) and ratios of circuli within the first annulus to circuli between the first and second annulus. T-tests were used to test for differences in ages assigned by the models. The percentage of annuli formed was calculated for each age class by dividing the number of recaptured fish with scales that had formed one additional annulus by the total number of recaptures.

Growth

Growth rate was determined using recaptures of marked fish. Fish over 120 mm (FL) were marked using visible implanted tags. Fish from 90 to 119 mm (FL) were left pelvic fin clipped and those under 90 mm (FL) received a right pelvic fin clip. I calculated daily growth rates for streams where there was an adequate sample size of recaptured fish. Only fish which were tagged and recaptured during the 1993 growth season, defined as May 1 through October 1, were used in this analysis to avoid potential biasing of the growth rate estimates due to differential growth rates between winter and summer. Daily growth rate (G) was calculated as follows:

$$G = (Y2 - Y1)/(t2 - t1)$$

where Y2 and Y1 represent lengths at time t2 and time t1, respectively.

Following calculation of daily growth rates, I correlated; initial length, initial age, stream conductivity, and mean stream elevation with daily growth rate to explore the relationships between these variables and growth.

Fecundity, Sexual Maturity, and Longevity

During May 1994 I collected fish from Cache Creek in the Taylor Fork drainage, West Fork Cottonwood Creek in the Smith River drainage, and Halfway Creek in the Boulder River drainage to determine fecundity, longevity, and ages at sexual maturity for headwater populations and to strengthen the fecundity to length relation of Rieman and Apperson (1989). Samples were stratified by 25 mm fork length groups to assure good size coverage and to be consistent with an earlier study conducted by Magee (1993).

Females were collected immediately prior to the onset of spawning. Both ovaries were removed from each mature female collected, fixed in Davidson's solution (Kent 1992), and ova later enumerated using a dissecting microscope at 7 power. One sample stream, Halfway Creek, was inaccessible until spawning had commenced. Consequently, I was unable to determine fecundity for females from this stream because most had initiated egg deposition.

Mean fecundity and associated standard deviations were calculated for each 25 mm length group. Linear regression was used to create a model for predicting fecundity based on length. Initially, I constructed fecundity to length relations using untransformed, log10, and natural log transformations of the data from my study and unpublished data from Cache Creek, Montana (A. Bowersox, Montana State University, personal communication) to create a model using only fecundities from headwater populations. The linear fit was poor due to the large variability in fecundity at length and small sample size. I then combined my data with the unpublished data from Cache Creek, Montana, and data from Averett (1962) and Johnson (1963) to increase sample size and produce a model that would make reasonable fecundity predictions for a wide range of sizes. A scatter plot of the data indicated a curvilinear relationship, so natural log and log10 transformations were applied to the raw data. Chattergee and Price (1991) suggested a natural log transformation of the Y axis (fecundity) was most appropriate.

Ages at sexual maturity were determined for both sexes using females collected for estimating fecundity and all incidental mortalities collected during spring sampling. Additional males were collected to ensure an adequate sample size by length group. Status of sexual development was determined by laboratory examination of ovaries and testes. The difference between immature and mature ovaries was distinct. Immature ovaries were granular in appearance and located dorsally, rarely extending back beyond the origin of the dorsal fin. Mature ovaries were much larger, possessing eggs in an advanced stage of development, usually filling the abdominal cavity. Males were classified as immature if testes were dorsally located and appeared threadlike. Samples were pooled across streams to increase sample size for statistical analysis.

Percent sexual maturity was calculated by sex and age class. I calculated mean lengths of immature and mature by age class and sex and used a t-test to test for significant differences between mature and immature fish. Logistic regression (Hosmer and Lemeshow 1989) was used to analyze the relationship between age and length of fish versus sexual maturity. Sexual maturity was entered into logistic regression models as a binomial variable, mature or not mature. Age, length, and the interaction of length and age were entered as covariates. Akiake's Information Criterion (AIC; Akaike 1973, 1985) and Chi-square probability values for significance of individual variables within each model were examined by sex. AIC values were used to select the best models, as recommended by Burnham and Anderson (1992). Significant differences between models were tested by using differences in log likelihood values tested under a Chi-square distribution with 1 df using a $p \leq 0.05$ significance level (Hosmer and Lemeshow 1989). Field classifications of sexual maturity status were used to test the predictive capability of the best model.

Longevity was estimated using otoliths taken from fish sacrificed for genetic and fecundity analyses, tests of age at maturity, and incidental mortalities. Fish were not intentionally sacrificed to obtain longevity information because of concerns over the long-term population effects of removing the largest mature individuals from small populations.

RESULTS

Age Determination

Ages interpreted from otoliths were consistently older than ages interpreted from scales for the 424 paired age structure samples (Figure 2). The discrepancies increased with increasing age (Figure 3). Agreement between the structures, prior to scale age adjustment, was 25%. Older ages were estimated from otoliths for 74% of the pairs, while older ages were estimated from scales for only 1% of the pairs. Chi-square analysis indicated that ages interpreted from otoliths were significantly higher than ages interpreted from scales ($X^2 = 295.5$, $p < 0.001$).

The "Index of Average Percent Error" (AEI%) was 3.2% for otoliths and 11% for scales (Table 3.). The precision of estimated ages was higher for otoliths than for scales. Age estimates for replicate readings of otoliths were not significantly different (t-test; $p = 0.80$) while age estimates between replicate readings of scales samples were significantly different (t-test; $p < 0.001$). Percent agreement between readers was 87 % for otoliths while only 55 % for scales.

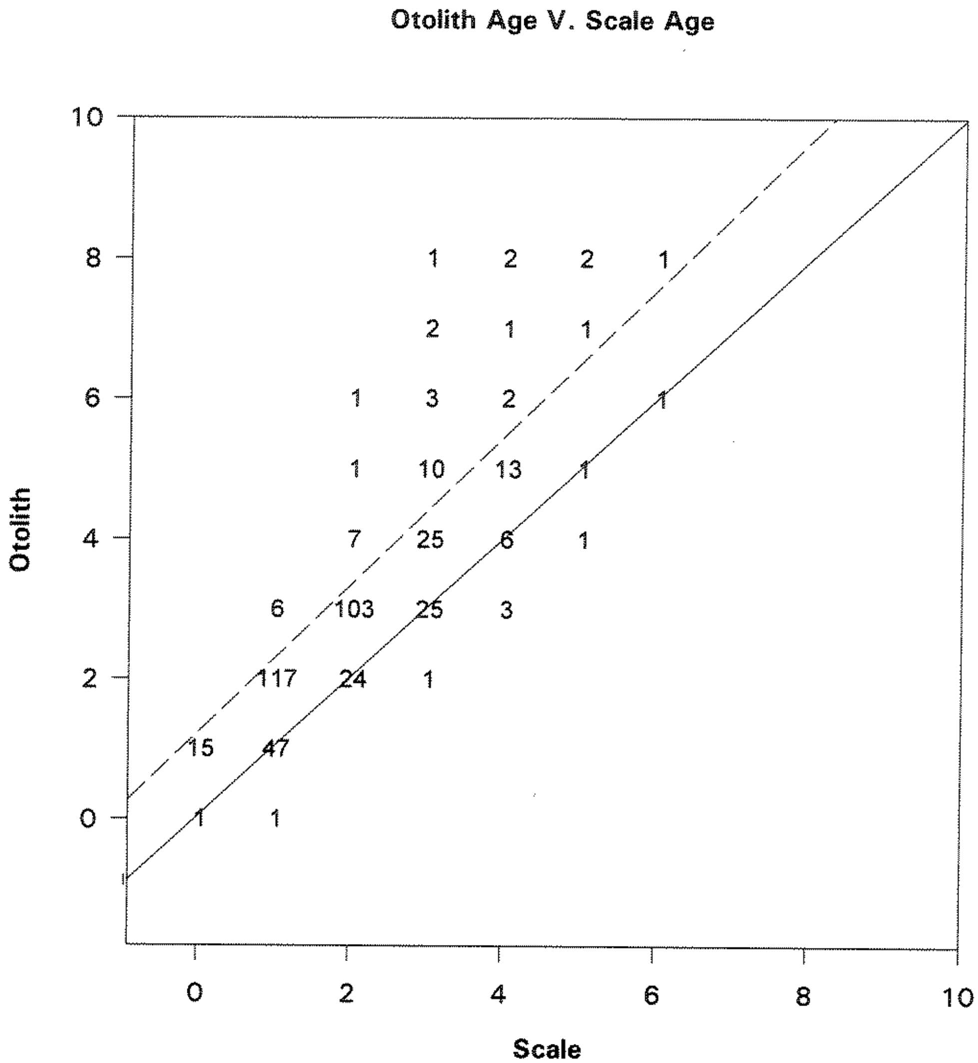

Figure 2. Scatter plot of age frequencies interpreted from paired otolith-scale samples of westslope cutthroat trout. Solid line shows agreement (1:1 relationship) between otoliths and scales and the dashed line represents the best fit linear regression line through the data.

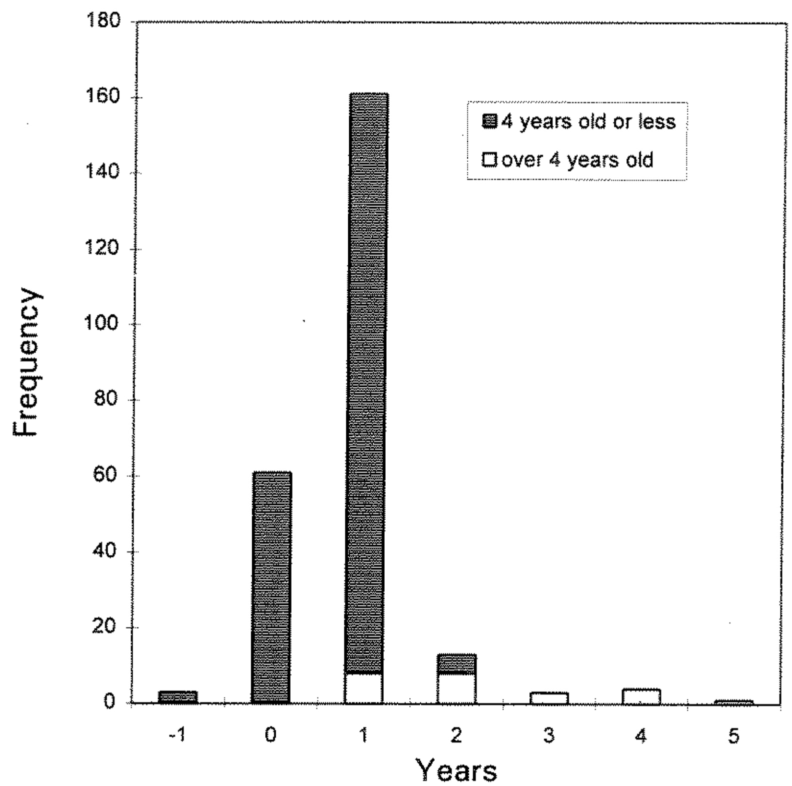

Figure 3. Age discrepancies in years between paired otolith and scale samples from westslope cutthroat trout stratified by fish 4 years old or less and those over 4 years of age.

Table 3. "Index of Average Percent Error" (AEI%) and p-values based on t-tests for differences between independent, experienced readers for ages of westslope cutthroat trout interpreted from otoliths and scales.

