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[Article]

Sex Ratio, Fecundity, and Models Predicting Length at Sexual Maturity of Redband Trout in Idaho Desert Streams

DANIEL J. SCHILL* AND GEORGE W. LABAR
Department of Fish and Wildlife Resources, University of Idaho, Post Office Box 441136, Moscow, Idaho 83844, USA

ELIZABETH R. J. M. MAMER AND KEVIN A. MEYER
Idaho Department of Fish and Game, 1414 East Locust Lane, Nampa, Idaho 83686, USA

Abstract.—Factors affecting length at maturity and other important reproductive characteristics have not been investigated for Idaho redband trout *Oncorhynchus mykiss gairdneri* residing in desert streams. Prespawning redband trout were collected from nine streams, and estimates of length at sexual maturity, median age at maturity, sex ratio, and fecundity were developed along with models predicting length at maturity from physical stream conditions. Males first matured 1–2 years prior to females in seven of nine streams, while in the remaining two populations a few fish of both sexes first matured at the same age. Total length (TL) was strongly related ($P < 0.0004$; $n = 49$) to fecundity (F) via the curvilinear function $F = 0.0002\mathrm{TL}^{2.5989}$. Redband trout residing in Idaho desert streams appeared to be less fecund than several other stream-dwelling populations of Pacific salmon *Oncorhynchus* spp. The best estimate of sex ratio for all fish, including immature fish, was 1:1. The best two-variable logit model for predicting length at maturity in males included stream order and conductivity, whereas the best model for females included drainage area above the sample site and stream gradient. These models can be used by fishery managers to estimate the total number of mature redband trout present in Idaho streams and, in combination with other data, can be used to approximate effective population sizes across southwestern Idaho desert stocks.

Behnke (1992) defined native rainbow trout *Oncorhynchus mykiss* populations in the Columbia River basin east of the Cascade Mountains as redband trout *O. mykiss gairdneri*. Those residing in desert environments are perhaps the least studied of western salmonids (Schill et al. 2007). Basic reproductive data, including size at maturity, age at maturity, fecundity, and sex ratio, have not been collected for redband trout stocks residing in desert basins of Idaho. Outside the state, the sole study appears to be that of Kunkel (1976), who reported a maturity schedule and sex ratio for a stock of redband trout in an Oregon stream and a pooled fecundity relationship for a small number of fish ($n = 16$) from three streams.

The redband trout is considered a sensitive species in Idaho by a number of agencies, including the Idaho Department of Fish and Game (IDFG), U.S. Forest Service, and Bureau of Land Management (Zoellick and Cade 2006). A petition to protect redband trout residing in the Snake River upstream from Brownlee Reservoir under the federal Endangered Species Act (ESA) was submitted in 1995, although the petition was not found to be warranted (U.S. Office of the Federal Register 1995). Regardless of their ESA status, the present lack of life history information for redband trout residing in desert environments prevents an informed assessment of their general status.

Sex ratio, fecundity, and fish maturity status, including length and age at maturity, all play important roles in salmonid population dynamics (Scott 1962; McFadden et al. 1965) and are thus important factors in species or subspecies status assessments (Rieman and Allendorf 2001; Meyer et al. 2006; Swenson et al. 2007). Recently, a series of logistic regression models that predict length at maturity for Yellowstone cutthroat trout *O. clarkii bouvieri* across Idaho streams as a function of physical stream attributes were developed (Meyer et al. 2003). Meyer et al. (2006) subsequently used those models in combination with other demographic and abundance data to approximate effective population size (Wright 1938) for Yellowstone cutthroat trout populations across southeast Idaho. To our knowledge, no method exists for predicting maturity status of individual fish in desert redband trout populations based on habitat variables; therefore, attainment of such an approach became our chief aim.

As was stated by Downs et al. (1997) for westslope cutthroat trout *O. clarkii lewisi*, a general goal of this study was to provide parameter estimates for modeling persistence probabilities and genetic risk in a stream

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* Corresponding author: dan.schill@idfg.idaho.gov

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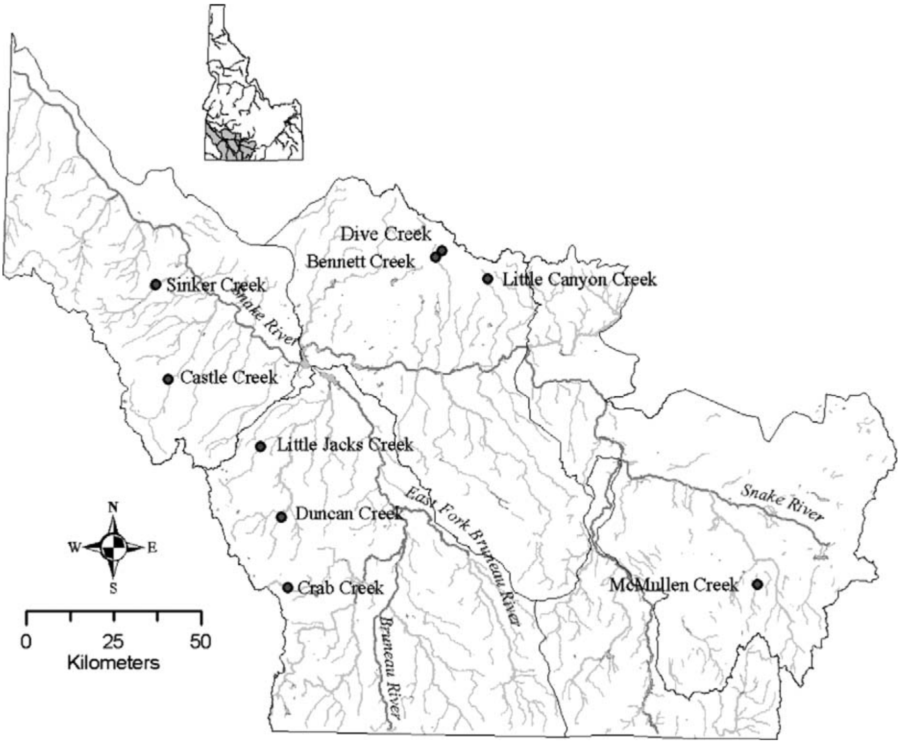

