North American Journal of Fisheries Management 17:85–92, 1997

Age at Sexual Maturity, Sex Ratio, Fecundity, and Longevity of Isolated Headwater Populations of Westslope Cutthroat Trout

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Abstract.—We sampled 19 isolated headwater populations of westslope cutthroat trout *Oncorhynchus clarki lewisi* in Montana to provide estimates of fecundity, longevity, sex ratio, and age at sexual maturity. Fecundity was estimated for 31 fish collected from two streams in the upper Missouri River drainage. Females smaller than 149 mm fork length (FL) were generally immature and their fecundities could not be estimated. Mean fecundities (SD) were 227 eggs (41.1) for 150–174-mm fish, 346 eggs (85.6) for 175–199-mm fish, and 459 eggs (150.8) for 200-mm and larger fish. A linear regression model (two stream samples combined) to predict fecundity (E) from fork length was developed ($E = -494.9 + 4.4 \cdot \text{FL}$; $r^2 = 0.51$, $P < 0.001$) for westslope cutthroat trout in the upper Missouri River drainage. Regression slopes of fecundity against fish length differed significantly ($P < 0.01$) between these and some of the previously studied populations. Steeper slopes were associated with lacustrine–adfluvial populations. The average sex ratio was 1.3 males per female across all sampled streams. Males began to mature sexually at age 2 and all were mature by age 4. Some females (27%) were sexually mature at age 3 and most of them (93%) were mature by age 5. Length was a better predictor of sexual maturity than age. Males matured at 110–160 mm and females at 150–180 mm FL. The maximum estimated age was 8 years based on otoliths from 475 fish collected from our 19 study streams and 14 additional streams.

Westslope cutthroat trout *Oncorhynchus clarki lewisi* have undergone major reductions in distribution and abundance since the turn of the century because of land use practices, introductions of nonnative fishes, and overexploitation (Liknes and Graham 1988; Behnke 1992). Genetically pure populations of westslope cutthroat trout occupy about 2.5% of the subspecies' historic range in Montana (Liknes and Graham 1988). Isolation of salmonid populations due to habitat fragmentation increases deterministic, stochastic, and genetic risks of extinction (Rieman and McIntyre 1993). Westslope cutthroat trout populations have become highly fragmented throughout their range and are primarily relegated to headwater habitats. Fish managers need to assess extinction risk and develop conservation and recovery strategies for this native subspecies.

Our study of headwater westslope cutthroat trout populations was undertaken to provide parameter estimates for an extinction risk model being developed by biologists of the U.S. Forest Service's Intermountain Research Station. This model will be used to assess extinction risk associated with isolation and small population size. Our goal was to improve an existing fecundity–length relationship (Rieman and Apperson 1989) by examining small females (125–250 mm fork length, FL), document lengths and ages at sexual maturity, estimate sex ratios, and determine longevities of westslope cutthroat trout in headwater populations in Montana.

Methods

From May through October in 1993 and 1994, fish were collected by using a backpack electrofishing unit (Smith-Root model 15-B). We selected 19 study streams that supported isolated, genetically pure populations of westslope cutthroat trout (Figure 1). Fifteen of the streams drained into the upper Missouri River and four were tributaries to the Clark Fork River in the Columbia River System. The Wild Trout and Salmon Genetics Laboratory at the University of Montana, Missoula, provided fish from an additional 14 streams. We combined the samples from the Wild Trout and Salmon Genetics Laboratory with our own samples to estimate longevity for this study and in a related age structure study.

Fish were aged by viewing, with a binocular

[1] The Unit is jointly sponsored by Montana State University, Montana Department of Fish, Wildlife, and Parks, and the U.S. Geological Survey.