Structure	n	AEI%	p-value
Otolith	89	3.2	0.80
Scale	72	11.0	0.00

Ages interpreted from otoliths agreed with ages assigned by length-frequency analysis for ages 1 (n=5), 2 (n=22),and 3 (n=3). Beyond age 3, ages could no longer be clearly interpreted from the length-frequency histogram (Figure 4).

Time of annulus formation ranged from May to early July. Using westslope cutthroat trout which were VI tagged in 1993 and subsequently recaptured in 1994, I evaluated annulus formation by age at initial capture. The proportion of fish which formed an annulus over the 1993-94 winter generally decreased with increasing age. Eighty-six percent of age 2 fish had formed a discernible annulus by the time of recapture (Figure 5). Only 13 % of age 4 fish possessed one additional annulus upon recapture.

Some individuals from each sampled population failed to form a first year annulus on their scales. The proportion of fish with a missing first year scale annulus varied between streams. Halfway Creek contained the lowest proportion (49%) of fish missing a first year scale annulus while Half Moon Creek supported the population with the highest proportion (85%) (Table 4).

One hundred seventy-six paired samples were used to construct models for predicting the occurrence of missing first year annuli (training sample) and 195 different paired samples to test them (testing sample). Fifteen models were constructed (Table 5). The first set of models utilized only the number of circuli present to the first annulus as an indicator of a missing first year annulus. I varied the number used to identify a missing annulus from 5 to 7 circuli and ran my training sample through each model.

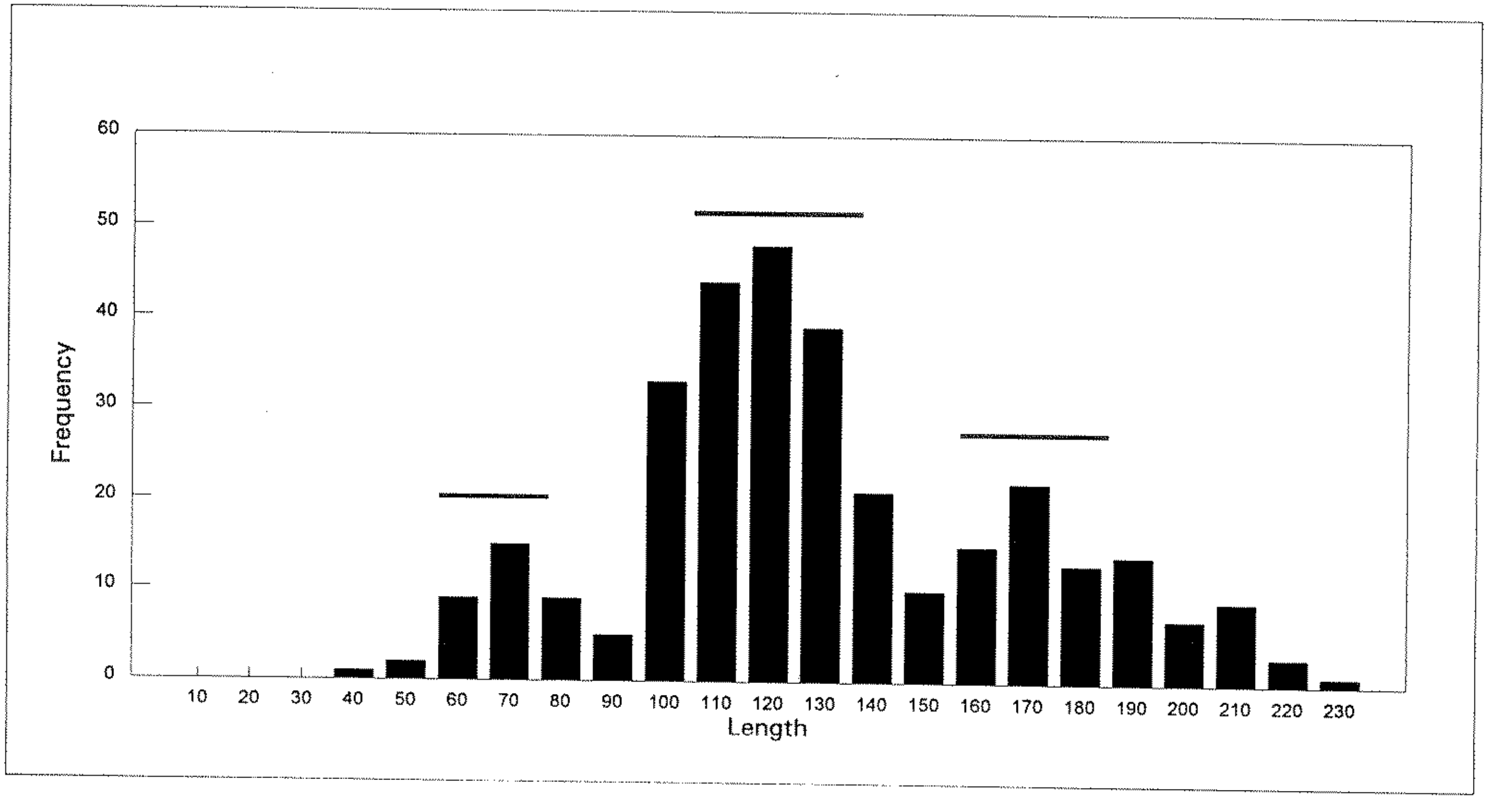

Figure 4. Length-frequency histogram for westslope cutthroat trout from West Fork Cottonwood Creek, MT. Horizontal bars represent length ranges for ages 1, 2, and 3 as interpreted from otoliths.

I then ran a second set of models which incorporated varying ratios of circuli to the first annulus to circuli present from the first annulus to the second. When there was no second annulus present, the model used the number of circuli to the first annulus.

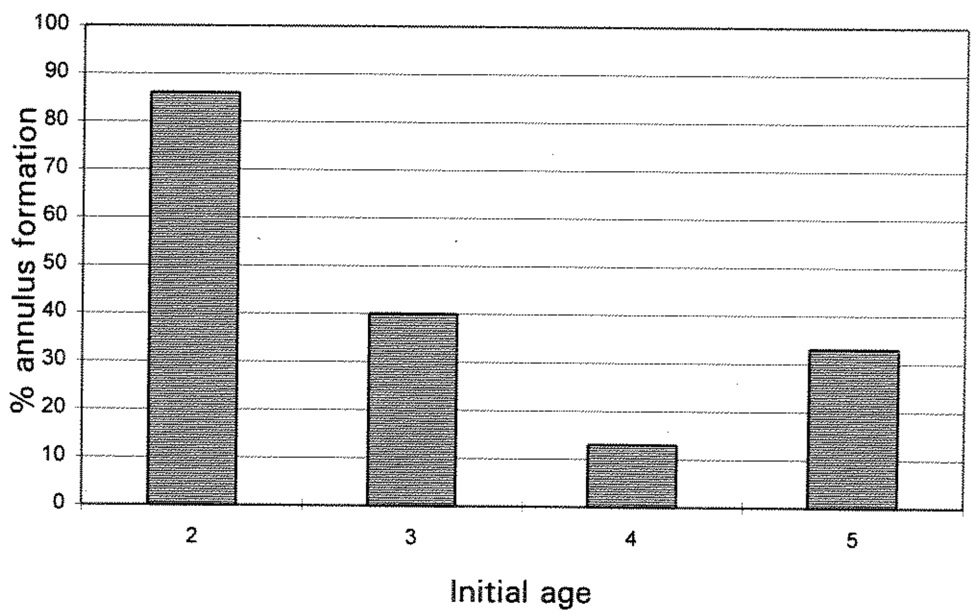

Figure 5. Percent annulus formation by age class based on recapture of visible implant (VI) tagged westslope cutthroat trout one summer later.

The three "best" models were selected by identifying the models which brought the most paired age structure samples into agreement. I included a fourth model that did not correct for a missing first year annulus as well as the three I selected for further testing to examine if using the ratio of circuli within the first annulus to the number of circuli within the second improved the corrective capability of models. I then ran the testing sample through each of these models to determine which model corrected the highest proportion of the testing sample. Once the most appropriate model was identified, I applied it to all of the scale samples collected in 1994. The percent of samples missing a first year annulus was calculated for each stream based on the percentage of scale samples the model adjusted.

Table 4. Proportion of westslope cutthroat trout missing a first year annulus on their scales by stream based on application of corrective age model IVB (Table 5) to all scales collected during 1993.

Stream	Proportion missing first year annulus	n
Collar Gulch	79	125
Cottonwood (Ruby)	79	82
Cottonwood (Smith)	80	90
W.F. Cottonwood	68	209
N.F. Deadman	55	12
Delano	60	115
Douglas	62	135
N.F. Douglas	66	143
Geyser	80	201
N.F. Gold	63	147
Half Moon	85	13
Halfway	49	152
Jerry	63	134
McVey	53	79
Muskrat	71	21
Soap	82	149
Tenderfoot	50	62
Whites	57	101

Table 5. Models constructed to predict and correct for missing first year annuli based on circuli counts on westslope cutthroat trout scales.

Model	Condition	number of circuli
IA	> * circuli to the first annulus, add one year	5
IB		6
IC		7
IIA	If number of circuli from first annulus to second < number of circuli to the first annulus, add one year. If no second annulus and number of circuli to the first > * , add one year	5
IIB		6
IIC		7
IIIA	If number of circuli from first annulus to second ≤ number of circuli to the first annulus, add one year. If no second annulus and number of circuli to the first > * , add one year	5
IIIB		6
IIIC		7
IVA	If number of circuli from first annulus to second ≤ number of circuli to the first annulus plus one, add one year. If no second annulus and number of circuli to the first > * , add one year	5
IVB		6
IVC		7
VA	If number of circuli from first annulus to second ≤ number of circuli to the first annulus plus two, add one year. If no second annulus and number of circuli to the first > * , add one year	5
VB		6
VC		7

* = number of circuli (5-7)

The initial agreement between the paired otolith and scale samples utilized to develop age adjustment models was 22%. Following application of the corrective age models, agreement improved to between 60% and 72% (Table 6). The model utilizing 7 circuli (IC) to the first annulus as the sole indicator of a missing first year annulus, did the poorest job of bringing ages into agreement. Models IA, IVA, and IVB brought the highest percentages of the samples into agreement.

Table 6. Agreement between paired age structure samples from westslope cutthroat trout following application of all age correction models to the training sample.

Model	% Agreement
IA	70
IB	65
IC	60
IIA	64
IIB	63
IIC	64
IIIA	68
IIIB	67
IIIC	63
IVA	72
IVB	71
IVC	67
VA	67
VB	69
VC	66

I selected models IA, IVA, and IVB as the best potential corrective age models. I also included model IB to test for significant differences between models using only the number of circuli to the first annulus and models incorporating both the number of circuli to the first annulus and the ratio of circuli within the first annulus to the number of circuli from the first annulus to the second. Initial agreement between the paired age structure samples used in the testing data set was 24%. The testing sample was run through all four models and model IVB performed the best, bringing 73% of the samples into agreement (Table 7). The single variable model, incorporating 6 circuli to the first annulus, corrected the lowest proportion of the testing sample (66%). Results of t-tests indicated that model IVB produced a significantly different mean age than the other three models (Table 8).