FIGURE 1.—Study area and distribution of nine redband trout study streams across southern Idaho. Inset shows location of study area within the state.

salmonid—in our case, redband trout. Such modeling efforts allow fisheries managers to better assess current population status and genetic risk (Hilderbrand and Kershner 2000; Rieman and Allendorf 2001). The specific objectives of the present study were to (1) quantify sex ratio and fecundity in redband trout populations, (2) characterize variation in redband trout length and age at sexual maturity in select streams, and (3) develop models for predicting length at maturity for redband trout across the landscape using readily obtained physical stream attributes.

Study Area

The study area includes streams in the Snake River drainage upstream from its confluence with the Owyhee River to Shoshone Falls, Idaho, excluding the Wood River system. The study area is vegetated primarily with shrub-steppe communities dominated by big sagebrush *Artemesia tridentata*. Streamside vegetation is typically dominated by willows *Salix* spp. (Zoellick and Cade 2006). Most of the study area receives less than 30 cm of rainfall per year (IDWR 2004). Such xeric basins dominated largely by sagebrush communities have been referred to as high desert (Li et al. 1994). Many streams in the study area become intermittent during midsummer at lower elevations, where complete channel desiccation is common (Zoellick 1999).

Nine streams believed to contain native redband trout populations across their longitudinal distribution in the study area were identified (Figure 1). Streams were selected based on stream size, known or suspected differences in water temperature regimes, and perceived ability of the redband trout populations to withstand a small amount of lethal sampling. Study streams varied in width from 1.2 to 2.7 m, and elevation at sampling sites ranged from 942 to 1,749 m (Table 1). Water conductivity varied from 33 to 315 μS/cm.

Native fishes found in sympatry with desert redband trout within one or more of the study streams included the mountain whitefish *Prosopium williamsoni*, bridgelip sucker *Catostomus columbianus*, mottled sculpin *Cottus bairdii*, shorthead sculpin *Cottus confusus*, redside shiner *Richardsonius balteatus*, speckled dace *Rhinichthys osculus*, chiselmouth *Acrocheilus alutaceus*, and northern pikeminnow *Ptychocheilus oregonensis*. Anadromous stocks of steelhead (anadromous

TABLE 1.—Physical attributes and electrofishing sample sizes for redband trout in nine southern Idaho streams, March–April 2001.

Creek	*n*	Elevation (m)	Stream order (1:100,000)	Conductivity (μS/cm)	Gradient (%)	Stream width (m)	Drainage area (km^2)
Bennett	32	1,420	2	63	1.6	1.6	36
Castle	69	1,085	3	105	2.7	2.2	316
Crab	45	1,749	1	63	2.1	1.2	21
Dive	42	1,419	1	51	2.9	1.6	20
Duncan	75	1,374	2	95	1.7	2.0	55
Little Canyon	41	1,561	2	33	3.8	1.6	51
Little Jacks	69	1,088	3	96	1.3	2.2	192
McMullen	56	1,310	3	58	2.0	2.0	55
Sinker	55	942	4	315	2.5	2.7	217

rainbow trout) and Chinook salmon *O. tshawytscha* were once found in some of the study streams (Miller and Miller 1948; Fulton 1968) but were eliminated due to the construction of Swan Falls Dam on the mainstem Snake River in 1901. The brown bullhead *Ameiurus nebulosus*, a nonnative species, was present in one study stream.

Methods

Fish collection and physical stream data.—To ensure accurate assessment of maturity status, redband trout were collected from study streams immediately before the spawning season by means of DC backpack electrofishing during March and April 2001. Target sample size was 50–75 fish/stream, distributed evenly across the observed length range where possible (Table 1). The length of stream sampled depended on the amount of effort required to approach the target sample size but ranged from 300 to 600 m. Upon collection, 484 fish were euthanized with an overdose of tricaine methanesulfonate (MS-222), placed on ice, transported to the laboratory, and frozen for later analysis.

