

Reproductive Demographics and Factors that Influence Length at Sexual Maturity of Yellowstone Cutthroat Trout in Idaho

KEVIN A. MEYER,* DANIEL J. SCHILL, F. STEVEN ELLE, AND
JAMES A. LAMANSKY, JR.

*Idaho Department of Fish and Game,
1414 East Locust Lane,
Nampa, Idaho 83686, USA*

Abstract.—Length and age at sexual maturity for Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* vary across their historical range, but the factors that influence this variation are poorly understood. We collected 610 Yellowstone cutthroat trout from 11 populations across southeastern Idaho from streams and rivers with a variety of physical characteristics to determine length and age at sexual maturity and other reproductive demographics. The oldest Yellowstone cutthroat trout captured (age 10) was from the South Fork Snake River; most fish (90%) were between ages 2 and 4, and only three (<1%) were older than age 7 (all from the South Fork Snake River). Cutthroat trout from the South Fork Snake River did not mature until they were 300 mm long and 5 years of age, whereas cutthroat trout from other migratory and resident sites began maturing at ages 2–3 and lengths of 100–150 mm. Fish 100–250 mm long were much more likely to be mature if they were from sites with resident rather than migratory reproductive life histories. The sex ratio (expressed as the percentage of females) averaged 46% and varied from 27% to 66% among sites. At all but one study site, males matured at a smaller size than females. For both male and female Yellowstone cutthroat trout, length at maturity was directly related to stream order and width, negatively related to gradient, and weakly correlated with conductivity, elevation, mean aspect, and mean summer water temperature. Length-at-maturity models were stronger and fit the data better than age-at-maturity models. Our results enable prediction of length at maturity for Yellowstone cutthroat trout by using readily derived physical data from streams. As such, the results could be useful in estimating risk assessment parameters, such as the number of breeders in and the genetic effective population size of Yellowstone cutthroat trout populations.

Salmonids typically exhibit variation in adult life history patterns among populations (e.g., Ricker 1972; Scarnecchia 1983; Quinn and Unwin 1993; Hutchings 1996; Morita et al. 2000), reflecting differences in rearing conditions or genetic adaptations to local environments. For Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*, length and age at sexual maturity vary across their historical range (Thurow et al. 1988; Varley and Gresswell 1988; Gresswell et al. 1994), presumably in response to biotic and abiotic factors such as stream productivity and size, migratory spawning pattern (i.e., migratory or resident), and possibly genotypic variation—although genetic divergence in Yellowstone cutthroat trout is low (Allendorf and Leary 1988). That much variation exists in the reproductive life history traits of Yellowstone cutthroat trout among populations is well known, but the factors influencing this variation are poorly understood (Gresswell et al. 1997).

Because length and age at maturity to a degree define the reproductive potential for a particular population, understanding when fish mature and what factors influence that maturity would be useful for population modeling and risk assessment. Despite a few reviews discussing general sizes and ages at maturity for Yellowstone cutthroat trout (Thurow et al. 1988; Gresswell et al. 1994), we were unable to find maturity schedules or other pertinent demographic information. The few maturity data available were based solely on spawners observed on redds or captured during migration and did not include fish that were not migrating or spawning. If an understanding of the factors that affect length at maturity could be ascertained, the results could be used in conjunction with other reproductive demographic data and with existing data on presence/absence, abundance, and length frequency to estimate such things as effective population size, reproductive potential, and other risk assessment parameters across a broad geographical area. The recent petition to list Yellowstone cutthroat trout under the Endangered Species Act, although considered unwarranted at this time (USFWS 2001), underscores the importance of

* Corresponding author: kmeyer@idfg.state.id.us
Received February 26, 2002; accepted August 8, 2002