Table 7. Agreement between paired aging structures of westslope cutthroat trout for the testing sample following application of four age adjustment models.

Model	% Agreement
IA	70
IB	66
IVA	72
IVB	73

Table 8. T-test results for significant differences between adjusted ages of westslope cutthroat trout following application of four age adjustment models to the testing sample.

Models	p-value	Significant difference
IA, IVA	0.76	No
IVA, IVB	0.00	Yes
IB, IVB	0.00	Yes
IA, IVB	0.01	Yes

Growth

Daily growth rate varied with stream. For those individuals marked with visible implant tags (> 125 mm FL), Delano Creek had the lowest average daily growth rate (0.025 mm), while West Fork Cottonwood Creek had the highest average daily growth rate (0.285 mm) (Table 9). Scatter plots of growth increments by stream did not indicate any relationship between initial capture size and subsequent daily growth rate (Figures 6-14). The correlation between initial length and growth rate was insignificant ($p=0.89$, $r=-0.03$). Although not significant ($p=0.06$), when the relationship between growth rate and age was examined, a stronger relationship was apparent as indicated by the increased correlation value ($r=-0.33$). I ran correlations between conductivity and daily growth in an effort to use some measure of productivity to explain growth rate. The correlation between conductivity and daily growth was insignificant ($p=0.97$, $r=-0.02$).

Correlation's between mean stream elevation and growth rate were also insignificant ($p=0.21$, $r=-0.46$).

Table 9. Average daily growth increments calculated for study streams based on VI tag recaptures during the 1993 field season.

Stream	Average daily growth (mm)	Conductivity (µmhos)
Collar	0.25	206
Delano	0.025	180
Geyser	0.135	447
Halfway	0.049	78
Jerry	0.062	160
McVey	0.173	78
N.F. Douglas	0.111	253
Soap	0.143	81
W.F. Cottonwood	0.285	126

Daily growth rates for those fish which were marked with a right pelvic fin clip (< 90 mm (FL)) could not be calculated for study streams because sample sizes were extremely small for recaptures during the defined 1993 growing season. Daily growth rates for those fish marked with a left pelvic fin clip (90-125 mm) were calculated for 5 study streams (Table 10). Growth rates for the length group 90-125 mm were higher than those of fish >125 mm for given streams. Correlation's between mean elevation and conductivity remained insignificant.

Table 10. Average daily growth increments calculated for study streams based on recaptures of marked fish in the length group 90-125 mm.

Stream	Average daily growth (mm)	Conductivity (μmhos)
Delano	0.104	180
Geyser	0.165	447
Jerry	0.1	160
N.F. Douglas	0.23	253
Soap	0.153	81

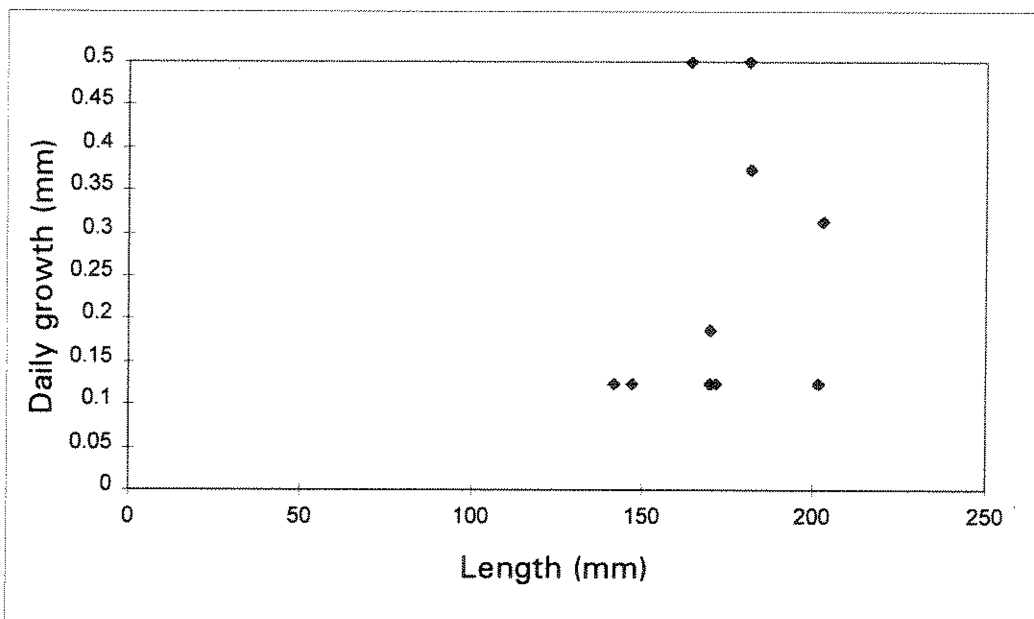

Figure 6. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Collar Gulch.

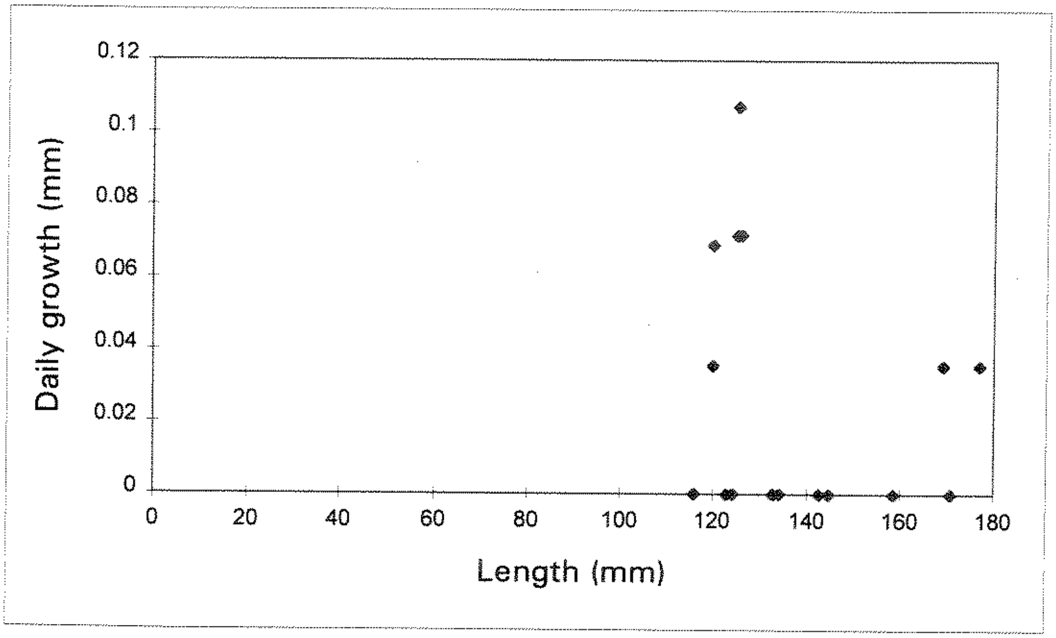

Figure 7. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Delano Creek.

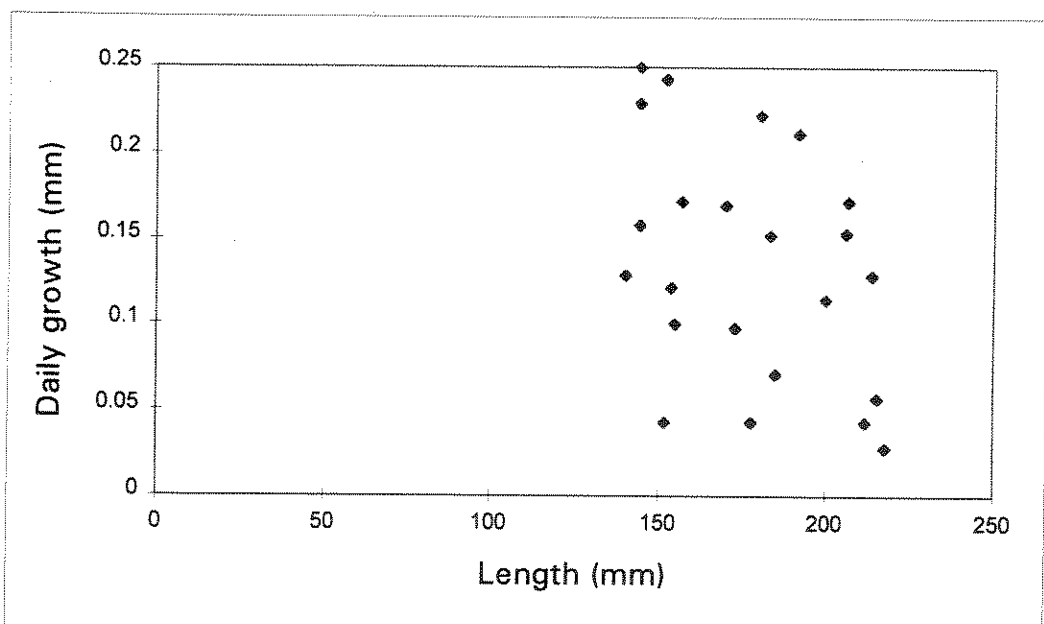

Figure 8. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Geyser Creek.

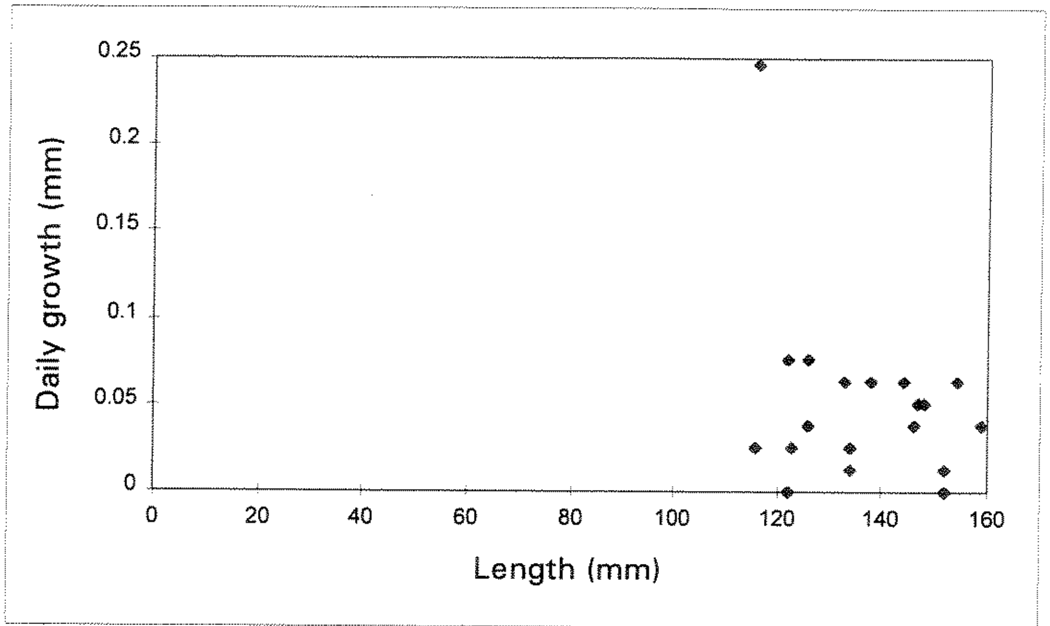

Figure 9. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Halfway Creek.