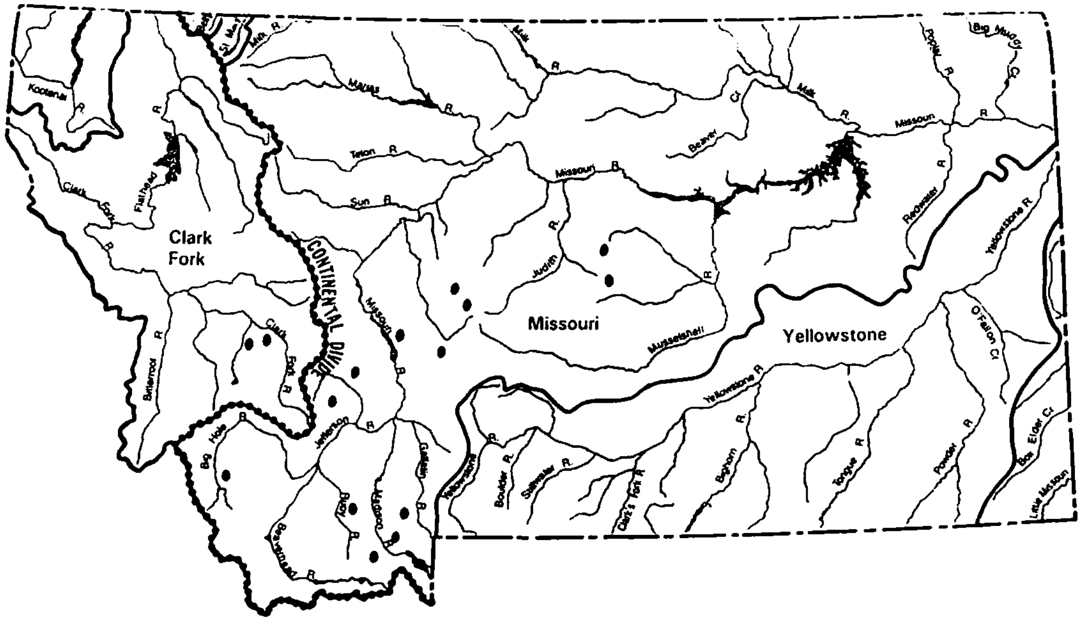

FIGURE 1.—Distribution of headwater streams (black points) in central and western Montana selected for study. Some points represent more than one study stream.

dissecting microscope and reflected light, whole sagital otoliths submerged in distilled water. Whole otoliths provide more accurate and precise age estimates than scales for westslope cutthroat trout from headwater habitats (Downs 1995). In addition, Fraley et al. (1981), Shepard et al. (1984), and Lentsch and Griffith (1987) all reported problems with interpreting ages from scale samples from cutthroat trout inhabiting cold headwater streams. Otoliths have been used to age other salmonids such as chinook salmon *Oncorhynchus tshawytscha* (Neilson and Green 1983); sockeye salmon *Oncorhynchus nerka* (Marshall and Parker 1982); steelhead *Oncorhynchus mykiss* (Campana 1983); and brook trout *Salvelinus fontinalis* (Hall 1991).

Eggs were enumerated from mature females collected from three Missouri drainage streams immediately prior to the onset of spawning in 1994. We attempted to collect at least 10 females in each of four fork length groups—125–149 mm, 150–174 mm, 175–199 mm, and 200 mm and larger—to be consistent with an earlier study (Magee 1993). Fecundity samples from one of the three streams were not used in our analysis because spawning had already begun and some captured fish released eggs in live-cars and during handling. Samples from the other two streams—Cache and Cottonwood creeks—did not yield 10 mature females in the two smallest length-groups. Both ovaries were removed from each mature female and fixed in Davidson's solution (Kent 1992). Ova were enumerated under a binocular dissecting microscope.

We regressed our fecundity data and unpublished data from Cache Creek (A. Bowersox, Montana State University, personal communication) against fish length with both transformed ($\log_{10}$ and $\log_e$) and untransformed variables. We then combined these fecundity–length data with those of Averett (1962) and Johnson (1963) and repeated the analysis.

We collected 50 males and 79 females (in total) from 11 streams to determine age and length at maturity. Status of sexual development was determined by laboratory examination of ovaries and testes. The difference between mature and immature ovaries was distinct. Immature ovaries were granular, dorsally restricted, and rarely extended posterior of the dorsal fin. Mature ovaries were much larger, posessed eggs in an advanced stage of development, and extended ventrally to nearly fill the abdominal cavity. Males were classified as immature if testes were dorsal and threadlike. Because these populations all exhibit resident life histories in headwater habitats, we felt it was appropriate to pool samples across streams to increase sample sizes for statistical analyses.