A suite of physical stream attributes, including four characteristics related to stream size, was measured to assess possible effects on maturity schedules of redband trout. Stream width (nearest 0.1 m) was calculated from a mean of 10 measurements taken at points equidistant throughout the sampled reach. Stream order (Strahler 1964) was determined from 1:100,000-scale land status maps. Stream drainage area above the lowermost end of each sample site was calculated using digitized U.S. Geological Survey (USGS) 1:24,000-scale topographic maps and ArcGIS version 9.1 software (ESRI 1998). Stream gradient was measured using All Topo Maps version 2.1 software (iGage 1998).

Other features that were likely to affect maturity schedule were also measured at sample sites. Conductivity (μS/cm) was measured with a handheld digital meter accurate to within 2%. Elevation, a surrogate for temperature (Rieman and McIntyre 1995; McGrath et al. 2008), was determined at the lower end of each stream reach sampled using 1:24,000-scale USGS topographic maps and Universal Transverse Mercator coordinates obtained from a handheld Global Positioning System unit.

Laboratory analysis.—Age of redband trout was determined using sagittal otoliths (Williams and Bedford 1974). Prior to otolith removal (Schneidervin and Hubert 1986), fish were thawed, weighed to the nearest 0.01 g, and measured to the nearest millimeter in total length (TL). Digital images of whole otoliths immersed in water were taken under a compound microscope (40× magnification) using oblique reflected light. Otoliths were subsequently embedded in epoxy resin and sectioned transversely (0.60-mm width) through the nucleus along the dorsoventral plane (Chilton and Beamish 1982). Sections were covered with type B immersion oil, and digital images were recorded. Ages were initially assigned by two independent readers who had no prior knowledge of the lengths of sampled fish; readers viewed sectioned otolith images as the primary structure and whole-otolith images as corroboratory structures. Opaque zones were counted as annuli, assuming that the fish had completed their current year of life on 1 January (Devries and Frie 1996; Hining et al. 2000). To improve accuracy, different age estimates obtained by the two readers for the same fish were reconciled in joint readings to produce a final age estimate (Buckmeier 2002).

Sex and maturity status were determined by visual examination of ovaries and testes as described by Strange (1996) and Downs et al. (1997). During necropsies, a small number of females ($n = 6$) from Little Jacks Creek contained well-developed eggs, but regression of the entire egg mass was occurring (Scott 1962). Although these fish appeared to be large enough to spawn during the ensuing spring spawning season, they were classified as immature. In addition, a total of 55 immature fish across all study sites had gonads that were too underdeveloped to allow differentiation of sex (mean TL = 78.4 mm; range = 45–118 mm). Such fish were excluded from further analysis.

Fecundity was evaluated by obtaining actual counts of developed eggs present in 49 prespawn females that were collected from the study streams. A predictive length–fecundity relationship was developed by pooling data across sampling sites (Downs et al. 1997; Meyer et al. 2003).

Sex ratio estimates, expressed as the percentage of females in each population, were calculated for fish collected from all study streams. Two sex ratio estimates were made for each population: (1) among mature redband trout only and (2) among all redband trout for which sex could be determined, including immature fish. Ninety-five-percent confidence intervals (CIs) were calculated for both estimates on individual streams as described by Fleiss (1981). Sex ratio estimates with 95% CIs that did not overlap 50% were considered to be significantly different from a ratio of 1:1 (i.e., 50% female).

On Little Jacks Creek, we compared the sex ratio estimate from a single location with that from a more dispersed sample. A total of 276 redband trout were collected and euthanized from four 200–500-m locations scattered throughout the Little Jacks Creek drainage. These samples were collected between 29 September and 29 October 2003 from the sole tributary, Ox Prong Creek, and from three sites on Little Jacks Creek about 5, 13, and 22 km downstream from the confluence of Ox Prong Creek. Sex ratios and associated 95% CIs were calculated for this combined sample as described above.

Maturity modeling.—We first sought to characterize variation in length and age at maturity for redband trout across a variety of streams in the study area. For length at maturity, this was done by estimating the length at which the probability of being mature was 0.50 (ML50) using logistic regression (Meyer et al. 2003). Separate estimates of ML50 were developed for each stream population by sex. Statistical validity of regression models was assessed using the Hosmer–Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989) and an α value of 0.05. For each logistic regression model constructed, McFadden's rho-squared (ρ^2) statistic was calculated to evaluate the predictive strength of the model, with ρ^2 values between 0.2 and 0.4 considered acceptable (Hensher and Johnson 1981; Meyer et al. 2003).

This approach was not as useful for characterization of age at maturity since in many cases statistically significant logistic regression models could not be developed. Thus, only the oldest immature and youngest mature fish collected in each stream are reported for each sex separately.

Physical stream data and maturity information were then used to construct a broader model for predicting length at maturity in Idaho redband trout populations. Modeling efforts were limited to those predicting length at maturity because length data could conceivably be available from hundreds of sites with minimal effort, whereas age data are available from relatively few sites. The physical stream attributes described previously were all considered possible independent variables in a multiple logistic regression analysis. Potential combinations of independent variables with correlations greater than 0.70 were removed from consideration (Tabachnick and Fidell 1989). If the correlation coefficient for two such variables in study streams exceeded this threshold, we removed the variable for which data were more difficult or costly to obtain (Meyer et al. 2003).