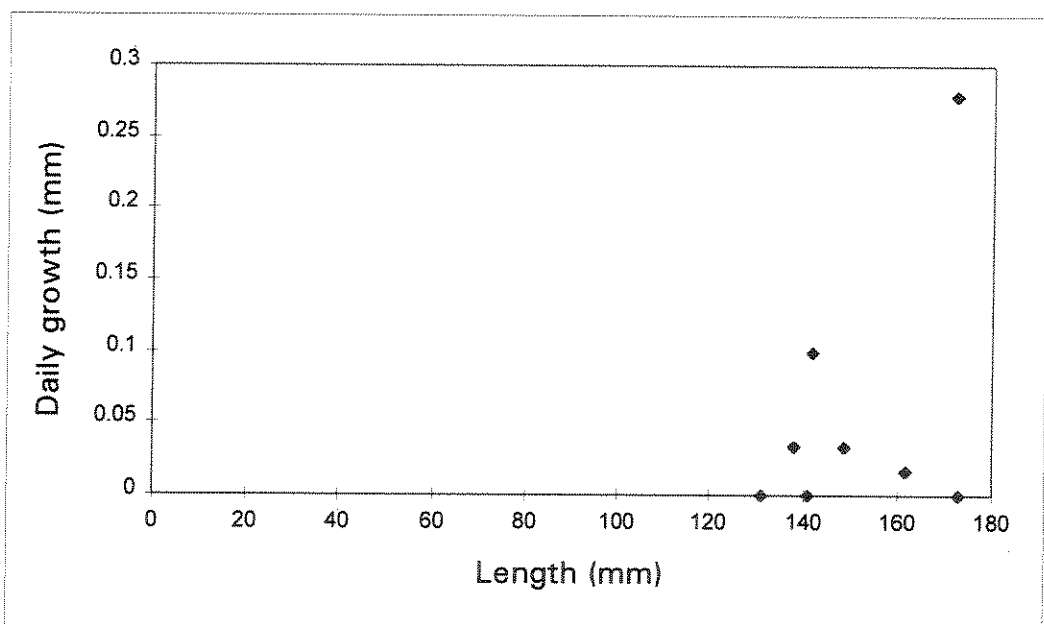

Figure 10. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Jerry Creek.

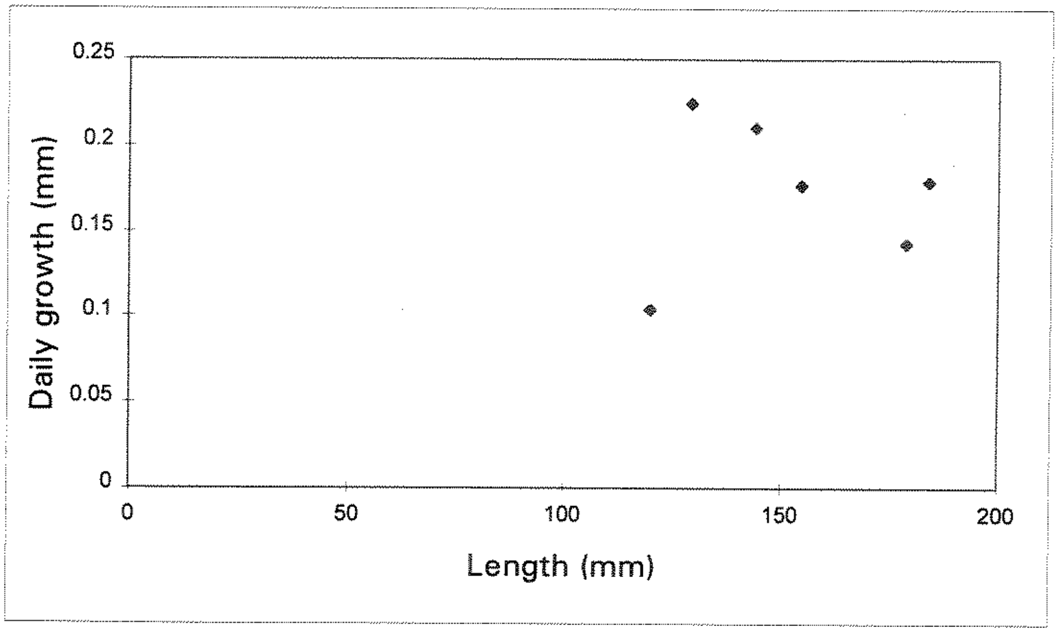

Figure 11. Individual daily growth increments of westslope cutthroat trout plotted against length initial capture for McVey Creek.

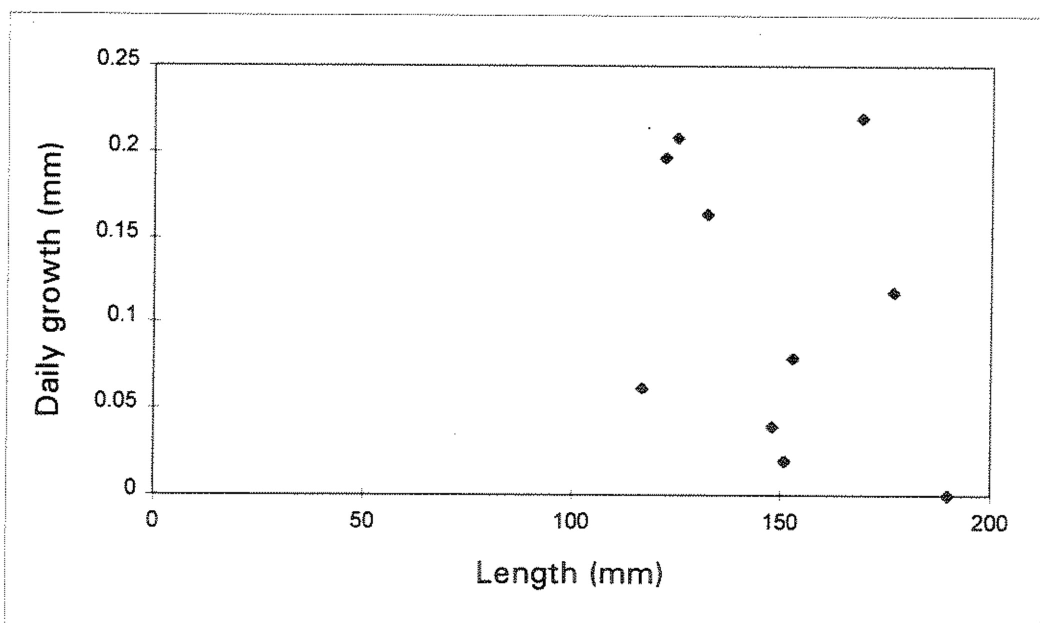

Figure 12. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for North Fork Douglas Creek.

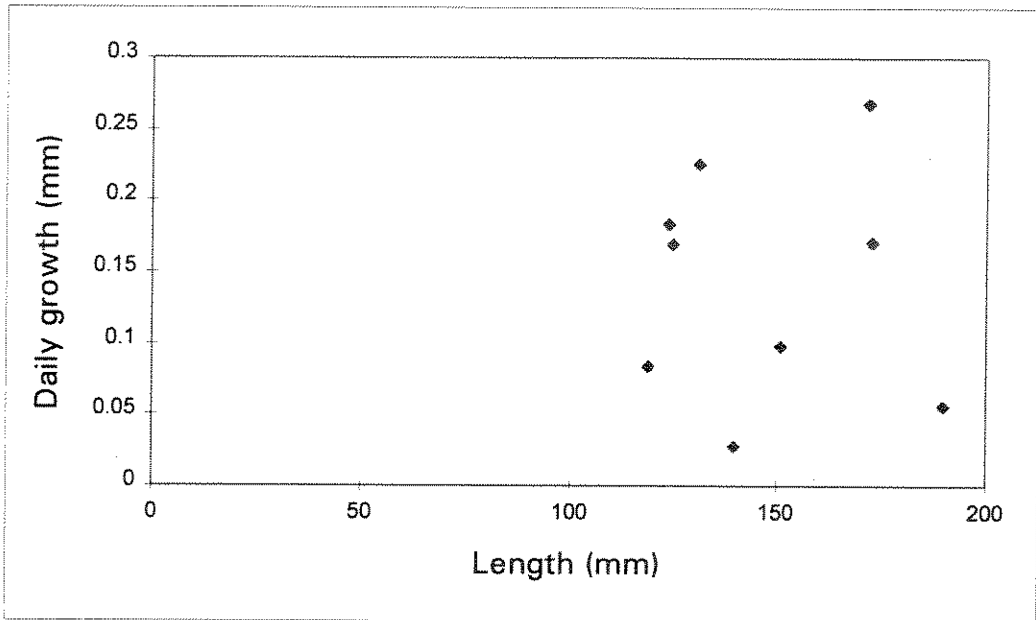

Figure 13. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for Soap Creek.

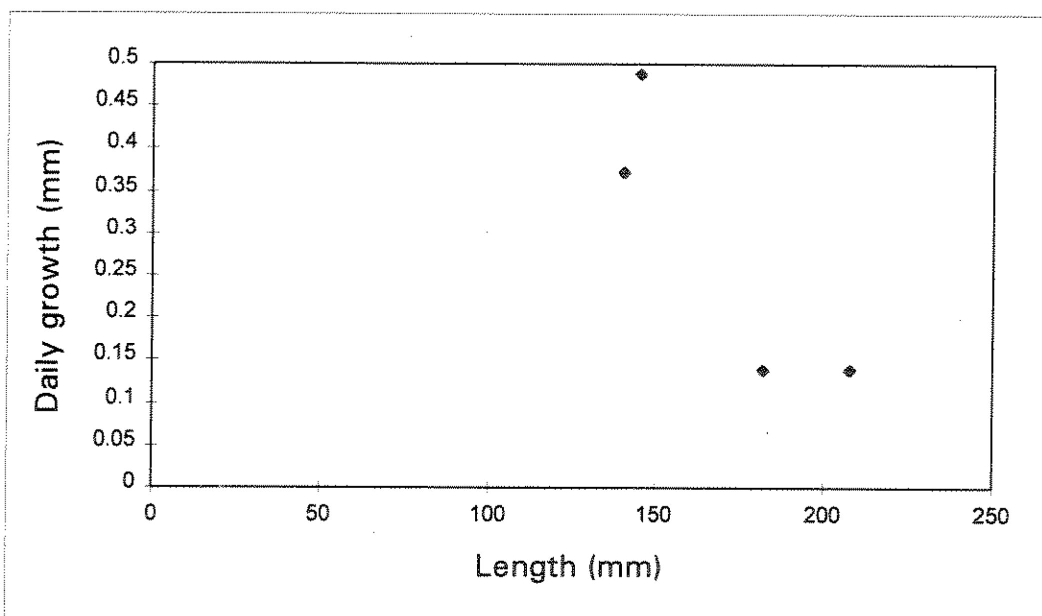

Figure 14. Individual daily growth increments of westslope cutthroat trout plotted against length at initial capture for West Fork Cottonwood Creek.