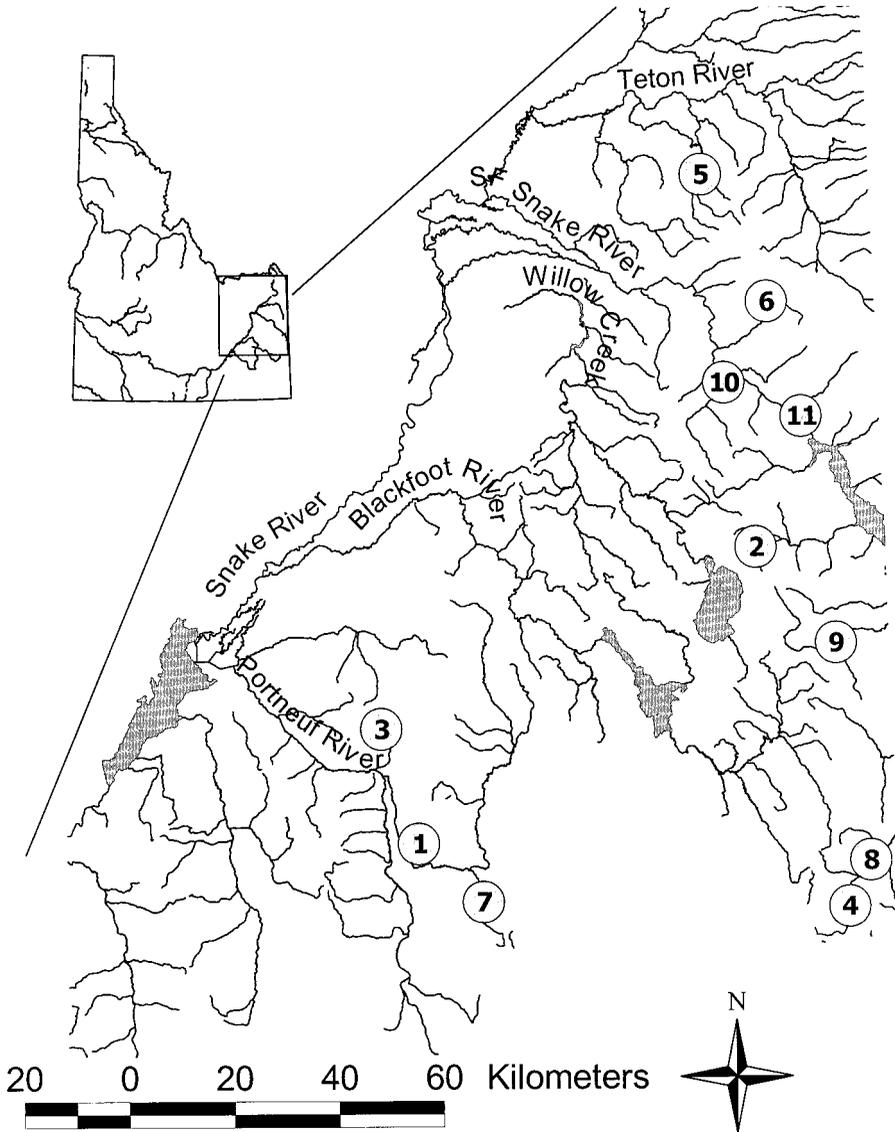


FIGURE 1.—Distribution of study sites across the range of Yellowstone cutthroat trout in southeastern Idaho. Numbers correspond to those in Table 1.

gaining such an understanding for this species. Thus, the primary objectives of this study were to (1) determine length and age at sexual maturity of Yellowstone cutthroat trout across their historical range in Idaho; (2) determine fecundity, longevity, and sex ratios of individuals from several populations; and (3) develop a model to predict Yellowstone cutthroat trout length at maturity based on easily obtained physical stream attributes.

Methods

Using backpack and boat-mounted electrofishing units, we collected 499 Yellowstone cutthroat

trout from 10 streams in April 2000. An additional 111 Yellowstone cutthroat trout were collected from the South Fork Snake River in February and March 2001. Sample streams and the study sites within the streams were selected arbitrarily, but we purposefully distributed study sites across a broad geographic area in southeastern Idaho (Figure 1) containing a wide variety of stream conditions (Table 1). Three streams were sampled in the Portneuf River drainage, one in the Teton River drainage, three in the Salt River drainage, and three in the South Fork Snake River drainage. The

TABLE 1.—Stream attributes for study sites in southeastern Idaho. Stream numbers correspond to those in Figure 1.

Number	Stream Name	Elevation (m)	Stream order (1:100,000)	Conductivity ($\mu\text{S}/\text{cm}$)	Gradient (%)	Stream width (m)	Drainage area (km^2)	Aspect (degrees from true north)	Fish life history	Average daily summer (Jun–Aug) water temperature ($^{\circ}\text{C}$)		
										Minimum	Mean	Maximum
1	Harkness Creek	1,707	1	295	6.3	1.7	7.9	60	Resident	9.0	10.9	14.0
2	Spring Creek	2,042	1	415	2.0	2.4	6.8	129	Migratory	10.5	13.7	17.2
3	North Fork Rapid Creek	1,561	2	452	1.2	3.1	34.7	35	Resident	12.9	16.1	19.3
4	Upper Crow Creek	2,091	2	440	1.7	5.2	36.5	135	Migratory	NA	NA	NA
5	Canyon Creek	1,798	2	183	0.9	4.4	148.1	161	Migratory	11.5	15.5	19.8
6	West Pine Creek	1,768	2	332	1.5	3.2	23.8	42	Migratory	6.8	10.4	15.3
7	Dempsey Creek	1,670	2	285	2.8	3.6	49.0	146	Resident	10.3	14.8	20.0
8	Lower Crow Creek	1,984	3	502	0.4	5.4	143.3	147	Migratory	12.8	13.9	15.1
9	Tincup Creek	1,856	3	358	1.1	5.8	104.8	80	Migratory	12.3	15.0	18.3
10	Fall Creek	1,664	4	652	0.8	6.0	193.4	172	Resident	NA	NA	NA
11	South Fork Snake River	1,640	6	239	0.2	79	13,527	136	Migratory	11.4 ^a	12.1 ^a	12.9 ^a

^a Data from 1996.

length of stream electrofished at a site varied, depending on the amount of effort needed to capture an adequate number of fish, but generally was from 200 to 400 m. Captured fish were transported directly to a freezer for storage.

Several physical and physiochemical stream attributes were measured to assess their effect on the maturity of the captured Yellowstone cutthroat trout. The stream characteristics we measured were selected on the basis of their ecological importance, previous research into factors related to fish growth as well as age and length at maturity, and ease of collection. We generally focused on variables we felt reflected stream size (e.g., stream order, width, drainage area) or conditions associated with fish growth (e.g., elevation, water temperature, stream aspect, conductivity). At each collection site, we determined elevation from U.S. Geological Survey (USGS) 1:24,000 topographic maps, using Universal Transverse Mercator coordinates obtained at the lower end of the reach that was electrofished. Stream order (Strahler 1964) was determined from both USGS 1:24,000 and Bureau of Land Management 1:100,000 topographic maps. We suspected that stream order from the 1:24,000 scale would more precisely reflect stream size and flow patterns. However, because stream order between these map scales is highly correlated across southeast Idaho streams ($r = 0.75$, $n = 320$; K. Meyer, unpublished data), we used data from the 1:100,000 scale for the remaining analysis because the Idaho Department of Fish and Game (IDFG) geographical information systems coverage for stream hydrology is at that scale. Gradient was determined by using the software package All Topo Maps Version 2.1 for Win-