TABLE 1.—Length-stratified fecundities of westslope cutthroat trout sampled from Cottonwood and Cache creeks, Montana, during this study combined with unpublished data from Cache Creek, Montana (A. Bowersox, Montana State University, personal communication). Lengths are fork lengths.

Length-group (mm)	N	Length (mm)		Fecundity (number of eggs)		
		Mean	SD	Mean	SD	Range
150–174	5	162	9.6	227	41.1	166–264
175–199	15	189	6.9	346	85.6	198–533
over 200	11	218	11.8	459	150.8	224–644

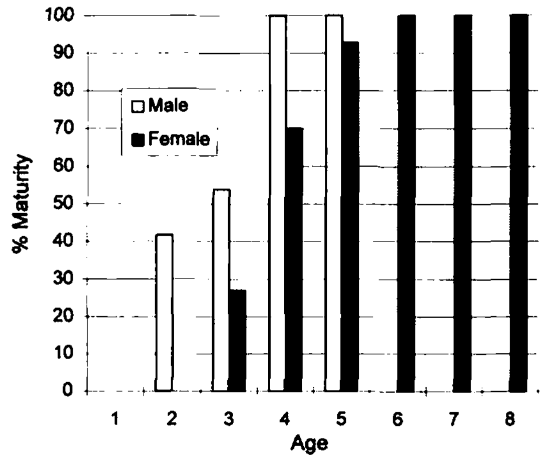

FIGURE 2.—Proportions of male and female westslope cutthroat trout mature at age, based on 129 fish from 11 headwater streams in Montana.

We used logistic regression (Hosmer and Lemeshow 1989; SAS Institute 1994) to explore relationships between age and length and sexual maturity. Sexual maturity was entered into logistic regression models as a binomial variable, mature (1) or not mature (0). Age, length, and their interaction were entered as covariates. Akaike's information criterion (AIC; Akaike 1973, 1985) and chi-square probability values for significance of individual variables within each model were examined for each sex. We used AIC values to select the best models, as recommended by Burnham and Anderson (1992). We tested for significant differences between models using differences in log likelihood values tested against a chi-square distribution with 1 df and an alpha of 0.05 (Hosmer and Lemeshow 1989).

All fish captured during May and June 1994 were externally examined to determine their gender and sexual condition. Sexual condition was rated as immature, mature, ripe, or spent. Immature fish could not be sexed. All males that exuded milt were rated as ripe. Females were considered ripe if eggs could be easily extruded or spent if the abdomen seemed hollow and some residual eggs could be extruded. Gravid females were rated as mature. Sex ratios were calculated for all fish rated as mature, ripe, and spent.

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

Results

Larger fish were more fecund, but fecundity was highly variable within length-groups (Table 1). We were unable to determine fecundity for our smallest length-group (125–149 mm) because only two females in this group possessed mature eggs. These two had several mature, residual eggs and ovaries developing for the next spawning period.

We regressed fecundity (E) against fork length, but the fit was poor. The best model, $E = -494.9 + 4.4 \cdot \text{FL}$ ($r^2 = 0.51$, $P < 0.001$), was for untransformed data. Including data from previous studies (Averett 1962; Johnson 1963) yielded a better fit ($E = -790.7 + 6.2 \cdot \text{FL}$; $r^2 = 0.88$, $P < 0.001$) with untransformed fecundity and length data.

Sampled male westslope cutthroat trout first reached sexual maturity at age 2 (Figure 2). All males sampled were mature by age 4. The youngest sexually mature females were age 3, and most age-5 females sampled were mature. All sampled females greater than age 5 were mature.

Length was a better predictor of maturity than age, especially for females. Logistic regression identified highly significant differences between the single-variable (length or age) models for both sexes ($P < 0.001$). For females, there was no significant difference between the full model (length, age, and their interaction) and the length-only model ($P > 0.50$). For males, the difference between full model and length-only models approached significance ($0.05 < P < 0.10$). Plots of predicted probabilities of maturity versus fish length showed that females matured at longer lengths, but over a narrower length range, than males (Figure 3).