Fecundity

Fecundity increased with increasing length group, however variability was high both between and within length groups (Table 11). Mean fecundity ranged from 258 for the 150-174 mm size group to 421 for the largest size group. I was not able to document fecundity for females in the smallest pre-established length group (125-149 mm) because the only two mature females captured in this size group appeared to have already spawned. These two fish, both from Halfway Creek, contained several mature, residual eggs in addition to ovaries that appeared to be developing for the next spawning period.

Table 11. Fecundity of westslope cutthroat trout inhabiting tributaries of the upper Missouri River.

Length group (mm)	n	Mean length (mm)	S.D.	Mean fecundity	S.D.	Fecundity range
150-174	2	169	1.4	258	9.2	251-264
175-199	10	190	6.3	336	81.4	198-444
over 200	8	217	11.1	421	157.8	224-630

I regressed fecundity against fish length to develop a model for predicting fecundity based on female length for populations from slow growth environments. I combined my data with unpublished data from Cache Creek, Montana (A. Bowersox, Montana State University, personal communication). Because of high variation in fecundity, linear fits as determined by coefficients of variation (r^2) of the regression models using both untransformed and transformed variables were poor (r^2 ranging from 0.49 to 0.52) (Table 12). The single variable model with the highest r^2 value used untransformed variables only.

Table 12. Transformations used for regression models constructed to predict fecundity of westslope cutthroat trout based on female length using data from my study combined with unpublished data from Cache Creek, Montana (A. Bowersox, Montana State University, personal communication).

Fecundity	Length	r^2	Model
None	None	0.52	$E = -515.5 + 4.5(FL)$
nLog	None	0.49	$E = 30.532 * e^{0.012358\,(FL)}$
Log10	Log10	0.49	$E = 0.0043187 * FL^{2.36464}$

In an effort to improve the model, I combined my fecundity data with that of Bowersox (Montana State University, personal communication), with data from Averett (1962), and Johnson (1963) to produce additional regression models incorporating a larger sample size. I converted the reported total lengths of Johnson to fork length by dividing by 1.05 (Carlander 1969). I again regressed fecundity against length using both transformed and untransformed variables. The r^2 values improved in all cases. The best fit model resulted in an r^2 of 0.88 (Table 13). This model did not employ any transformations of the data. A scatter plot of the combined raw fecundity data identified the possibility of different fecundity to length relations for individual stocks of westslope cutthroat trout (Figure 15).

Table 13. Transformations used for regression models constructed to predict westslope cutthroat trout fecundity based on female length using data from this study and from Cache Creek, Montana (A. Bowersox, Montana State University, personal communication), and data published by Averett (1962), and Johnson (1963).

Fecundity	Length	r^2	Model
None	None	0.88	$E = -797.756 + 6.184(FL)$
nLog	None	0.84	$E = 69.838 * e^{0.008403(FL)}$
Log10	Log10	0.73	$E = 0.0022637 * FL^{2.26}$

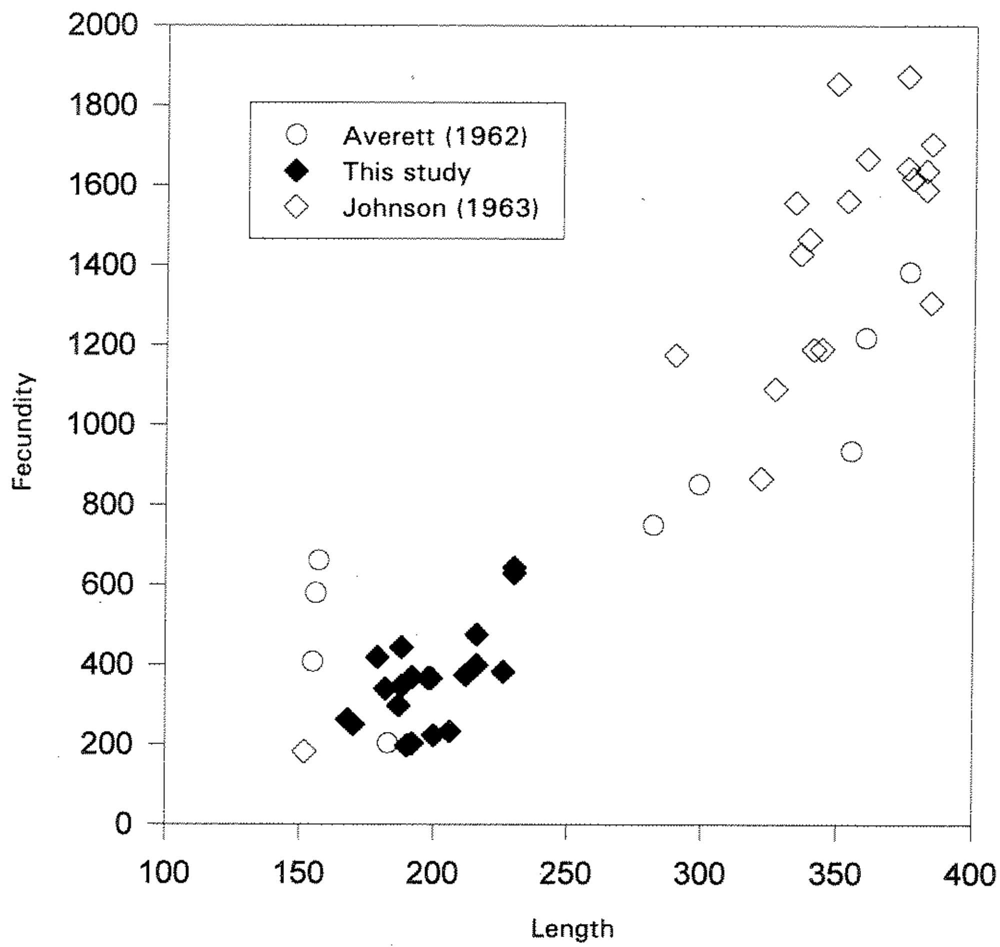

Figure 15. Scatter plot of fecundity at length of westslope cutthroat trout from this study and the studies of Averett (1962) and Johnson (1963) showing differences in fecundity at length associated with different stocks of westslope cutthroat trout.

Sexual Maturity

Male westslope cutthroat trout from study streams first matured at age 2 (Figure 16). All sampled males (n = 51) were sexually mature by age 4. Females began to mature at age 3 (n = 79), with most females mature by age 5. All sampled females were sexually mature by age 6. The mean lengths for mature fish were significantly longer than the mean lengths for immature fish within each age class for both sexes (t-Test; $p < 0.05$) (Figures 17 and 18).

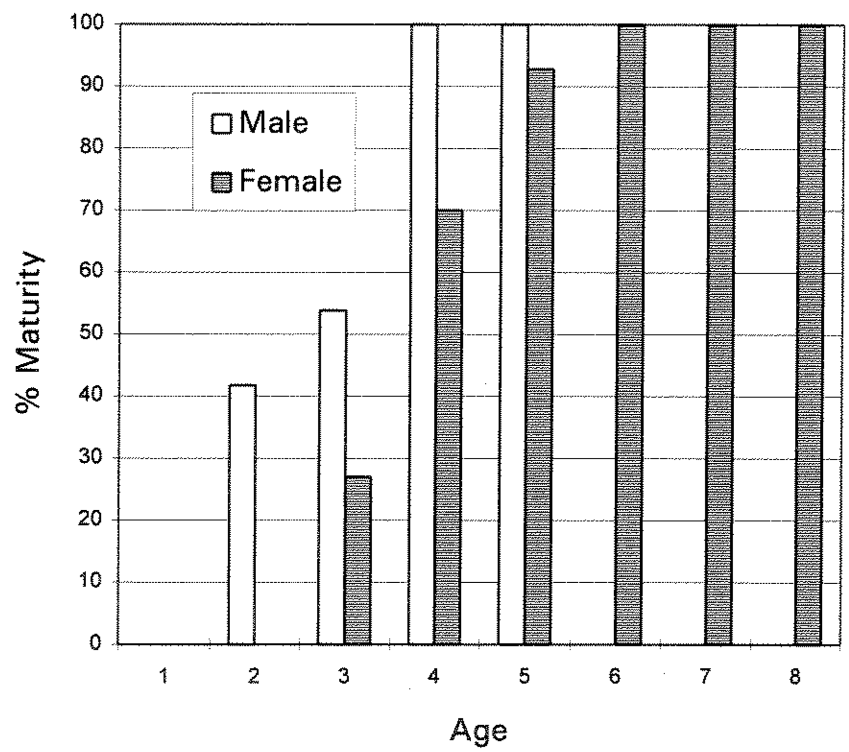

Figure 16. Ages at sexual maturity for male and female westslope cutthroat trout.

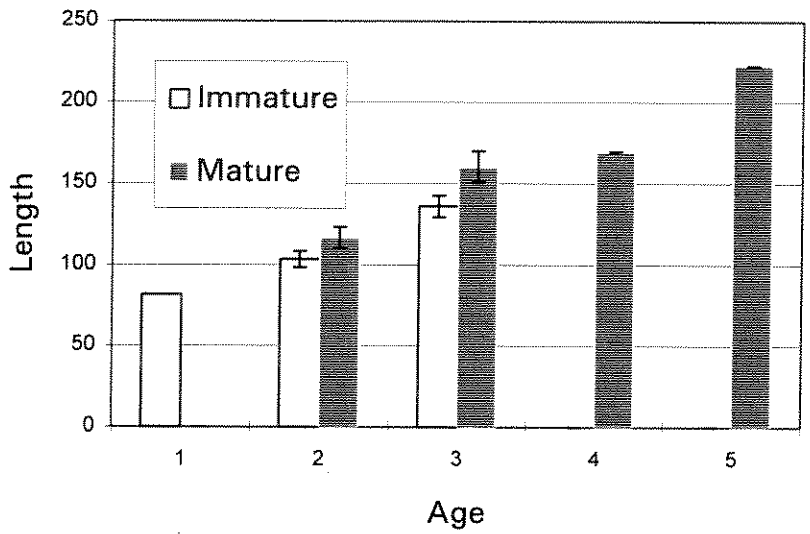

Figure 17. Length of mature and immature male westslope cutthroat trout by age with associated 95% confidence intervals.

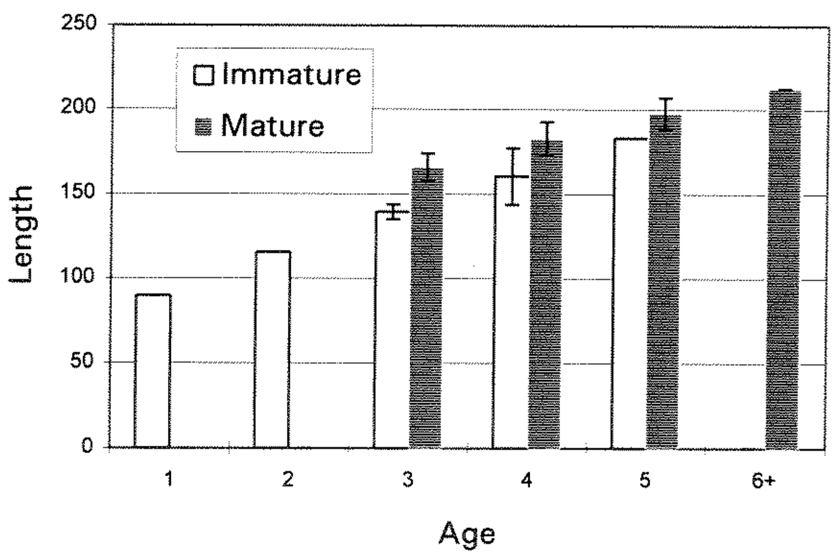

Figure 18. Length of mature and immature female westslope cutthroat trout by age with associated 95% confidence intervals.