The physical stream attributes were all considered as possible independent variables in logit model construction. All physical attribute variables were continuous. Maturity status was considered a binary dependent variable (0 = immature, 1 = mature), and individual fish were considered the sample unit (Meyer et al. 2003). Statistical significance and strength of logit models were assessed for individual stream models, and those not meeting the Hosmer–Lemeshow goodness-of-fit test were discarded. Akaike's information criterion (AIC; Akaike 1969) was used to pick the best of the remaining models, and the weight of evidence for the model selected was evaluated by calculating Akaike weights (w_i; Burnham and Anderson 1998). The rescaled coefficient of determination ($\check{R}^2$; Nagelkerke 1991) was calculated to quantify how much variance could be explained by candidate models. Classification error rates of statistically valid models were also evaluated in Statistical Analysis System software by using the CTABLE option (SAS 2000).

Results

Length and Age at Maturity

We observed age-related differences in maturity schedules in small (first- and second-order) versus large (third- and fourth-order) streams. In both small and large streams, a sizeable fraction of age-2 males (38–53%) were mature. However, only 12% of age-2 females were mature in large streams, while none were mature in small streams. For both sexes at ages 3–5, maturity rates in large streams were lower than those in small streams (Figure 2).

Males generally matured earlier in life than females. Based on observations of the youngest mature fish, males began to mature 1–2 years earlier than females in

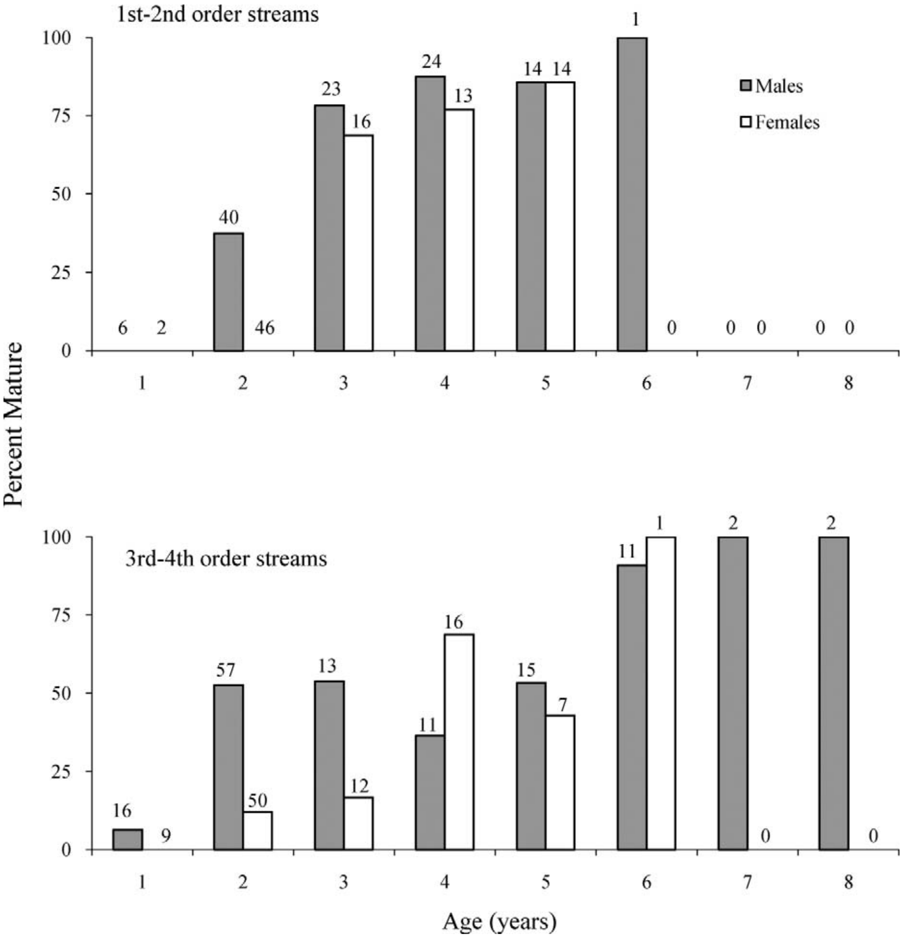

FIGURE 2.—Percentages of male and female redband trout that were mature at age in nine southern Idaho streams between 20 March and 5 April 2001. Numbers above bars are sample sizes.

seven of nine streams (Table 2). In the remaining two instances, McMullen and Little Jacks creeks, both sexes first matured at age 2 and age 4, respectively.

Males matured at smaller lengths than females, while both sexes matured at greater lengths in larger streams. Estimates of ML50 for males were smaller than those for females in all instances except Duncan Creek (Table 2). Six percent ($n = 16$) of males smaller than 100 mm TL were mature in first- and second-order streams (Figure 3). No females matured in this length range in any stream.