We used sexual maturity data we gathered from external examination of fish to evaluate the pre-

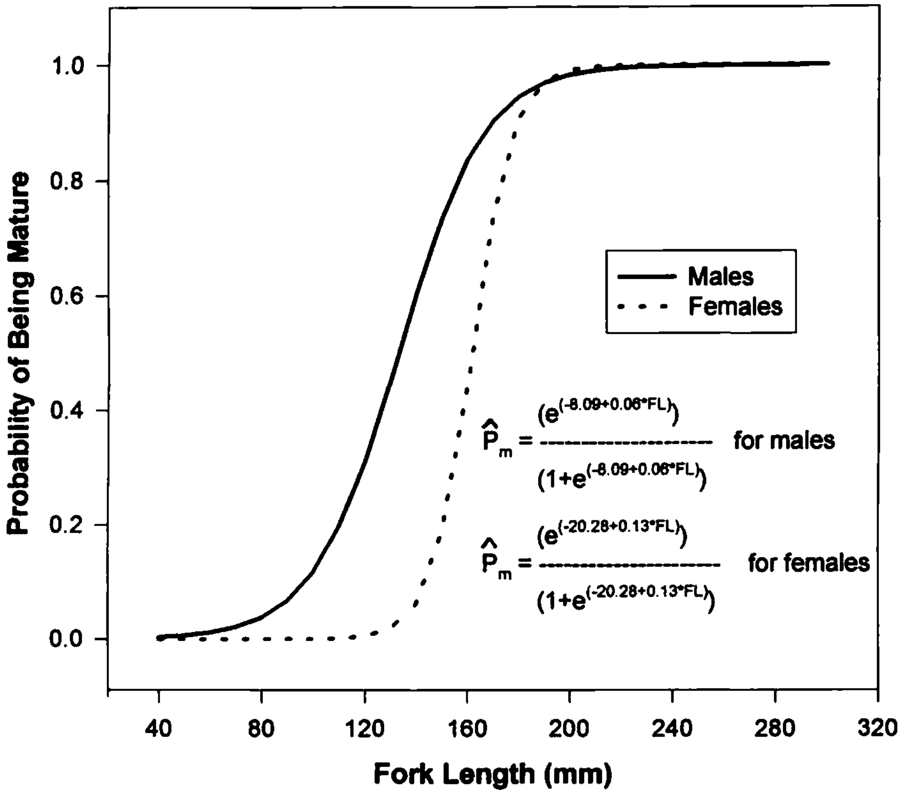

FIGURE 3.—Predicted probabilities ($\hat{P}_m$) of maturity at fork length (FL) for male and female westslope cutthroat trout in headwater streams of Montana, estimated by logistic regression analyses.

dictive capability of the logistic regression models. We compared the number of males and females we visually classified as mature during the spawning season with probabilities of maturity predicted by the length-based logistic models of Figure 3. The model for males predicted that 75% of those we visually classified as mature had a 50% or higher probability of being mature based on length. The predictive ability of the model for females was lower: only 56% of the females we visually classified as mature had a 50% or higher probability of being mature.

TABLE 2.—Numbers of mature males and females (visually classified as mature, ripe, or spent) and sex ratios of westslope cutthroat trout sampled from Montana headwater streams sampled during spring 1994.

Stream	Dates sampled	Males (M)	Females (F)	Sex ratio (M:F)
Collar Gulch	Jun 2, 3	38	46	0.8:1
Cottonwood (Ruby)	Jun 15, 16	59	52	1.1:1
Cottonwood (Smith)	May 6, 24; Jun 28, 29	87	50	1.7:1
Douglas Creek	Jun 13, 14	22	26	0.8:1
Halfway Creek	May 25	45	31	1.5:1
Jerry Creek	Jun 6, 7	70	47	1.5:1
North Fork Gold Creek	Jun 16	14	7	2.0:1
Soap Creek	Jun 16	13	6	2.2:1
All		348	265	1.3:1

Sex ratios in our study streams varied from 0.8 to 2.2 males per female (Table 2); overall, it was 1.3:1. Sex ratios of more than two males per female were associated with small sample sizes.