Logistic regression analyses indicated that fish length was a better predictor of maturity than fish age. Models using age or length as the sole predictor of sexual maturity were significant ($p<0.001$). However, the single variable model using length was better than the model using age, based on AIC values (males: AIC = 49.8 for length and AIC = 60.9 for age; females: AIC = 41.6 for length and 67.6 for age). There was no significant difference between the full models and the models using the single variable of length for either males or females ($0.50<p<0.75$, $0.05<p<0.10$, respectively). Probability plots of maturity indicated that sampled females matured between 150-180 mm while males matured at smaller lengths but over a wider range of sizes (110-160 mm) (Figure 19). The predicted probabilities of being mature based on fork length (FL) from the samples are:

$$(e^{(-8.0933+0.0608*FL)})/(1+e^{(-8.0933+0.0608*FL)}) \text{ for males}$$

$$(e^{(-20.2754+0.1254*FL)})/(1+e^{(-20.2754+0.1254*FL)}) \text{ for females}$$

The above logistic regression equation predicted that 75% of the males visually classified as mature in the field had at least a 50% chance of being mature based on length (Table 14). For females, the results were poor. The logistic model predicted only 56% of the fish visually classified as mature had at least a 50% chance of being mature. However, when only fish classified as ripe or spent were run through each model, the male model predicted with approximately the same accuracy (74%) while the female

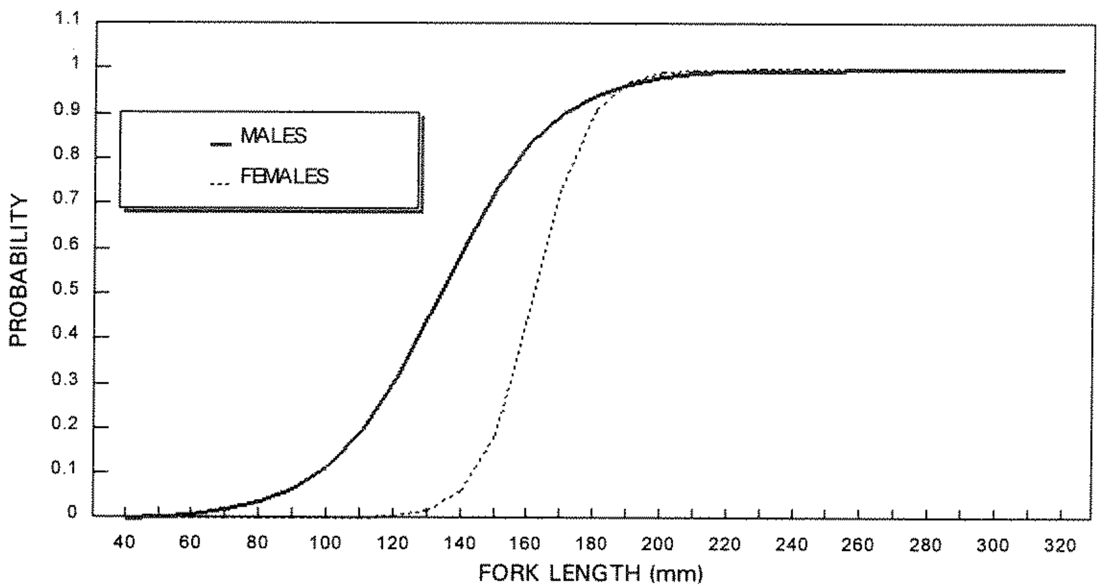

Figure 19. Probability plots of sexual maturity for male and female westslope cutthroat trout based on length.

model improved from 56% to 71%. Because sex determination of immature fish under field conditions was not reliable, all immature fish were analyzed under both of the logistic models. The logistic model developed for males predicted 87% of the fish visually classified as immature had a >50% chance of being immature. The logistic model developed for females predicted 95% of the fish visually classified as immature had a > 50% chance of being immature.

Table 14. Results of logistic model runs using field classifications of maturity status of westslope cutthroat trout to test the predictive capability of the length-based models.

Sex	Field classification	Number (%) predicted mature ≥0.5	<0.5	Total
Male	All Mature	199 (75)	67 (25)	266
	Ripe	189 (74)	66 (26)	255
	Immature	44 (13)	298 (87)	342
Female	All Mature	122 (56)	94 (44)	216
	Ripe/Spent	32 (71)	13 (29)	45
	Immature	16 (5)	326 (95)	342

Longevity

The maximum age found in study populations was 8 years (Table 15). A large proportion of streams had maximum ages sampled of 4 or greater (75%)(Table 16), however the length of the oldest fish sacrificed was often much smaller than that of the longest fish captured, indicating a potential under-estimate bias. I present length ranges from both the sample of fish aged and for all fish captured by stream and summarized by maximum age so the reader can assess this potential bias (Table 16). Examining only those streams where longevity was estimated from fish near the maximum length captured, typical longevity is 4 years or greater.

Table 15. Longevity of isolated, headwater populations of westslope cutthroat trout.

Stream	Collection year	Max. age captured (years)	Size at max. age captured (mm)	Total capture range (mm)
Cabin Ck.	1994	6	210	90-252
Cache Ck.	1994	8	226	113-230
Collar Gulch	1993-94	4	178	45-230
Cottonwood Ck.	1993-94	6	246	41-324
E. F. Cottonwood	1994	4	178	62-256
W.F. Cottonwood	1993-94	6	212	46-268
S.R. Cottonwood	1993-94	4	222	64-258
N.F. Deadman Ck.	1993-94	7	164	40-216
Delano Ck.	1993-94	6	159	37-209
Douglas Ck.	1993-94	3	207	45-227
N.F. Douglas Ck.	1993-94	4	204	23-204
Geyser Ck.	1993-94	6	188	37-270
N.F. Gold	1993-94	4	198	35-270
Halfway Ck.	1993-94	5	185	27-278
Jerry Ck.	1993-94	4	154	33-235
Muskrat Ck.	1993	4	262	73-262
Soap Ck.	1993-94	5	230	38-239
Whites Gulch	1993-94	4	183	62-251
Badger Cabin Ck.*	1993	2	145	to 229
Bear Ck.*	1993	3	165	64-180
E.F. Blue Ck.*	1993	5	141	N/A
W.F. Blue Ck.*	1993	3	160	75-173
Brushy Fork Ck.*	1993	8	175	53-210
Upper Cabin Ck.*	1993	5	193	N/A
W.F. Dyce Ck.*	1993	2	158	140-170
W.F. Fishtrap Ck.*	1993	3	188	N/A
Four Mile Ck.*	1993	5	203	102-254
Green Gulch*	1993	3	140	to 190
Hall Ck.*	1993	4	169	102-178
Prickly Pear Ck.*	1993	3	158	76-178
Sauerkraut Ck.*	1993	4	116	51-152
Wilson Ck.*	1993	1	92	51-127

N/A Data not available

* Samples from University of Montana Wild Trout and Salmon Genetics Laboratory

Table 16. Maximum ages collected from study streams and genetic collections.

Maximum age	Number of streams	Size at maximum age (mm)	Total capture range (mm)
3	6	140-207	45-227
4	10	116-262	23-270
5	5	141-230	27-278
6	5	159-246	37-324
7	1	164	40-216
8	2	175-226	53-230

DISCUSSION

Age Determination

One of the major assumptions of the scale aging technique is that annual scale growth maintains a constant ratio with annual body growth throughout the life of the fish (Van Oosten 1929). Therefore, when body growth slows, there will be an associated reduction in scale growth. Another important assumption is that a distinguishable annulus is deposited each year of life. If body growth is very slow, however, it becomes difficult to discern and interpret individual annuli on scales. Westslope cutthroat trout living in headwater habitats are generally slow growing and problems associated with accurate age determination from scales are apparent. Slow growth may occur after a fish reaches sexual maturity because more energy is devoted to the maturation of gametes than to growth or simply because physical stream conditions are not conducive to rapid growth.

My data indicate that scales underestimate the true age of westslope cutthroat trout from headwater streams. This is based on comparisons with otoliths which are present at hatching and have been shown to provide older age estimates than scales for slow growing or mature salmonids (Craig and

Poulin 1974; Erickson 1979; Sikstrom 1983; Barnes and Power 1984; Sharp and Bernard 1988). Otoliths indicated that a large proportion of yearling trout from individual streams (49-85%) did not form a first year annulus.

I typically did not encounter age 0 fish until mid August, and in some cases as late as September. Scarnecchia and Bergersen (1986) reported peak emergence of young-of-the-year greenback cutthroat trout (O. c. stomias) and Colorado River cutthroat trout (O. c. pleuriticus) from headwater systems in Colorado peaked near mid-August and few individuals exceeded lengths of 30-35 mm before they entered their first winter. Shepard et al. (1984) reported that in the Flathead River basin, Montana, scales first form on westslope cutthroat trout at lengths of 38 to 44 mm and Brown and Bailey (1952) reported that scales did not cover the entire body of cutthroat trout until 63-68 mm in length. When juveniles residing in headwater systems emerge late in the growing season, they often do not grow large enough either to form scales or, if scales form, to lay down a discernible first year annulus. If not accounted for, this missing first year annulus results in an underestimate of age through the life of the fish.

When missing first year annuli are compounded with slow growth as an adult, large underestimates of age from scales are likely. This was evident when the discrepancies between paired age structure samples were plotted by fish age (Figure 3). For fish under age 4, assumed to be mainly immature, ages determined from scales were usually 1 year less than those determined from otoliths. Fish beyond age 4 exhibited larger discrepancies. Scales may be suitable aging structures for immature westslope cutthroat living in headwater streams if missing first year annuli are accounted for. This is supported by Sharp and Bernard (1988) who concluded that scales could be used to age immature lake trout Salvelinus namaycush from interior Alaska, but ages interpreted from the scales of mature fish were lower and less precise that ages interpreted from otoliths.

The level of exploitation a population undergoes influences the reliability of scales as an aging structure. Headwater populations of westslope cutthroat trout experience low levels of exploitation by virtue of their physical locations, slow growth rates, and small population sizes. Fish from unexploited populations achieve older ages than fish from exploited populations which can result in greater discrepancies between ages assigned from otoliths and scales (Power 1978; Erickson 1979; O'Gorman et al. 1987), providing further support for my conclusion that ages interpreted from scales underestimate the true ages of westslope cutthroat trout from headwater populations.