Fecundity and Sex Ratio

Fecundity varied markedly for individual redband trout at a given age. Mean fecundities at age varied from 116 to 149 eggs/female for age-3–5 fish in small streams and from 190 to 366 eggs/female for age-2–4 fish in large streams. Egg counts in two age-5 females residing in the smallest stream (Crab Creek; mean stream width = 1.2 m) were exceptionally low (range = 38–44 eggs/female). Total length was strongly related ($P < 0.0004$; $n = 49$) to fecundity (F) when data were pooled across all sites via the curvilinear function $F = 0.0002\text{TL}^{2.5989}$ (Figure 4), but there was considerable variation in fecundity at given lengths ($r^2 = 0.57$).

Sex ratio of redband trout collected during spring sampling differed when considering all fish that could be sexed versus only those categorized as mature. For all redband trout that could be sexed (including immature fish), the sex ratio expressed as the percentage of females ranged from 34% to 54% across all study sites and averaged 44%; 95% CIs overlapped 50% at all individual sites but did not include 50% when considering all fish combined (Table 3). When only redband trout classified as mature were considered, the average sex ratio of spring-caught fish

TABLE 2.—Variation in size (total length [TL]) and age (years) of 421 immature and mature redband trout and variation in estimates of TL at which the probability of being mature was 50% (ML50) at study sites across nine southern Idaho streams in 2001 (McFadden's rho-squared [ρ^2] evaluates the predictive strength of each logistic regression model).

				TL at maturity (mm)					
						Logistic regression		Age at maturity	
Creek	Date sampled	Sex	*N*	Largest immature	Smallest mature	ML50	McFadden's ρ^2	Oldest immature	Youngest mature
Bennett	22 Mar	M	17	137	126	128	0.57	3	2
		F	14	146	145	147	0.69	2	3
Castle	20 Mar	M	32	195	143	174	0.39	4	2
		F	28	185	156	178	0.58	4	3
Crab	2 Apr	M	20	128	83	107	0.38	5	2
		F	16	128	117	125	0.58	5	4
Dive	23 Apr	M	19	128	113	121	0.70	2	2
		F	19	148	140	148	0.68	2	3
Duncan	21 Mar	M	36	183	121	141	0.36	4	2
		F	23	135	130	133	0.86	3	3
Little Canyon	21 Mar	M	16	133	101	121	0.56	3	2
		F	19	130	128	129	0.79	3	3
Little Jacks	20 Mar	M	42	238	153	129	0.30	6	4
		F	21	195	153	177	0.36	5	4
McMullen	4 Apr	M	25	161	137	149	0.51	3	2
		F	19	170	157	167	0.73	5	2
Sinker	23 Mar	M	28	150	128	136	0.69	2	1
		F	27	166	162	164	0.73	2	2

declined to 30% female (95% CI = 23–37% female); 95% CIs for individual streams did not include 50% in five streams (Table 3).

A difference in sex ratio when comparing the same two groups was not apparent in the more dispersed fall sample from Little Jacks Creek. For all sexed redband trout, including immature fish, the sex ratio was exactly 50% female ($n = 276$; 95% CI = 44–56% female). For mature fish only, the sex ratio increased slightly to 56% female, but this estimate was not statistically different ($n = 117$; 95% CI = 47–66% female).

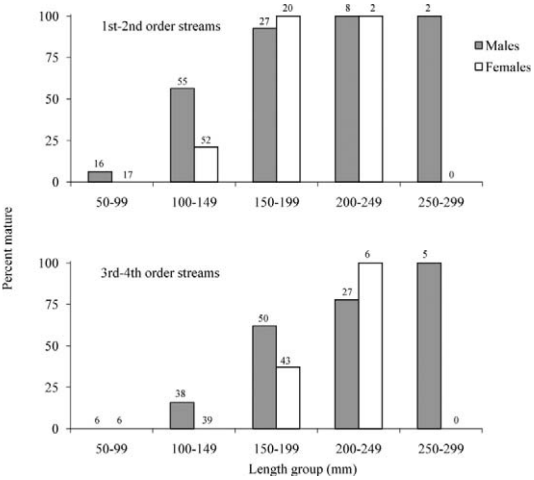

FIGURE 3.—Percentages of male and female redband trout that were mature at length (total length, mm) in nine southern Idaho streams sampled during spring 2001. Numbers above bars are sample sizes.

Maturity Modeling

Considerable variation in length at initial maturity, age at initial maturity, and ML50 was observed across the study streams. Overlap in size of mature and immature redband trout occurred for both sexes in all streams (Table 2). Logistic regression relating length to maturity status (mature or immature) resulted in statistically useful regressions in all 18 cases attempted based on the Hosmer–Lemeshow goodness-of-fit test. All models were considered satisfactory

TABLE 3.—Sex ratio (SR) expressed as percentage of females among redband trout collected from nine streams in southwestern Idaho, 20 March–5 April 2001 (CI = confidence interval).