The maximum age estimated for westslope cutthroat trout in our sample was 8 years (Table 3). Fish in 23 (70%) of the streams had maximum ages of 4 years or more. However, the length of the oldest fish aged from otoliths was often much less than the longest fish captured. Genetic collections not directly associated with this study accounted for 8 of the 10 population samples with maximum age estimates under 4 years.

Discussion

Fecundity increased with increasing fish length but was highly variable even within size groups,

TABLE 3.—Maximum ages, lengths at maximum age, and length ranges of westslope cutthroat trout sampled from Montana headwater streams (NA means data not available).

Stream	Collection year	Maximum age	Fork length (mm) At maximum age	Fork length (mm) Sample range
Cache Creek	1994	8	226	113–230
Brushy Fork Creek[a]	1993	8	175	53–210
North Fork Deadman Creek	1993–1994	7	164	40–216
Cabin Creek	1994	6	210	90–252
Cottonwood–Ruby	1993–1994	6	246	41–324
West Fork Cottonwood	1993–1994	6	212	46–268
Delano Creek	1993–1994	6	159	37–209
Geyser Creek	1993–1994	6	188	37–270
Halfway Creek	1993–1994	5	185	27–278
Soap Creek	1993–1994	5	230	38–239
East Fork Blue Creek[a]	1993	5	141	NA
Upper Cabin Creek[a]	1993	5	193	NA
Four Mile Creek[a]	1993	5	203	102–254
Collar Gulch	1993–1994	4	178	45–230
East Fork Cottonwood	1994	4	178	62–256
Cottonwood–Smith	1993–1994	4	222	64–258
North Fork Douglas Creek	1993–1994	4	204	23–204
North Fork Gold Creek	1993–1994	4	198	35–270
Jerry Creek	1993–1994	4	154	33–235
Muskrat Creek	1993	4	262	73–262
Whites Gulch	1993–1994	4	183	62–251
Hall Creek[a]	1993	4	169	102–178
Sauerkraut Creek[a]	1993	4	116	51–152
Douglas Creek	1993–1994	3	207	45–227
Half Moon Creek	1994	3	202	56–270
Bear Creek[a]	1993	3	165	64–180
West Fork Blue Creek[a]	1993	3	160	75–173
West Fork Fishtrap Creek[a]	1993	3	188	NA
Green Gulch[a]	1993	3	140	To 190
Prickly Pear Creek[a]	1993	3	158	76–178
Badger Cabin Creek[a]	1993	2	145	To 229
West Fork Dyce Creek[a]	1993	2	158	140–170
Wilson Creek[a]	1993	1	92	51–127

[a] Samples from University of Montana Wild Trout and Salmon Genetics Laboratory, Missoula; all other samples are from the present study.

resulting in poor predictive capability. Rieman and Apperson (1989) developed a predictive model for westslope cutthroat trout fecundity using data from Averett (1962) and Johnson (1963). We hoped to improve the predictive ability of their model for smaller fish, but it appeares that differences in length–fecundity relationships exist between populations (Figure 4). We compared the slopes for regressions of length versus fecundity between populations using Zar's (1984) methodology for multiple comparisons between slopes and found that the slopes were significantly different ($P <$ 0.01). Although lacustrine–adfluvial populations (Liknes and Graham 1988) had steeper slopes than resident ones, a Tukey multiple-comparison test (Zar 1984) showed no consistent differences between slopes of the two life history types. The Flathead Lake lacustrine–adfluvial population had a significantly steeper slope ($P < 0.001$) than the other populations. The slope of the resident Cottonwood Creek population did not significantly differ from that of the adfluvial Hungry Horse Reservoir, the adfluvial Coeur d'Alene, or the resident Cache Creek populations. The slope of Cache Creek fish was significantly smaller ($P < 0.01$) than that of the adfluvial populations. These comparisons suggest that length–fecundity relationships must be developed for each life history type and, perhaps, for each population.

Our fecundity model was statistically significant ($P < 0.001$), but a large proportion of the variance remained unexplained ($r^2 = 0.51$). We recommend applying this fecundity model ($E = -494.9 + 4.4 \cdot FL$) only to isolated headwater populations occupying the upper Missouri River drainage in Montana. This recommendation reflects uncertainties in combining fecundity relations across drainage basins and populations of westslope cutthroat trout.