dows (iGage 1998); stream length (m) was traced between the two contour lines that bounded the study site (average traced distance was 1,575 m), and gradient was calculated as the elevational increment between the contours divided by the traced distance. Conductivity was measured with a calibrated handheld conductivity meter accurate to within 2%. Stream width was calculated from the average of 10 readings through the reach that was electrofished, except for the South Fork Snake River, where width was determined by using aerial photographs. Drainage area was calculated by using digitized USGS topographic maps and the ArcView Version 3.1 software package (ESRI 1998). Mean aspect was measured along a line from the upstream extent of perennial stream on 1:24,000 topographic maps to the study site as the number of degrees from true north (oriented in either an easterly or westerly direction); thus, 180 $^{\circ}$ was the maximum value for aspect. We deployed electronic temperature recorders at each site to record hourly water temperature throughout the summer months (June–August), from which we calculated summer average daily minimum, daily mean, and daily maximum water temperature; only summer mean water temperature was used in our analysis. Each site was classified as having Yellowstone cutthroat trout with either a resident or migratory reproductive life history strategy, based on professional knowledge of the systems. For example, sites known to be isolated from or including no downstream Yellowstone cutthroat trout populations were classified as sites containing resident populations, whereas migratory sites were defined as those known to provide spawning grounds for migratory Yellowstone cutthroat trout, or those

that we assumed supported migratory fish (i.e., sites where migratory cutthroat trout were present in a larger system downstream and no migration barriers existed).

The frozen captured fish were thawed in the laboratory and then measured for total length (mm) and weight (g). Sagittal otoliths were removed and stored dry in vials, and scales were removed and spread on strips of paper, which were then stored in envelopes. Age was determined primarily by viewing whole otoliths, dry or submersed in saline, with a dissecting microscope using reflected or transmitted light. Because of the difficulty in interpreting ages for cutthroat trout from scales (Lentsch and Griffith 1987; Downs 1995), we read scales only for corroboratory assistance when age from otoliths was difficult to ascertain ($n = 14$). In these few instances, we pressed scales on acetate slides with a heat press at 6,895 kPa and 110°C for 20–30 s and viewed the scales with a microfiche reader. Otoliths from several ($n = 15$) South Fork Snake River fish were particularly hazy and unusually difficult to read, and scales from this location have been unreliable in the past (W. Schrader, IDFG, personal communication). To age these fish, we placed the otoliths in epoxy and sliced them with a Bronwill crosscutting saw, roasted the otoliths on a hot plate, and viewed the sectioned otoliths with a binocular microscope. All fish were considered to be 1 year old when they reached their first January. The same two readers aged all fish, and agreement between readers was high; for our 11 study sites, the mean index of average error (Beamish and Fournier 1981) between readers for fish age 1 and older was 3.1% (range, 0.4–6.8%).

Gender and maturity were determined by laboratory examination of the gonads. Males were classified as immature if testes were opaque and threadlike and as mature if they were large and milky white. Females were classified as immature if the ovaries were small, granular, and translucent and as mature if they contained large, well-developed eggs that filled much of the abdominal cavity (Strange 1996). Eggs were counted from 77 mature females across all sites. Curvilinear (i.e., power function) regression equations to predict fecundity (F) from fish length (TL) were developed for all females combined and for resident and migratory life histories separately. To test for differences in regression slope between life histories, we log-transformed the length and fecundity data to create a linear relationship, then used 95% confidence intervals (CIs) around the difference be-

tween the regression coefficient estimates ($\beta_1 - \beta_2$; Zar 1996); nonoverlapping CIs indicated a significant difference. Because testing for a difference between y -intercepts ($\alpha_1 - \alpha_2$) is inappropriate (Zar 1996), we used t -tests to compare regression estimates of elevation. To evaluate sex ratio at each site, we calculated 95% CIs around the percentage of the population that was female, following Fleiss (1981); CIs not overlapping 50% indicated a statistically significant departure from a 50:50 ratio.

For ecological perspective, we wished to characterize the variation in length and age at maturity across the study sites. For length at maturity, we did this by estimating the length at which the probability of being mature was 0.5 (termed ML50), using one of two methods. If there was no overlap between the largest immature and smallest mature fish, we selected the midpoint between the length of these two fish as ML50. If there was overlap, we related fish length to maturity by logistic regression, using a binary dependent variable (0 = immature, 1 = mature), and selected ML50 as the fish length at which the probability of being mature was equal to 0.5. We followed the above guidelines with one exception: At Harkness Creek, we caught no male cutthroat trout that were immature, and the smallest mature male was 97 mm, so we used 97 mm as the best estimate of ML50. Separate estimates were developed for males and females because males tended to mature at a smaller size than females and because selection forces for size at maturity differ between the sexes (Roff 1992). If we found overlap between immature and mature fish at a site and could fit no suitable logistic regression to the data for that site, we did not estimate ML50 for the site.

These guidelines were not appropriate for age-at-maturity characterization because in most instances (12 of 22) there was no age overlap in immature and mature fish for males or females; where there was overlap, suitable logistic regression models generally could not be developed. Instead, we simply reported the oldest immature and youngest mature fish for each site.

We assessed the relationship between length and age at maturity and the stream attributes we measured with logistic regression. Our ultimate goal was to use this information to model maturity across the range of Yellowstone cutthroat trout in Idaho. Because length frequency information is available from hundreds of locations but age structure information is available for only a few streams, we were most interested in developing

TABLE 2.—Sex ratio (expressed as the percentage of females) and longevity for Yellowstone cutthroat trout across study sites in southeastern Idaho. Data include all fish (immature and mature) for which sex could be determined; CI = confidence interval.