	All sexed fish			Mature fish only		
Creek	*n*	SR (%)	95% CI	*n*	SR (%)	95% CI
Crab	37	43	27–60	20	35	14–56
Dive	38	50	34–66	14	21	0–43
Bennett	31	45	27–63	14	21	0–43
Duncan	65	38	26–51	42	40	25–56
Little Canyon	35	54	37–71	13	31	5–56
Castle	60	47	34–60	24	29	11–48
Little Jacks	64	34	37–68	25	28	10–46
McMullen	44	43	28–58	15	27	4–50
Sinker	55	49	36–63	23	22	5–39
Total	429	44	39–49	190	30	23–37

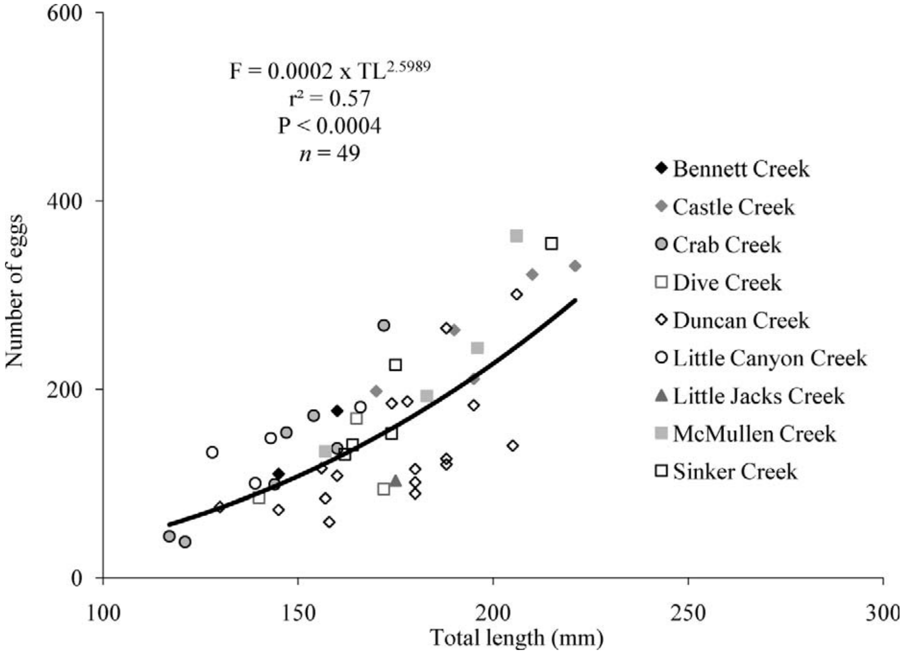

FIGURE 4.—Relationship between total length (TL) and fecundity (*F*) of female redband trout residing in nine southern Idaho streams between 20 March and 5 April 2001.

TABLE 4.—Summary of logistic regression models relating redband trout total length (TL; mm) at maturity (dependent variable) to Idaho stream attributes (independent variables; cond = conductivity; order = stream order; drain = drainage area; grad = gradient; elev = elevation; width = stream width). Coefficients with positive values indicate inverse relationships to TL at maturity, and those with negative values indicate direct relationships. Standard errors are shown in parentheses; asterisks indicate coefficients that do *not* differ significantly from zero. Akaike's information criterion (AIC), change in AIC (ΔAIC) between the given model and the best model, Akaike weight (w_i), rescaled R^2 (R^2), and percent correct classification are shown.

				Estimated coefficients		
Variable	*n*	Constant	TL	1st	2nd	3rd
Male logistic regression models						
Cond + order + (cond × order)	240	−2.008 (1.445)	0.057 (0.007)	−0.037* (0.021)	−2.53 (0.503)	0.013 (0.005)
Drain + grad + (drain × grad)	240	−6.714 (1.385)	0.059 (0.008)	−0.041 (0.009)	−0.082* (0.432)	0.012 (0.003)
Grad + elev + (grad × elev)	240	−28.97 (5.226)	0.054 (0.007)	6.848 (1.863)	0.015 (0.003)	−0.005 (0.001)
Grad + order + (grad × order)	240	−1.792* (1.687)	0.053 (0.007)	−1.517 (0.735)	−2.750 (0.667)	0.824 (0.282)
Order	240	−4.238 (0.734)	0.047 (0.006)	−0.998 (0.020)		
Elev	240	−11.66 (1.803)	0.044 (0.006)	0.004 (0.001)		
Drain	240	−5.347 (0.778)	0.044 (0.006)	−0.009 (0.002)		
Width	240	−2.419 (0.864)	0.040 (0.005)	−1.729 (0.452)		
Grad	240	−6.672 (1.030)	0.035 (0.005)	0.712 (0.245)		
Cond	240	−4.601 (0.697)	0.032 (0.005)	−0.0004* (0.002)		
Female logistic regression models						
Drain + grad + (drain × grad)	189	−12.981 (2.935)	0.112 0.189	−0.083 (0.020)	−0.869* (0.642)	0.026 (0.007)
Grad + order + (grad × order)	189	−4.196* (3.192)	0.104 0.017	−3.270 (1.244)	−5.297 (1.315)	1.518 (0.512)
Grad + elev + (grad × elev)	189	−47.419 (9.738)	0.108 0.018	8.354 (2.975)	0.021 (0.006)	−0.005 (0.002)
Cond + order	189	−11.444 (1.968)	0.103 0.017	0.012 (0.004)	−2.490 (−0.492)	
Order	189	−10.100 (1.674)	0.090 0.014	−1.742 (0.328)		
Elev	189	−24.130 (3.677)	0.088 0.014	0.008 (0.001)		
Drain	189	−10.925 (1.639)	0.078 0.012	−0.015 (0.003)		
Width	189	−5.904 (1.447)	0.076 0.011	−3.254 (0.730)		
Cond	189	−8.703 (1.338)	0.056 0.009	−0.006 (0.002)		
Grad	189	−10.907 (1.924)	0.058 0.010	0.535* (0.335)		

based on the minimum ρ^2 guideline of 0.2–0.4 (Table 2). The predicted ML50 ranged from 107 to 174 mm for males and from 125 to 178 mm for females. Overlap in age of mature and immature redband trout occurred for both sexes at all but two study sites, Bennett and Dive creeks, where no overlap occurred for females.