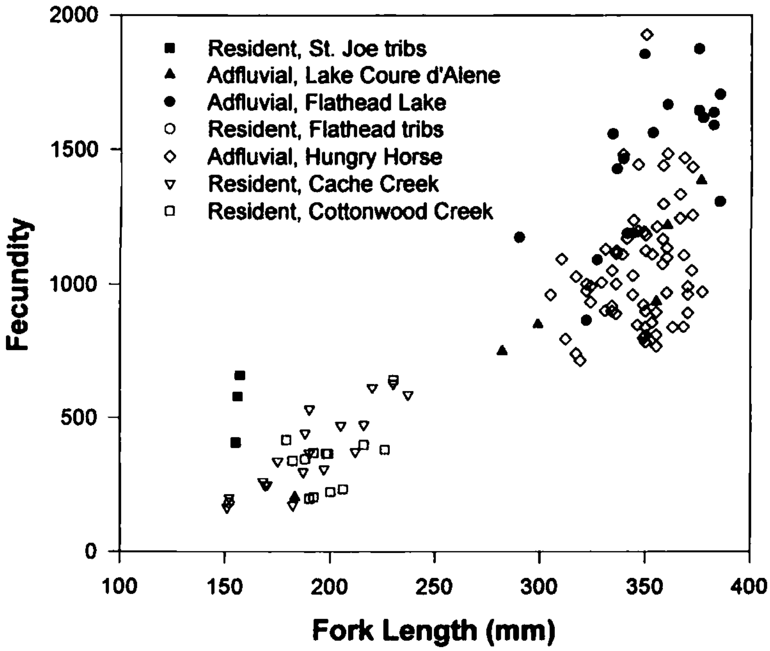

FIGURE 4.—Scatter plots of fecundity versus fork length for populations of westslope cutthroat trout. Data sources are Averett (1962) for resident, St. Joe River tributaries, Idaho; and adfluvial, Lake Couer d'Alene, Idaho; Johnson (1963) for adfluvial, Flathead Lake, Montana, and resident, Flathead River, Montana; J. Huston (Montana Fish, Wildlife and Parks, personal communication) for adfluvial, Hungry Horse Reservoir, Montana; and this study for resident, Cottonwood and Cache creeks, Montana.

Genetic control of sexual maturation notwithstanding, our results indicate that length is more important than age in determining sexual maturity of westslope cutthroat trout. Thus, populations that inhabit streams supporting faster growth should, on average, mature at younger ages. In river and lake systems, westslope cutthroat trout reach sexual maturity between ages 3 and 6 (Brown 1971; Lukens 1978; Liknes and Graham 1988; Behnke 1992). In our study streams, males first reached sexual maturity at fork lengths from 110 to 160 mm (age 2), whereas females first reached sexual maturity between 150 and 180 mm (age 3). This probably reflects the different energy requirements for maturation between testes and ovaries (Wootton 1985). Fish that grow faster may have different mortality rates within a given age (Busacker et al. 1990). Earlier maturation may compensate for higher mortality rates. In systems where predation by piscivorous fish species occurs, fast growth may be a means of avoiding predation. We do not believe this situation exists in our study streams because piscivorous fish species were not present. Because age and length at maturity may vary among streams, they should be evaluated for each stream.

When the predictive capability of the length-based logistic models was tested against field classifications of sexual maturity, results were better for males than for females. Because only males that exuded milt were classified as mature, they were easier to identify than females. The need to rely on appearance to assess female maturity may have biased our results. We recommend additional sampling of females to better document variation in maturation rate between streams. All ovaries examined from females older than age 5 contained mature ova, and we interpret this as evidence for annual rather than alternate-year spawning. Because resident westslope cutthroat trout do not perform extended migrations associated with spawning, more energy may be available for annual reproduction. This could maximize recruitment in a harsh environment.