Location	<i>n</i>	Sex ratio		Maximum age	
		Estimate	95% CI	Male	Female
Harkness Creek	33	42	25–60	4	4
Spring Creek	29	48	30–67	4	4
North Fork Rapid Creek	42	48	32–63	5	4
Upper Crow Creek	50	48	34–62	3	4
Canyon Creek	59	37	25–49	5	4
West Pine Creek	44	27	14–41	6	6
Dempsey Creek	43	44	29–59	4	4
Lower Crow Creek	29	66	48–83	4	5
Tincup Creek	57	33	21–46	5	5
Fall Creek	53	53	39–67	5	7
South Fork Snake River	80	55	44–66	10	8

length-at-maturity models. However, we compared the strength of the length-at-maturity models with the age-at-maturity models to assess whether environmental variables influenced one differently or more strongly than the other. Before performing logistic regression analysis, we removed from consideration any combination of independent variables with bivariate correlations greater than 0.70 (Tabachnick and Fidell 1989). If two independent variables were highly correlated, we removed the variable for which data were more difficult to obtain. Multicollinearity comparisons involving stream width and drainage area were skewed high because values for the South Fork Snake River were orders of magnitude higher than for other sites. However, with or without inclusion of the South Fork Snake River data, stream width, stream order, and drainage area were all highly correlated with each other ($r > 0.80$). We therefore removed drainage area from consideration in the logistic regression models and included either stream order or stream width (but never both) in the models we developed.

Each fish was considered a sample unit. As above, a binary dependent variable was used for maturity. All independent variables were continuous except for the discrete variable “life history,” for which dummy values were used (migratory = 1, resident = -1). Only first-order interactions were tested for significance. Of the 610 Yellowstone cutthroat trout collected, gender could not be determined for 91 fish (mean length, 77.6 mm; range, 50–112 mm); these fish were not included in further analysis. The Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 1989) was used to determine whether a particular logistic regression model adequately fit the data; those models not satisfying the goodness-

of-fit test were discarded. We then used Akaike’s information criteria (AIC) and McFadden’s Rho² to assess the best logistic regression models. AIC is an extension of the maximum likelihood principle with a bias correction term that penalizes for added parameters in the model (Akaike 1973); models with lower AIC values are better. McFadden’s Rho², a transformation of the likelihood ratio statistic, mimics an r^2 value (SYSTAT 1998) but tends to give much lower scores; values between 0.20 and 0.40 are considered very satisfactory (Hensher and Johnson 1981).

Because the South Fork Snake River was much larger than any of the other streams included in our analysis, we were concerned that data from this location might exert undue leverage or influence on modeling results, especially for those models including stream width. We therefore developed predictive models both with and without the inclusion of South Fork Snake River fish; however, because the results were similar for both models, we present only those models that include South Fork Snake River fish.

Results

Most Yellowstone cutthroat trout whose sex could be determined were age 2 (29%), 3 (49%), or 4 (13%), and only three fish (<1%) in the entire study were older than age 7, all three being from the South Fork Snake River. The oldest cutthroat trout captured was 10 years old from the South Fork Snake River (Table 2).

In the South Fork Snake River, only 5% of Yellowstone cutthroat trout smaller than 300 mm long were mature. In contrast, cutthroat trout smaller than 300 mm at other migratory sites and resident sites were mature 22% and 50% of the time, respectively (Figure 2). Similarly, only 5% of South