The proportion of fish missing a first year annulus was highest for Half Moon Creek and lowest for Halfway Creek. Water temperature (number of degree days during the first year of life), which strongly influences growth rate, explains a large proportion of the variability in first year annuli formation between populations of salmonids (Laakso and Cope 1956; Jensen and Johnsen 1982; Lentsch and Griffith 1987). Lentsch and Griffith (1987) identified the number of degree days as the major environmental factor controlling first year annulus formation. They concluded that if trout were exposed to less than 720 degree days, no fish formed a first year annulus. If fish were exposed to more than 1500 degree days, all fish formed the annulus. I did not have thermographs installed in study streams. By using elevation, aspect, and basin morphology as a relative measure of degree days study streams were exposed to, my results are consistent with the results of Lentsch and Griffith (1987). The elevation of Halfway Creek (1830 m - 2290 m) is moderate when compared to other study streams, but other physical characteristics of the drainage basin suggest a relatively high number of degree days. The aspect is south facing, and the headwaters and the majority of Halfway Creek supporting westslope cutthroat trout are of the B channel type (Rosgen 1985), meandering through open meadows until it reaches a small, shallow pond where more warming likely occurs. Below the pond stream characteristics change to a higher gradient, A type channel (Rosgen 1985), but lower segments are still likely influenced by warm headwater temperatures. When attempting to collect fish from Halfway Creek for fecundity analysis, I documented earlier spawning than in other study streams sampled, also indicating a longer growing season. Half Moon Creek is located at a slightly lower elevation (1710 m - 2010 m), but the aspect is northeast facing. The stream originates near the top of a northeast facing basin and travels over most of its length in a constrained, A type channel (Rosgen 1985) with reduced exposure to solar radiation due to steep canyon walls and vegetative overstory. These physical stream parameters indicate a relatively lower number of degree days. I believe that the number of degree days age 0 fish are exposed to during the first growing season would be the best predictor of missing first year annuli on scales, but I do not have these data on study streams.

The results of annulus validation based on recaptured fish provides further evidence that scales are a poor overall choice for an aging structure for headwater populations of westslope cutthroat trout. It appeared that interpretable annulus formation broke down after age 3, with only 40% of recaptured individuals forming an interpretable annulus on scales when recaptured at age 4. The proportion of fish forming annuli on their scales generally decreased with increasing age. The apparent increase in the rate of annulus formation for 5-year-olds (Figure 5) likely reflects the influence of a small sample of fish in this age class. This indicates that ages interpreted from scales would decrease in accuracy with increasing fish age. This is similar to findings of Casselman (1987), who reported no significant correlation between assessed scale age and actual age for lake trout ranging in age from 9 to 36 years.

Managers should therefore use scales as aging structures with caution. If the ages interpreted from scales are accepted without validation, errors in the estimation of production, growth, and mortality may occur (Beamish and McFarlane 1983). In addition, longevity and the age at sexual maturity may be under estimated. In relatively unexploited populations, these types of errors may not be of major concern. However, in stream systems near roads or population centers where harvest is occurring, errors in population parameter estimates could have a negative influence on managing small populations. Ages assigned using scales should be viewed as conservative estimates of age instead of absolute estimates and acknowledgment of errors associated with age estimation should lead to more cautious management.

Use of fin rays for aging small, slow growing westslope cutthroat trout was unsuccessful. Annuli were not interpretable on pectoral fin ray sections using the preparation methods described. Fin ray samples were prepared from fish ranging in length from 107 mm to 222 mm. Shirvell (1980) concluded that the validity and accuracy of ages interpreted from fin rays is highly dependent on differential growth rates during the year. Growth rates in headwater systems in Montana may not be sufficient to produce identifiable, contrasting seasonal zonations on fin rays. In addition, it is necessary to clip fins collected for aging as close to the body as possible so as not to miss the first year annulus and the possibility of serious injury or mortality to a small fish exists.

My study produced a "Index of Average Percent Error" (AEI) of 3.2% for otoliths and 11% for scales, demonstrating that ages interpreted from otoliths were more precise than those interpreted from scales for headwater populations of westslope cutthroat trout. Studies of arctic grayling Thymallus arcticus (Craig and Poulin 1974, Sikstrom 1983), and lake trout Salvelinus namaycush (Sharp and Bernard 1988) support these results. Knapp and Dudley (1990) examined headwater populations of golden trout Oncorhynchus aguabonita and found no interpretable annuli on scales, while annuli on otoliths were easily interpreted. Hubert et al. (1987), however, concluded that scales were appropriate for aging Yellowstone Lake cutthroat trout Oncorhynchus clarki bouvieri and that otoliths were less precise aging structures than scales. The authors reported an AEI of 33% for otoliths and 15% for scales, indicating lower precision of aging using otoliths, although otoliths did provide older age estimates in general. The high AEI% associated with the ages interpreted from otoliths of Yellowstone Lake cutthroat population may identify problems associated with precision. Low precision indicates problems associated with annulus recognition. If a study is designed to test the precision of ages interpreted from various hard structures and annulus recognition is a problem in a particular structure, other methods of sample preparation should be explored. If other methods are not attempted, conclusions regarding the precision of age estimates from a given structure may not be valid. I viewed otoliths whole without applying a clearing technique because the annual zones were readily apparent as was indicated by the low AEI% (3.2%). Hubert et al. (1987) employed the otolith clearing technique described by Reimers (1979). It is possible that their high AEI% (33%) for otoliths was a result of preparation techniques.

The agreement between ages interpreted from otoliths and a length-frequency histogram for West Fork Cottonwood Creek indicates that otoliths are valid aging structures for westslope cutthroat trout. The negative side of using otoliths for aging is the necessity to sacrifice the fish. The impact to the population can be reduced by examining a subsample of otoliths for comparison with ages interpreted from scales. Biologists could then determine if aging from scales is appropriate for a given population. Otoliths from small trout are easily extracted, prepared, and viewed. If a population is so small that sacrificing fish would put it at risk, then it should be closed to angling. Given the relative consistency in physical parameters of headwater streams between years, annual examination of otoliths would not be required. A one-time collection of fish from various age classes in a given stream would provide guidance on the validity of scale ages out to maturity.

The number of fish to be sacrificed should be left to the discretion of the biologist most familiar with the population.

I developed models to predict and correct for a missing first year annulus. These models allow managers of headwater populations of westslope cutthroat trout to use scales as aging structures up to the age of sexual maturity. Of the models created using a single variable (the number of circuli to the first annulus), the model employing 5 circuli as the indicator of a missing first year annulus performed the best when applied to the testing sample, improving agreement between paired otoliths and scales from 24% to 70%. Of the models utilizing 2 circuli variables, model IVB performed the best. This model improved initial agreement of the testing sample pairs from 24% to 73% following correction.

Westslope cutthroat trout fry in headwater streams emerge from the gravel late in the growing season; therefore, they probably lay down fewer circuli on their scales during their first year of growth than during their second year of growth. Lentsch and Griffith (1987) documented mean numbers of circuli to the first and second annuli of 7 and 19, respectively, for 733 rainbow-cutthroat hybrids from Emerald Lakes, Colorado. Thus, 7 circuli were laid down the first year and 12 circuli were laid down during the second year. This supports the idea that incorporating a ratio of circuli between first and second annuli versus simply counting the number of circuli to the first annulus should more accurately predict a missing first year annulus within and across streams. Although a t-test indicated significant differences in the mean predicted ages between these two models, the difference between 70 and 73% is not significant for management purposes.

A fishery biologist is likely to be more concerned with accurate age determination than reducing potential aging biases. Most fishery biologists do not follow techniques to reduce bias in aging (i.e. reading samples without *a priori* knowledge of length) because knowledge of fish length can help assign the correct age. The additional time required to count the number of circuli to the second annulus would probably outweigh any improvement in aging accuracy because of biases inherent in scale aging techniques. Shepard et al. (1984) used 7 circuli as an indicator of a missing first year annulus for westslope cutthroat from the Flathead River basin, Montana, and Lukens (1978) reported that all westslope cutthroat trout from the Wolf Lodge Creek drainage, Idaho formed a first year annulus preceded by an average of 7 circuli. My 7 circuli model detected the lowest proportion of missing first year annuli (Table 6). Although my single variable model utilizing 5 circuli corrected for a missing first year annulus better than the 6 circuli model (70% versus 66%, respectively), I recommend using the 6 circuli model for management purposes since it will provide substantial improvement in age accuracy while maintaining a conservative approach to age correction.

I was able to document the missing first year annulus phenomena in populations by using only incidental mortalities and calculating the frequency of occurrence based on circuli counts entered into my age correction model. This may be the most efficient means of determining the presence and magnitude of a missing first year annulus in small populations.

A potential problem associated with the application of this corrective age model to other headwater populations of westslope cutthroat trout lies in differential growth rates associated with individual streams. A stream with a higher trout growth rate than those streams used to develop this model could potentially be identified as supporting fish which do not form a first year annulus based on circuli counts, when in fact age 0 growth is fast and subsequent over-age estimation could result. By taking a conservative approach and using the 6 circuli model, over-age estimation will be reduced.

Growth

Selected study streams differed with respect to productivity, flow regimes, and temperature, resulting in differential growth rates. This is supported by Averett (1962) who documented higher growth rates for westslope cutthroat trout from lower versus higher elevation tributaries of the St. Joe River, Idaho.

Daily growth rates ranged from 0.025 mm for Delano Creek to 0.285 mm at West Fork Cottonwood Creek. The two major external factors controlling fish growth are water temperature and food availability (Weatherly and Rogers 1978). West Fork Cottonwood Creek is located at a lower elevation (1850-2110 m) and has a southeast facing aspect while Delano Creek has an east facing aspect and a higher elevation (2120-2260 m). In addition, the slopes above West Fork Cottonwood Creek have been extensively logged, increasing surface runoff and subsequently, stream temperature. Delano has a smaller wetted width than West Fork Cottonwood Creek (1.2 versus 2.1 m, respectively) and has a dense overstory serving to reduce the amount of solar radiation which can reach the stream. Overall productivity is greater in West Fork Cottonwood as indicated by higher densities of fish and higher fish growth rates. Neither of these two streams were identified as those supporting the highest or lowest proportions of fish with missing first year annuli. It appears that some streams may offer better growth environments for juveniles than adults, while others offer better growth for adults than juveniles.

The calculation of mean length at age for the headwater study populations was confounded by the low level of reliability of ages interpreted from scales. The growth rates I observed for age 1 resident westslope cutthroat trout (Appendix A) appeared slightly higher than reported for fluvial and adfluvial populations (Appendix B). Even following the application of the corrective age model to my scale samples, some age 1 fish were classified as age 0 because growth was extremely slow. They neither possessed an age 1 annulus or produced greater than 6 circuli on their scales during the first growing season. This produced a bias against slow growing fish and inflated my estimates of mean lengths at age 1 and likely, all subsequent ages (Appendix A). Length at age was similar for age 2 adfluvial, fluvial, and resident westslope cutthroat trout (Appendix A and B). By age 3, length at age was similar for fluvial and resident fish, but higher for the majority of the adfluvial populations. Beyond age 4, length at age was higher for adfluvial and most fluvial populations resulting from migration to a better growth environment in larger systems. The similarities in length at ages between migratory and resident forms of westslope cutthroat trout prior to migration to larger systems by migratory forms indicates a possibility may exist to recover lost populations of fluvial and adfluvial westslope cutthroat trout if these life-histories can be adopted by resident fish.

The weak correlation between initial size at capture and subsequent growth rate was unexpected based on an idealized sigmoid growth curve (Bond 1979) (Figures 6-14). I expected to see a decrease in growth rate with increasing size within a stream, however, this pattern was not apparent in the data. A stronger relationship was apparent when the relationship between growth rate and age was examined as indicated by the increased correlation value ($r=-0.33$). The negative correlation between growth rate and age indicates that as fish age increases (as opposed to length), growth rate slows. The mean daily growth increments (Tables 9 and 10) support this, if size can be used to reflect relative age within a population. It may be that growth rate and length did not show a strong correlation because at a given length, a younger fish will have a higher growth rate than an older fish.