Sex ratios favored males in most of our study streams, unlike ratios reported for fluvial and adfluvial westslope cutthroat trout populations. Values ranging between 0.2 and 0.9 males per female were reported by Bjornn (1957), Johnson (1963), Lukens (1978), Thurow and Bjornn (1978), May and Huston (1983), and Shepard et al. (1984). Irving (1955) reported that the ratio of males to females decreased during the fishing season and suggested that mature male cutthroat trout were more susceptible to angling. We suspect that sex ratio differences between lacustrine–adfluvial and resident headwater populations of westslope cutthroat trout may be explained by the greater susceptibility to angling of mature male trout. Headwater populations receive less angling pressure than lacustrine–adfluvial populations by virtue of their more remote locations and environments that are less conducive to fish growth. (B. Shepard, personal observation).

Our results demonstrate that westslope cutthroat trout in headwater habitats live at least 8 years. Behnke (1992) reported that the life spans of most western trout are 6–7 years. Johnson (1963) and Lukens (1978) estimated maximum ages of 6 for westslope cutthroat trout and, based on two tag returns, ages of 13 years have been documented for this subspecies in Idaho (N. Horner, Idaho Department of Fish and Game, personal communication). Shepard et al. (1984) estimated maximum ages of 7 for westslope cutthroat trout inhabiting waters in the Flathead River–Lake basin in Montana. Large fish size does not necessarily translate into older age. As described earlier, fish with different growth rates may have different mortality rates. We did not intentionally select for any size-group to determine longevity. If incidental mortalities resulting from electrofishing or handling stress form a random sample of a population, our longevity estimates should be reasonable within the limits of sample size considerations. Electrofishing may cause higher voltage gradients (Ellis 1975) and injury rates (Sharber and Carothers 1988) in larger fish, but we do not believe this was a problem over the relatively narrow size range of fish we sampled (<280 mm FL). The maximum ages we estimated from fish obtained for genetic analyses do not reflect maximum longevity because smaller individuals often were selected to minimize potential negative effects of removing the largest or fastest-growing individuals from small populations.

These estimates of demographic parameters were incorporated into an extinction risk model for westslope cutthroat trout developed by U.S. Forest Service staff. This parameterized model is presently being applied to known westslope cutthroat populations within federal lands in the upper Missouri River basin. Results from this assessment will allow land and fish managers to understand the relative risks of extinction for populations of westslope cutthroat trout over a broad geographic area and, we hope, they will lead to management actions to conserve this subspecies.

Acknowledgments

This study was made possible through funding provided by the U.S. Forest Service, Intermountain Research Station, Montana Department of Fish, Wildlife and Parks, and U.S. Bureau of Land Management. S. Ireland, D. Nixdorff, and D. Fuller assisted with field collections. A. Bowersox provided some of the fecundity samples from Cache Creek. F. Allendorf and R. Leary, Salmon and Trout Genetics Laboratory, University of Montana, also provided some westslope cutthroat trout samples.

References

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petran and F. Csaki, editors. International symposium on information theory, 2nd edition. Akademiai Iadi, Budapest.

Akaike, H. 1985. Prediction and entropy. Pages 1–24 *in* A. C. Atkinson and S. E. Fienberg, editors. A celebration of statistics: the ISI centenary volume. Springer-Verlag, New York.

Averett, R. C. 1962. Studies of two races of cutthroat trout in northern Idaho. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, Project F-47-R-1, Completion Report, Boise.

Behnke, R. 1992. Native trout of western North America. American Fisheries Society, Monograph 6, Bethesda, Maryland.

Bjornn, T. C. 1957. A survey of the fishery resources of Priest and Upper Priest lakes and their tributaries, Idaho. Idaho Department of Fish and Game. Federal Aid to Fish and Wildlife Restoration, F-24-R, Final Report, Boise.

Brown, C. J. D. 1971. Fishes of Montana. Big Sky Books, Bozeman, Montana.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pages 16–30 *in* D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science, New York.

Busacker, G. P., I. R. Adelman, and E. M. Goolish. 1990. Growth. Pages 363–387 *in* C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Campana, S. E. 1983. Feeding periodicity and production of daily growth increments in the otoliths of steelhead trout *Salmo gairdneri* and starry flounder *Platichthys stellatus*. Canadian Journal of Zoology 61:1591–1597.

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.