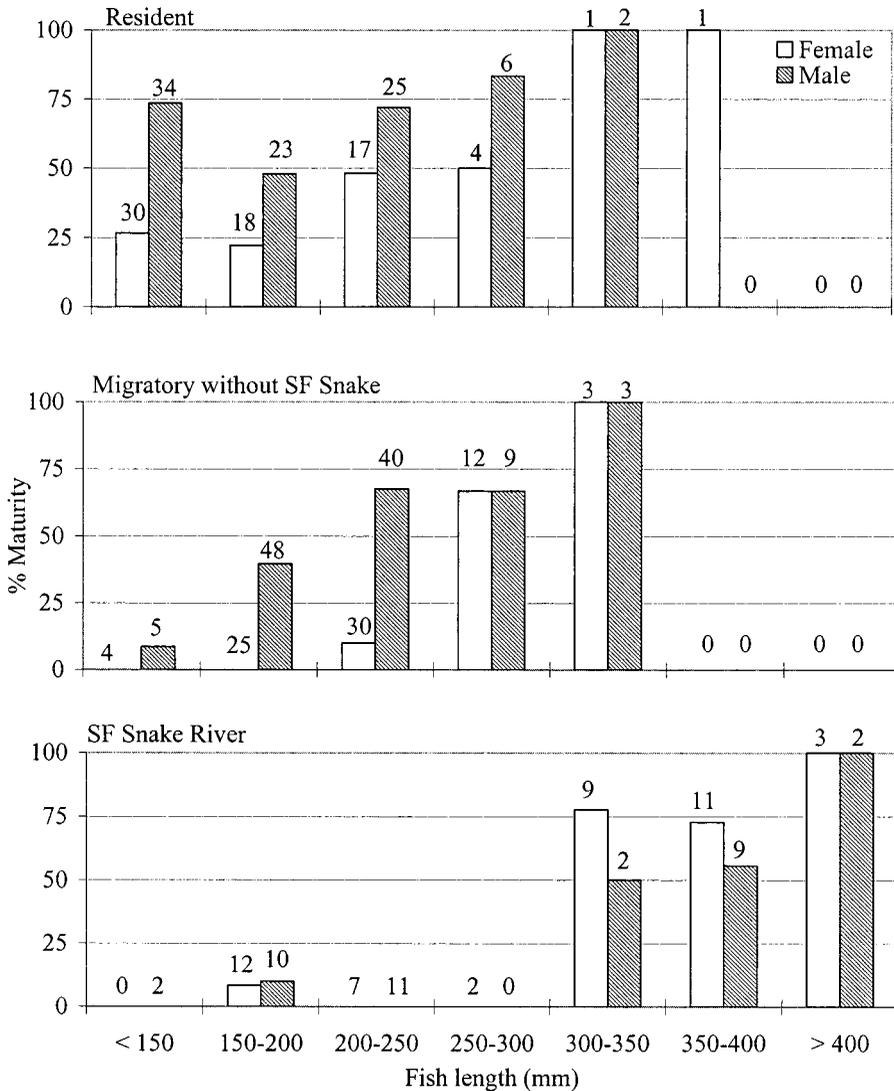


FIGURE 2.—Proportions of male and female Yellowstone cutthroat trout mature at length in southeastern Idaho. Numbers above bars are sample sizes; SF stands for South Fork.

Fork Snake River Yellowstone cutthroat trout younger than age 5 were mature, compared with 27% and 53% maturity for ages 2–4 cutthroat trout from other migratory and resident sites, respectively (Figure 3). Within most age- and 50-mm size-classes, percent maturity was greater for resident than migratory cutthroat trout (Figures 2 and 3).

Sex ratio, expressed as the percentage of females, varied from 27% to 66% among sites and averaged 46%. Males outnumbered females at 8 of 11 sites, but confidence limits around the proportion of the population that was female over-

lapped 50% at all sites except Canyon Creek, West Pine Creek, and Tincup Creek (Table 2).

The relationship between fish length and fecundity was strong across all sites ($r^2 = 0.86$; $n = 77$; Figure 4). However, there was little overlap in fecundity data between the South Fork Snake River and all other sites, and the relationship between fish length and fecundity for South Fork Snake River fish alone ($F = 0.0026 \cdot TL^{2.2255}$) was much weaker ($r^2 = 0.22$; $n = 37$) than for resident fish ($F = 0.0006 \cdot TL^{2.5124}$; $r^2 = 0.82$; $n = 26$) or for all other migratory fish ($F = 0.00009 \cdot TL^{2.8266}$; $r^2 = 0.63$; $n = 14$). We found no evidence of a

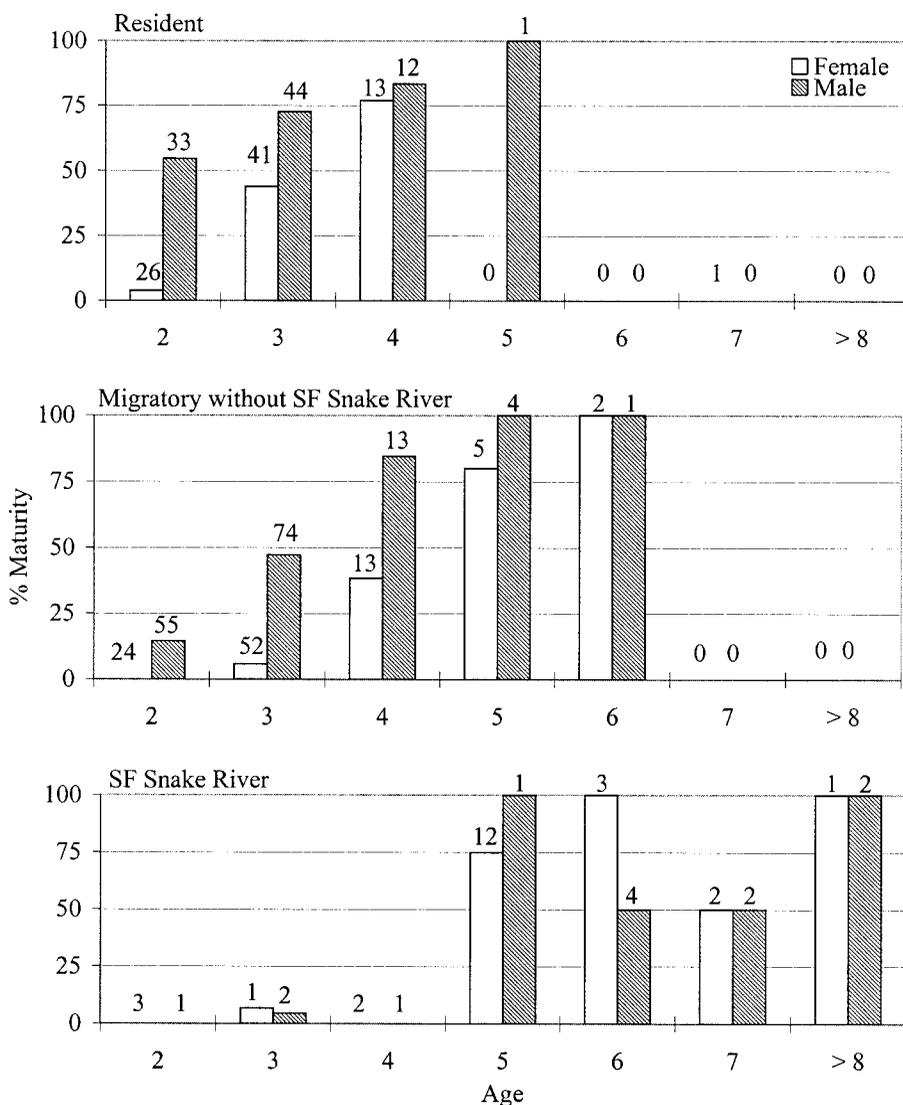


FIGURE 3.—Proportions of male and female Yellowstone cutthroat trout mature at age in southeastern Idaho. Numbers above bars are sample sizes; SF stands for South Fork.

difference between resident and migratory regression equations (using log-transformed data) in terms of slope ($\beta_1 - \beta_2 = 0.32 \pm 3.47$) or elevation ($t = 1.77$; $P = 0.09$). We did not test whether the regression equation for South Fork Snake River fish differed from that for other migratory fish or from resident fish because of the lack of data overlap in fish lengths.