A number of single-variable models successfully related redband trout maturity status to physical stream attributes across the study streams. Overall, the models for females were stronger than those for males; $\check{R}^2$ values ranged from 0.46 to 0.67 for females and ranged from 0.37 to 0.49 for males (Table 4). Stream order was the best single-variable model for predicting maturity for both sexes. These models resulted in the lowest AIC values and the highest $\check{R}^2$ values and also produced high correct classification rates. For both sexes, models incorporating elevation produced the next-best models, followed by models that included drainage area above the sampling site.

The addition of a second independent variable improved models for both sexes, but gains in $\check{R}^2$ and classification rate were relatively small. The best two-variable model for males included conductivity, stream order, and an interaction term (Table 4). The next-best model for males included drainage area, gradient, and an interaction term. The same two sets of variables produced the best models for females, but the model that included drainage area, gradient, and an interaction term was ranked highest (i.e., had the lowest AIC value and the highest $\check{R}^2$ value; Table 4). The resultant regression equations describing the best models for each sex are as follows:

Males:

$$p = 1 \div (\exp\{-[-2.008 + 0.057(L_{\mathrm{M}}) - 0.037(\mathrm{cond}) - 2.530(\mathrm{order}) + 0.013(\mathrm{cond} \times \mathrm{order})]\} + 1)$$

Females:

$$p = 1 \div (\exp\{-[-12.981 + 0.112(L_{\mathrm{F}}) - 0.083(\mathrm{drain}) - 0.869(\mathrm{grad}) + 0.026(\mathrm{drain} \times \mathrm{grad})]\} + 1),$$

where p = probability of being mature, L_{M} = length of a prospective male, L_{F} = length of a prospective female, cond = stream conductivity, order = stream order, drain = drainage area, and grad = stream gradient.

These two models explained 56% and 73% of the variation in length at maturity for males and females, respectively, and correctly classified maturity in nearly

TABLE 4.—Extended.

Variable	AIC	ΔAIC	w_i	$\check{R}^2$	Classification (% correct)
Male logistic regression models					
Cond + order + (cond × order)	209	0	0.716	0.56	77
Drain + grad + (drain × grad)	211	2	0.263	0.56	79
Grad + elev + (grad × elev)	217	8	0.013	0.54	78
Grad + order + (grad × order)	218	9	0.008	0.54	79
Order	227	18	0.000	0.49	76
Elev	233	24	0.000	0.47	77
Drain	236	27	0.000	0.46	76
Width	242	33	0.000	0.43	77
Grad	250	41	0.000	0.40	75
Cond	259	50	0.000	0.37	73
Female logistic regression models					
Drain + grad + (drain × grad)	99	0	0.735	0.73	89
Grad + order + (grad × order)	102	3	0.164	0.71	85
Grad + elev + (grad × elev)	104	5	0.060	0.71	87
Cond + order	105	6	0.037	0.70	88
Order	110	11	0.003	0.67	87
Elev	112	13	0.001	0.66	87
Drain	123	24	0.000	0.61	85
Width	129	30	0.000	0.59	84
Cond	152	53	0.000	0.47	80
Grad	154	55	0.000	0.46	81

8 of every 10 males and 9 of every 10 females (Table 4). Based on calculated w_i values, the weight of evidence in favor of these models being the best among those considered given the data are strong (Table 4). Models including drainage area and conductivity produced the next-best models. Models containing more than two independent variables were complicated by interaction effects and were not constructed.

Discussion

In the present study, length at maturity and age at maturity varied substantially across the landscape, a finding that has been observed elsewhere. Jonsson and L'Abeé-Lund (1993) reported clinal variation in age at maturity for anadromous brown trout *Salmo trutta* in northern Europe. Smaller-scale variation in age and size at maturity among nearby streams has also been reported for stream-dwelling brown trout (Olsen and Vollestad 2005) and for Yellowstone cutthroat trout (Meyer et al. 2003). Brown trout from infertile streams were older at first maturity relative to those in fertile waters, and maturation was dependent on both size and age (McFadden et al. 1965).

In our study streams, for a given length and age, male redband trout typically matured earlier in life and at a smaller size than did females. In terms of both length at first maturity and ML50, male redband trout matured earlier than females in eight of nine streams. In over two-thirds of the streams, some males matured at earlier ages than did females. These same general relationships have been reported in past literature reviews for a variety of rainbow trout populations (McAfee 1966; Scott and Crossman 1973). For all streams combined, 50% of age-2 males were mature compared with only 6% of the females. In the only previous study estimating maturity schedules in redband trout, Kunkel (1976) reported that 12.2% of age-2 males and 1.5% of age-2 females were mature in Threemile Creek, Oregon.