Ellis, J. E. 1975. Electrotaxic and narcotic responses of channel catfish to various electrical pulse rates and voltage amplitudes. Progressive Fish-Culturist 37: 155–157.

Fraley, J., D. Read, and P. Graham. 1981. Flathead River fishery study—1981. Report of Montana Department of Fish, Wildlife, and Parks to U.S. Environmental Protection Agency, Region 8 Water Division, Denver.

Hall, D. L. 1991. Age validation and aging methods for stunted brook trout. Transactions of the American Fisheries Society 120:644–649.

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

Irving, R. B. 1955. Ecology of the cutthroat trout in Henry's Lake, Idaho. Transactions of the American Fisheries Society 84:275–296.

Johnson, H. E. 1963. Observations on the life history and movement of cutthroat trout, *Salmo clarki*, in the Flathead River drainage, Montana. Proceedings of the Montana Academy of Sciences 23:96–110.

Kent, M. L. 1992. Diseases of seawater netpen-reared salmonid fishes in the Pacific Northwest. Canadian Special Publication of Fisheries and Aquatic Sciences 116.

Lentsch, L. D., and J. S. Griffith. 1987. Lack of first-year annuli on scales: frequency of occurrence and predictability in trout of the western United States. Pages 177–188 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Liknes, G. A., and P. J. Graham. 1988. Westslope cutthroat trout in Montana: life history, status, and management. Pages 53–60 *in* R. E. Gresswell, editor. Status and management of interior stocks of cutthroat trout. American Fisheries Society, Symposium 4, Bethesda, Maryland.

Lukens, J. R. 1978. Abundance movements and age structure of adfluvial westslope cutthroat trout in the Wolf Lodge Creek drainage, Idaho. Master's thesis. University of Idaho, Moscow.

Magee, J. P. 1993. A basin approach to characterizing spawning and fry rearing habitats for westslope cutthroat trout in a sediment rich basin, Montana. Master's thesis. Montana State University, Bozeman.

Marshall, S. L., and S. S. Parker. 1982. Pattern identification in the microstructure of sockeye salmon *Oncorhynchus nerka* otoliths. Canadian Journal of Fisheries and Aquatic Sciences 39:542–547.

May, B., and J. Huston. 1983. Kootenai River investigations final report: 1972–1982. Section C, fisheries investigations. Montana Department of Fish, Wildlife, and Parks report to the U.S. Army Corps of Engineers, Seattle District, Seattle.

Neilson, J. D., and G. H. Green. 1982. Otoliths of chinook salmon *Oncorhynchus tshawytscha*: daily growth increments and factors influencing their production. Canadian Journal of Fisheries and Aquatic Sciences 39:1340–1347.

Rieman, B. E., and K. A. Apperson. 1989. Status and analysis of salmonid fisheries, westslope cutthroat synopsis and analysis of fishery information. Idaho Department of Fish and Game, Federal Aid in Sport Fish Restoration, Project F-73-R-11, Boise.

Rieman, B. E., and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull-trout. U.S. Forest Service General Technical Report INT-302.

SAS Institute. 1994. SAS user's manual update for release 6.10. SAS Institute, Cary, North Carolina.

Sharber, N. G., and S. W. Carothers. 1988. Influence of electrofishing pulse shape on spinal injuries in adult rainbow trout. North American Journal of Fisheries Management 8:117–122.

Shepard, B. B., K. L. Pratt, and P. J. Graham. 1984. Life histories of westslope cutthroat trout and bull trout in the upper Flathead River basin, Montana. Report of Montana Department of Fish, Wildlife, and Parks to the U.S. Environmental Protection Agency, Region 8 Water Division, Denver.

Thurow, R. F., and T. C. Bjornn. 1978. Response of cutthroat trout populations to the cessation of fishing in the St. Joe River tributaries. Idaho Department of Fish and Game, Federal Aid to Fish and Wildlife Restoration, Project F-60-R, Final Report, Boise.

Wootton, R. J. 1985. Energetics of reproduction. Pages 231–254 *in* P. Tyler and P. Calow, editors. Fish energetics, new perspectives. Johns Hopkins University Press, Baltimore, Maryland.

Zar, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.