For sites where estimates could be made, ML50 ranged from 97 to 354 mm for males and from 193 to 311 mm for females (Table 3). ML50 was lower for males than females at all sites except the South Fork Snake River. Overlap in size of im-

mature and mature fish was more frequent for males (9 of 11 sites) than for females (6 of 11 sites); the same was true for age at maturity (7 of 11 sites for males versus 3 of 11 sites for females).

For both male and female Yellowstone cutthroat trout, length at maturity increased as stream order and width increased and as reproductive life history changed from resident to migratory but decreased as gradient increased (Table 4). Conductivity, elevation, and mean aspect did not appear to have a strong effect on length at maturity. Mean summer water temperature was indirectly related to length at maturity, but model output was in-

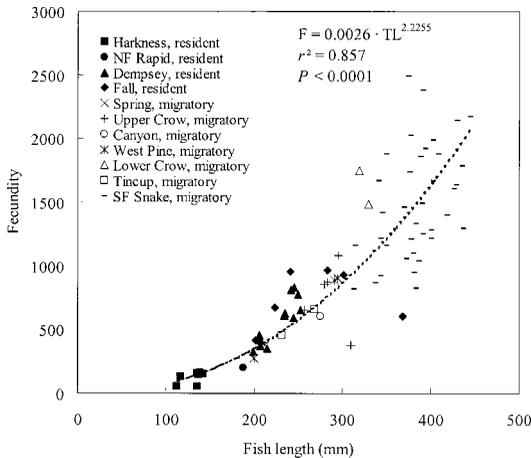


FIGURE 4.—Relation between fish length and fecundity for Yellowstone cutthroat trout across southeastern Idaho. The abbreviation NF stands for North Fork, the *F* in the equation for fecundity.

consistent, producing relatively low AIC values but also the lowest McFadden’s Rho^2 values of any single-variable model for both sexes (Table 4). The best logistic regression models for males appeared to be (1) stream order and life history (including an interaction term), (2) gradient and stream order, (3) gradient and width, and (4) stream order and summer water temperature. For

females, the best models appeared to be (1) gradient and life history, (2) gradient only, (3) summer water temperature and life history, and (4) summer water temperature and stream order. Length-at-maturity models were generally stronger and fit the data better than did the age-at-maturity models; of the independent variable combinations presented in Table 4, age-at-maturity models outperformed length-at-maturity models in only 1 of 12 comparisons for males and in 2 of 11 comparisons for females. However, the independent variables had the same effect on age at maturity that they did on length at maturity.

Discussion

Our results indicate that length at maturity varies greatly between populations of Yellowstone cutthroat trout and that stream size and gradient explain much of this variation. The positive relationship we observed between length at maturity and size of spawning stream may in part represent the phenotypic plasticity of the populations of cutthroat trout we studied. Phenotypic plasticity is the capacity of a genotype to produce different phenotypes in different environments (Bradshaw 1965). Larger rivers are typically characterized by larger substrate, greater flows, and bedload movement of larger particles than is seen in smaller rivers. Larger spawners presumably should be bet-

TABLE 3.—Variation in size and age of immature and mature Yellowstone cutthroat trout and in estimates of length at 50% maturity (ML50) in study sites across southeastern Idaho.

Location	Sex	<i>n</i>	Length at maturity (mm)			Age at maturity	
			Largest immature	Smallest mature	ML50	Oldest immature	Youngest mature
Harkness Creek	M	19		97	97		2
	F	14	150	112	NA	3	3
Spring Creek	M	15	178	181	180	3	4
	F	14	175	212	193	3	4
North Fork Rapid Creek	M	22	190	136	145	3	2
	F	20	258	127	NA	4	2
Upper Crow Creek	M	26	217	127	181	3	2
	F	24	228	257	242	3	3
Canyon Creek	M	37	175	133	173	4	2
	F	22	207	275	257	4	4
West Pine Creek	M	32	240	178	184	3	3
	F	12	202	200	201	3	5
Dempsey Creek	M	24	198	125	155	3	2
	F	19	192	199	195	3	3
Lower Crow Creek	M	10	297	181	NA	3	3
	F	19	277	319	298	5	5
Tincup Creek	M	38	254	161	214	4	3
	F	19	271	232	263	4	3
Fall Creek	M	25	274	213	236	4	3
	F	28	255	202	261	7	3
South Fork Snake River	M	36	398	198	354	7	3
	F	44	382	173	311	5	5

TABLE 4.—Summary of logistic regression models relating Yellowstone cutthroat trout length at maturity (dependent variable) to stream attributes (independent variables). Coefficients with positive values indicate inverse relationships to length at maturity, those with negative values direct relationships. Standard errors are shown in parentheses; asterisks indicate coefficients that do *not* differ significantly from zero. The acronym AIC stands for Akaike's information criteria.