Individual westslope cutthroat trout within streams did not demonstrate a great deal of movement (B. Shepard, Montana Department of Fish, Wildlife, and Parks, personal communication) which supports Northcote's (1992) contention that strong selective pressures make resident salmonids, particularly those isolated by barriers, minimize movements. Fish were generally recaptured in the same 100 m transect that they were originally captured in. Differential growth rates associated with variable quality in microhabitat may be masking relationships between fish length or age and growth rate. This idea is somewhat contrary to the findings of Newman and Waters (1989) who did not find significant differences in growth rates between eight contiguous 305 m-long sections of South Branch Creek, Minnesota over a 3-year period. However, the authors did not examine growth rate by microhabitat and did document significant differences in growth rates at age among sections for specific intervals (e.g. April-August 1981), sometimes two times as high. This may account for some of the variability I observed in growth rates within streams. Individuals inhabiting higher quality microhabitat may have higher growth rates than those inhabiting closely associated, but lower quality microhabitats.

I attempted to correlate mean stream elevation and conductivity with growth rate to address the effects of temperature and productivity on growth. Neither of these variables explained a significant amount of the variability in growth rate by stream and do not adequately represent either temperature or productivity.

Fecundity

Although fecundity increased with increasing fish length, high variability within length groups prevented the development of a strong predictive model from study streams. Small sample size is partially responsible for the poor r^2 values, but high variability in fecundity at length is apparent.

Rieman and Apperson (1989) developed a predictive fecundity model for westslope cutthroat trout using the data of Averett (1962) and Johnson

(1963). The fecundity data used to construct the model came primarily from larger, adfluvial fish. This model has been used to predict fecundity of westslope cutthroat trout from headwater habitats in Montana (Magee 1993). The predictions of the Rieman and Apperson (1989) model underestimated the fecundity I observed. The question arises not only as to the validity of application of Rieman and Apperson's (1989) predictive model to smaller, resident fish, but also combining my data with the data used to develop the model. Life history differences may influence fecundity to length relationships (Figure 14). Further sampling, incorporating appropriate statistical sample sizes and concentrated on several slow growing, resident populations would provide information on the validity of applying fecundity models across life histories or even populations with similar life histories.

The best models for predicting fecundity using length from several data sets, defined by r^2 values, did not employ data transformations. This indicates a linear relationship between fecundity and length for westslope cutthroat trout. This is in contrast to typical curvalinear length to fecundity relations requiring log-log transformations (Bagenal 1967). The r^2 value for the best regression using the combined data was 0.88. Because of uncertainties involving combining fecundity data from different life-histories, I recommend applying the fecundity model constructed using only fecundity samples from isolated, headwater populations ($E = -515.5 + 4.5(FL)$; $r^2 =$

0.52; $p<0.001$), to isolated, headwater populations in the upper Missouri River drainage in Montana.

Sexual Maturity

Males matured at earlier ages and smaller sizes than did females. Males were sexually mature as young as age 2 and as small as 110 mm while females did not mature until age 3 and at lengths of 150 mm in study populations. My findings are consistent with the findings of other authors who determined that westslope cutthroat trout reach sexual maturity between ages 3 and 5 (Brown 1971; Liknes and Graham 1988; Behnke 1992). The differences in ages and lengths at maturity for the sexes probably reflects the different energy requirements for maturation of testes and ovaries (Wooton 1985).

Anderson and Gutreuter (1983) noted that length is often a better indicator of maturity than age and Jonsson et al. (1984) documented that faster growing cutthroat trout matured, on average, younger than slower growing fish. The mean lengths of mature fish at a given age were longer than those of immature fish for both sexes of sampled fish, indicating that length or growth rate plays a more important role in sexual maturation of westslope cutthroat trout than age. Logistic regression also identified length as being more important than age in determining sexual maturity.

When the predictive capability of the length-based logistic models was tested using field classifications of sexual maturity status, the model to predict sexual maturity for males performed reasonably well and was far superior to the model predicting female maturity status. Field classifications of ripe (reproductive products can be easily extruded) are less subjective than simply assuming maturity based on the physical appearance of the individual fish. In the field, the differences between mature and immature males are more obvious than the differences between mature and immature females. During peak spawning, if a male extruded milt when pressure was applied to the abdomen, it was classified as mature. If it did not extrude milt the individual was classified as immature. For females, some fish that did not extrude eggs when pressure was applied to the abdomen were classified as sexually mature based on their physical appearance because not all females become ripe at the same time. When only females that were classified as ripe or spent (extruded eggs when pressure was applied to the abdominal walls) were run through the model, the results improved to the same level as the male predictive model. It is likely that field classification of the maturity status for some of the small, female westslope cutthroat trout was inaccurate.

Fish that grow at faster rates may have different mortality rates than slower growing individuals at a given age (Busaker et al. 1990). Given this scenario, faster growing fish would need to mature at younger ages if they are to be successful reproducers. By determining growth rates and knowing length at maturity, biologists can predict the number of years of growth to sexual maturity. This information can be used to develop management plans which assure fish reach sexual maturity and have reproduced at least once before harvest occurs.

Only 1 of the 21 sampled females age 5 or older did not appear sexually mature. This suggests that annual spawning, rather than alternate year spawning, is most common for the populations sampled. However, this could also reflect the small sample size of mature females collected beyond the age of 5. Ball and Cope (1961) reported that alternate year spawning was more common than annual spawning in Yellowstone cutthroat trout in Yellowstone Lake. Annual spawners suffered higher mortality rates than alternate year spawners. Based on recaptures, westslope cutthroat trout living in headwater habitats do not appear to have extended spawning migrations and Northcote (1992) noted that spawning migrations cause the most extensive movements in resident salmonid populations. This "saving" in terms of energy expenditures associated with migration to and from reproduction sites may allow for annual spawning without high levels of mortality, thus annual spawners could produce more progeny than alternate year spawners in the same system.

Longevity

I found that westslope cutthroat trout living in headwater habitats can live at least 8 years. Large fish size does not necessarily translate into older ages. As stated earlier, fish which grow at different rates may have different mortality rates and smaller, slower growing individuals may live longer. I did not intentionally select for any size group to determine longevity; therefore, where the largest fish sacrificed is near the size of the largest fish captured in a given population, the determination of longevity for that population is reasonable. The maximum ages presented in the longevity table for genetic collections should be viewed only as the maximum age sampled. Biologists collecting samples for genetic analysis often select for smaller individuals to minimize potential negative effects on populations from removing the largest and/or fastest growing individuals, especially from small populations.

Johnson (1963) and Lukens (1978) documented ages of 6 years for some Idaho populations and Shepard et al. (1984) reported 7-year-old westslope cutthroat trout inhabiting the Flathead River Basin system in Montana. These findings are consistent with my results, however these three studies utilized scales as aging structures and, therefore, may have underestimated age.

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APPENDICES

APPENDIX A

Length at age for study populations.

Table 17. Mean lengths at age for study populations. Ages were interpreted from scales and lengths represent point samples collected during 1993 summer sampling.

Stream	Age 0			Age 1			Age 2		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Collar Gulch	N/A			89.0	84-94	21.2	115.4	94-172	17.4
Cottonwood (Ruby drainage)	N/A			127.5	127-128	0.71	128.7	100-160	15.4
Geyser	72.3	58-88	10.2	100.0	72-131	17.9	120.8	84-168	21.2
Cottonwood (Smith drainage)	N/A			114.9	72-137	21.3	143.7	99-215	20.5
West Fork	75.7	68-84	6.0	90.6	68-108	14.4	132.4	89-219	23.4
Douglas	63.0	56-73	6.2	83.3	49-115	15.3	110.0	61-163	20.3
North Fork	66.0	53-78	7.0	83.2	63-119	11.6	119.2	86-160	17.9
Halfway	N/A			71.5	62-100	9.0	99.5	68-157	20.4
Jerry	74.5	65-83	6.5	89.4	59-124	18.2	107.5	81-146	14.6
Delano	77.7	72-83	3.6	93.5	80-113	10.2	115.5	81-172	21.7
McVey	72.9	62-86	6.6	104.7	94-130	9.8	119.2	92-156	19.9
Muskrat	N/A			98.0	77-119	29.7	132.5	103-188	23.9
North Fork Gold	69.7	57-100	10.9	88.6	64-105	10.7	109.1	77-166	20.1
Soap	72.3	70-76	3.2	111.9	69-142	28.9	121.5	89-195	23.6
Tenderfoot	N/A			119.0	114-124	7.1	153.3	113-178	21.2
White's Gulch	N/A			84.5	67-118	15.3	141.2	73-238	36.6

Table 17. Continued.

Stream	Age 3			Age 4+		
	Mean	Range	SD	Mean	Range	SD
Collar Gulch	164.7	109-219	23.2	179.0	144-216	25.3
Cottonwood (Ruby drainage)	183.4	149-247	25.5	234.9	174-324	38.1
Geyser	160.9	106-208	21.7	200.8	152-232	19.5
Cottonwood (Smith drainage)	185.0	153-220	25.8	220.1	197-245	14.4
West Fork	185.2	147-226	19.7	201.9	170-251	21.0
Douglas	146.6	92-207	21.5	167.0	137-203	27.5
North Fork	144.1	118-183	15.2	170.3	151-204	14.5
Halfway	127.6	88-173	18.2	158.3	103-243	27.2
Jerry	140.9	106-174	16.6	171.0	124-208	21.0
Delano	136.6	111-192	17.7	162.7	134-204	20.3
McVey	153.9	127-187	20.3	206.6	160-241	35.5
Muskrat	157.6	124-182	27.0	N/A		
North Fork Gold	140.3	99-205	26.5	162.8	125-201	22.5
Soap	172.0	141-213	18.6	190.6	150-230	25.0
Tenderfoot	186.9	128-216	21.1	225.9	200-258	15.8
White's Gulch	188.0	155-226	22.8	196.1	171-231	19.7

APPENDIX B

Mean length-at-age for fluvial and
adfluvial westslope cutthroat trout

Table 18. Estimated mean length-at-age (mm) for fluvial and adfluvial westslope cutthroat trout. Table was adapted from Rieman and Apperson (1989) and data were summarized by Lukens (1978) and Pratt (1985). Total lengths were converted to fork lengths by the equation: FL = TL/1.05 (Carlander 1969).

Migratory type	Water	Age 1	2	3	4	5	6	7
Fluvial								
	Middle Fork Salmon	57	95	166	242	307	353	
	Flathead	52	98	150	231	291	320	363
	Coeur d'Alene	71	110	167	257	333	400	
	St. Joe	49	87	136	183	231	277	
	Marble Creek	48	127	170	224	242		
	Kelly Creek	63	97	146	202	239	292	
Adfluvial								
	Wolf Lodge[a]	71	119	204	273	312	348	
	Wolf Lodge[b]	66	102	142	225	285	327	
	St. Joe	69	136	253	322	368		
	Flathead	61	114	180	249	296	333	364
	Pend Oreille	76	141	249	341			
	Priest Lake[a]	85	140	258	311	349		

[a] Two year migrants
[b] Three year migrants