Variable	n	Constant	Length	Estimated coefficients		AIC	McFadden's Rho ²
				1st	2nd		
Male logistic regression models							
Gradient (Grad)	284	-6.389 (0.812)	0.022 (0.003)	1.359 (0.238)		285	0.29
Stream order (SO)	284	-2.205 (0.455)	0.029 (0.004)	-1.333 (0.204)		294	0.27
Average temperature (AvgT)	233	-1.654* (1.034)	0.009 (0.002)	-0.017* (0.068)		308	0.06
Width	284	-3.114 (0.489)	0.018 (0.003)	-0.046 (0.009)		332	0.17
Aspect	284	-1.453 (0.476)	0.013 (0.002)	-0.011 (0.003)		354	0.11
Elevation	284	0.994* (1.604)	0.010 (0.002)	-0.002 (0.001)		366	0.08
Conductivity	284	-1.854 (0.526)	0.011 (0.002)	-0.001* (0.001)		370	0.07
SO + AvgT	284	-1.162* (1.181)	0.028 (0.004)	-1.401 (0.237)	-0.061* (0.078)	239	0.28
Grad + SO	284	-4.925 (0.782)	0.030 (0.004)	0.821 (0.205)	-0.864 (0.213)	266	0.34
Grad + Width	284	-6.784 (0.846)	0.028 (0.004)	1.109 (0.215)	-0.043 (0.011)	269	0.33
Grad + Life History (LH)	284	-6.052 (0.834)	0.022 (0.003)	1.263 (0.490)	-0.284* (0.168)	284	0.29
SO + LH + SO-LH ^a	284	-1.990 (0.547)	0.032 (0.004)	-1.725 (0.398)	-1.548 (0.225)	262	0.35
Female logistic regression models							
Grad	235	-9.917 (1.243)	0.033 (0.004)	1.016 (0.154)		160	0.43
AvgT	183	-2.130* (1.714)	0.015 (0.003)	-0.145* (0.112)		176	0.21
LH	235	-6.015 (0.777)	0.023 (0.003)	-0.979 (0.215)		190	0.32
SO	235	-5.346 (0.699)	0.030 (0.005)	-0.777 (0.197)		193	0.31
Aspect	235	-4.111 (0.685)	0.020 (0.003)	-0.011 (0.004)		207	0.26
Elevation	235	-0.397* (2.020)	0.018 (0.003)	-0.003 (0.001)		208	0.25
Width	235	-5.550 (0.734)	0.022 (0.003)	-0.017 (0.008)		209	0.25
Conductivity	235	-4.103 (0.775)	0.018 (0.003)	-0.002* (0.001)		211	0.24
AvgT + LH	235	-0.819* (1.737)	0.027 (0.004)	-0.414 (0.128)	-1.877 (0.337)	131	0.43
SO + AvgT	235	-0.021* (1.718)	0.031 (0.006)	-0.974 (0.254)	-0.358 (0.125)	154	0.32
Grad + LH	235	-10.259 (1.329)	0.035 (0.005)	0.888 (0.159)	-0.675 (0.260)	155	0.46

^a The third estimated coefficient was 0.357 (0.145).

ter adapted to build redds in larger rivers (van den Berghe and Gross 1984; Beacham and Murray 1987) and negotiate greater flows during upstream migration (Brett and Glass 1973). The indirect relationship we observed between length at maturity and gradient appears to contradict the premise that larger spawning substrate favors larger spawners, given that stream slope is directly related to substrate size (Leopold et al. 1964). In our study, however, changes in gradient were probably more reflective of changes in stream size from headwater streams to larger downstream rivers than of actual changes in substrate particle size. Indeed, correlations (r) were high between gradient and stream width (-0.65) and gradient and stream order (-0.60).

That stream size was directly related to length at maturity contrasts with the findings of Gresswell et al. (1997), who argued that spawner length was not a direct function of stream size but that mean aspect more strongly influenced the spawner length than did stream size. We found no such relationship between stream aspect and length at maturity. These discrepancies probably result from

the environmental differences encountered by fish in our study in comparison with those of the Yellowstone Lake watershed. Gresswell et al. (1997) did not attribute the relationship they observed between aspect and spawner length to stream orientation and the stream's exposure to the sun. Rather, they argued that aspect determined stream location in the Yellowstone Lake watershed. Because cutthroat trout in the Yellowstone Lake system remain littorally segregated on the basis of tributary spawning locations and because environmental conditions vary throughout the lake, fish may have experienced different growth rates while in the lacustrine environment, which may have resulted in differences in spawner lengths between tributaries.

Conductivity, a factor that has been used as an index of productivity (Northcote and Larkin 1956; McFadden and Cooper 1962), was not strongly related to length at maturity, although it has been shown to be related to growth (McFadden and Cooper 1962) and growth has been shown to affect age at maturity (Schaffer and Elson 1975; Chen and Harvey 1994).

Our results suggest that length at maturity may be related more to the physical than to the physiochemical characteristics of a stream. However, just because other variables that we measured showed no relationship to length at maturity does not necessarily mean that they have no influence on fish maturation. For example, temperature metrics such as accumulated thermal units, or degree-days, which would have incorporated the time of year that Yellowstone cutthroat trout gonads ripen, may have correlated better with length at maturity than did mean summer water temperature. Additionally, we measured temperature over only one summer, but most mature fish we encountered went through at least 2 years of growth. Moreover, we did not examine numerous other factors that can influence reproductive life history traits, such as fish density (Peterman et al. 1986; Kaeriyama 1996), survival (Hutchings 1993), growth (Hutchings 1993, 1996; Chen and Harvey 1994), angling pressure (Saunders and Power 1970; Jensen 1971; Ricker 1981), and migration distance (Schaffer and Elson 1975; Roff 1991). Such factors may have had an influence on length at maturity that we did not account for. For example, stream size may actually have had no direct effect on length at maturity but instead may have mediated an indirect response in length at maturity by directly affecting fish growth. Indeed, there could have been numerous interactions between factors that affect length at maturity that our study was not designed to detect. Scarnecchia (1983) discussed the dangers of viewing variation in a particular life history trait such as age or length at maturity as an isolated response to one or two environmental factors and argued that such traits are best viewed in the context of the entire life history pattern of a species. We agree with this assertion and suggest further research to improve understanding of the factors that influence length at maturity in stream-dwelling salmonids.

Length at maturity appeared to be more predictable from physical stream attributes than was age at maturity. This difference was not surprising, given that reproductive success may be more related to size than age (see review in Roff 1992). Maturation in fish depends to some extent on the attainment of a physiologically critical size and may depend less on the age at which that size is achieved.

The South Fork Snake River Yellowstone cutthroat trout population differed from fish from other locations in almost every aspect, including longevity, age at maturity, length at maturity, and the

fact that females matured earlier than males. The latter difference may have resulted from differences in iteroparity between genders. Several of the large cutthroat trout captured in the South Fork Snake River were not ripe, possibly because they were skipping a year of spawning. We believe that most of the South Fork Snake River fish 350–400 mm long that we had classified as immature had in fact spawned previously and thus were not truly immature fish. The South Fork Snake River was the only location where this situation occurred. Despite these differences, models with or without South Fork Snake River data were very similar. It is likely that the differences stem from the fact that the South Fork Snake River is a much larger system than any other in our study but that the differences probably do not cause the relationships between most of the stream attributes and length at maturity to change appreciably.

The fact that the South Fork Snake River was our only data point from a large river leads us to suggest caution in applying our results (and equations) to other large rivers without other supportive information. However, within the constraints of the parameters we measured, the equations we developed should be applicable to a wide variety of locations when predicting the length at which Yellowstone cutthroat trout mature. Verification of the fit of the models to data from one or more untested streams would further substantiate our results. To date, we have been unable to locate any existing datasets that would allow us to test the predictability of our models.

We found that fish from resident sites matured at a smaller size than did those from migratory sites, the main difference occurring between 100 and 250 mm (Figure 2). In this size range, females from resident sites were nearly 10 times more likely to be mature than were females from migratory sites, and males from resident sites were twice as likely as males from migratory sites to be mature. Such differences agree with the assertion of Roff (1991) that migrant fish tend to grow more rapidly than residents by taking advantage of resources unavailable to resident fish but tend to mature later because of their need for more energy reserves to migrate back to the natal spawning areas.

That we found such large differences in length at maturity between resident and migratory fish suggests our categorization of study sites, although admittedly somewhat subjective, was probably correct. Nevertheless, our study design did not allow a full assessment of the differences between resident and migratory life histories and their im-

pact on length at maturity. First of all, our sample size for each life history behavior was purposefully low (four resident sites and seven migratory sites) because of the need to sacrifice fish to obtain the necessary maturity and age data. In addition, probably both resident and migratory fish were present in at least some migratory sites, evidenced by the fact that mature males shorter than 150 mm were captured at the upper Crow Creek and Canyon Creek sites. The interaction of resident and migratory life history behaviors within a particular system is a subject that has been little studied in salmonid populations, although advances in the use of geochemical markers on otoliths for stock identification or for reconstructing migration history (see review in Campana 1999) promise to allow better assessment of such interactions.

Male Yellowstone cutthroat trout outnumbered females at most of the sites in our study; however, because sample size was relatively low for most study sites (<60 fish at all but one location) and because confidence limits around sex ratios overlapped at 8 of 11 sites, we cannot conclude the sex ratio was skewed towards males. Thurow et al. (1988) and Gresswell et al. (1997) found that female Yellowstone cutthroat trout were more numerous than males in migratory spawning populations. However, those studies involved relatively large fluvial and adfluvial populations that were captured during migration and did not include data from smaller streams where resident males may be more common. Such may have been the case in our study at the three locations where males outnumbered females. Differences in sex ratios typically indicate a mortality differential between sexes, usually reflecting angling effects (McFadden 1961) or a shorter life span resulting from earlier attainment of sexual maturity (Hoar 1957). Males did mature earlier than females at almost every location in our study, which is common in salmonid populations (McFadden 1961; Lachance and Magnan 1990), but such a difference should result in a greater mortality rate in males and thus a skew toward having more females in the population. Longevity between males and females was essentially equal in our study, providing further evidence that there was no difference in mortality between genders or in the sex ratio.

In general, the relationship of fish length to fecundity was strong, but certain aspects, such as the South Fork Snake River data, were weak. We found no evidence of a difference between resident or migratory regression equations, thus indicating that, at least in the streams we studied, females in

headwater streams with resident life histories were not producing any fewer eggs per unit body length than were females in larger systems with migratory life histories. In contrast, Downs et al. (1997) found that for westslope cutthroat trout *O. clarki clarki*, lacustrine-adfluvial populations had steeper slopes than did resident populations; they suggested that length–fecundity relationships be developed for each life history type and perhaps for each population.

Conclusions

The models we developed are simple and could explain much of the variation in length at maturity for the rivers we studied, suggesting that one can predict the size at which Yellowstone cutthroat trout mature in a variety of systems according to easily obtained physical stream attributes. Additional research is needed to further elucidate the factors that affect size at maturity in trout populations. Nevertheless, by applying our demographic results and the models we developed to the abundance and stock structure data already available throughout southeastern Idaho (K. Meyer, unpublished data), we should be able to estimate effective population size, reproductive potential, and other risk assessment parameters within individual cutthroat trout populations. Such estimates would be useful for managers concerned with prioritizing populations of Yellowstone cutthroat trout for conservation.

Acknowledgments

We thank W. C. Schrader for collecting fish from the South Fork Snake River and W. C. Schrader and L. Mamer for assistance in processing the fish in the laboratory. G. Labar and C. Downs reviewed an earlier version of the manuscript and provided helpful comments. Critiques from three anonymous reviewers also improved the manuscript substantially. This project was funded by the Bonneville Power Administration and by funds from Federal Aid in Sport Fish Restoration, project F-73-R-23.

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