Among both male and female redband trout in the larger streams, a fraction of individuals appeared to defer spawning until age 6–7 or alternatively did not spawn annually (Figure 2). In small (first- and second-order) streams, virtually all fish larger than 150 mm were sexually mature, but in large (third- and fourth-order) streams 22% of males in the 200–249-mm size-class had not yet matured (Figure 3). Redband trout in this size-class were well above the ML50 estimates for individual streams (Table 2) and should have been mature if annual repeat spawning is always the normal case. In a California rainbow trout population, repeat spawners in Kiln Meadow Tributary comprised 25–28% of the run (Erman and Hawthorne 1976).

TABLE 5.—Fecundity (eggs/female) at length for several salmonid populations, including redband trout in southern Idaho streams (present study).

	Population			
Mean length (mm)	Westslope cutthroat trout (Montana)[a]	Yellowstone cutthroat trout (Idaho)[b]	Redband trout (Oregon)[c]	Redband trout (present study)
172	227	245	184	129
200	346	343	272	191
230	459	473	391	278

[a] Table 1 of Downs et al. (1997), corrected to total length.
[b] From Figure 4 of Meyer et al. (2003).
[c] From the length–fecundity formula of Kunkel (1976).

Redband trout examined during this study appeared to be less fecund at a given length than those in several other small stream-dwelling *Oncorhynchus* spp. populations (Table 5). Female redband trout in Idaho contain 55–60% as many eggs as similar-sized westslope cutthroat trout residing in two small Montana headwater streams (Downs et al. 1997). Differences of nearly identical magnitude (53–59%) were observed between desert redband trout and resident Yellowstone cutthroat trout of similar size (Meyer et al. 2003). Kunkel (1976) presented a length–fecundity equation for a small sample of pooled redband trout from Threemile, Buck, and Rattlesnake creeks in Oregon ($n = 16$, $r^2 = 0.94$). Redband trout in southwestern Idaho contained about 70% of the number of eggs as the redband trout studied by Kunkel (1976; Table 5). Future studies should re-examine fecundity in the study streams to verify the present estimates. If fecundity levels are indeed this low over multiple years, this finding could have demographic implications.

There are no published fecundity estimates for other rainbow trout stocks maturing at sizes reported in the present study. The mean fecundity of all females in this study was 218 eggs/female, while Scott and Crossman (1973) and Carlander (1969) reported that fecundity of rainbow trout may be as low as 200 eggs/female, or nearly five times the average egg count (41 eggs/female) observed in the smallest two redband trout in Crab Creek (mean TL = 119 mm).

The overall sex ratio reported in our study differed depending on which sample was being used in the calculations. The sex ratio of all redband trout that could be reliably sexed, including immature fish, was roughly 50% female regardless of the data used (pooled spring samples across multiple streams versus extensive fall sampling on a single stream). However, when only mature fish were considered, the sex ratio of the pooled sample was about one-third female, while the sex ratio of the intensive sample from Little Jacks

Creek remained near 50% female. Sex ratio in salmonids may differ longitudinally along a stream (Meyer et al. 2003; Rodnick et al. 2008), and our own concern about estimating sex ratio from short stream sections was the impetus for sampling along the length of Little Jacks Creek. While it may be defensible to state that sex ratio of mature redband trout in this study was about one-third to one-half female, we believe the latter estimate is more credible because the associated sampling was much more representative of the entire drainage. We suggest that any future investigation into sex ratio in these or similar streams should involve collection of samples along a greater proportion of the study streams than was done in the spring sampling effort.

A possible limitation of this study is the potential effect of past hatchery stocking on the redband trout study populations, although we do not consider the likelihood of significant introgression levels to be great. No study streams are currently stocked with hatchery rainbow trout, typically coastal rainbow trout *O. mykiss irideus*, but stocking did occur historically in five of the nine study streams, mostly before 1968. Genetic tools available to assess introgression between the interior rainbow trout subspecies and coastal rainbow trout have only recently become available (Sprowles et al. 2006; Brunelli et al. 2008). In a companion study conducted by the IDFG genetics laboratory, a subsample of redband trout ($n = 328$) collected for growth analysis from our nine study streams was screened with a combination of single-nucleotide polymorphisms and microsatellite DNA markers. Analysis suggests that redband trout from eight of the nine study streams were pure native redband trout and that six trout from the remaining stream (Little Canyon Creek) were assigned as "unknown," indicating either pure redband trout or low levels of introgression (M. Campbell, IDFG, unpublished data). Thus, there is quantitative evidence that the genetic influence of hatchery rainbow trout on the redband trout collected for this study is very low.

This effort represents the first attempt to build models that predict maturity status of redband trout by using fish length and physical stream attributes. Our results were similar to those reported by Meyer et al. (2003) for Yellowstone cutthroat trout in that models for females were stronger than those for males, but our study differs from theirs in that stream order provided the best predictive results for single-variable models describing both sexes. For redband trout, we found consistency in two-variable models for both sexes, with the paired variables of conductivity–stream order and drainage area–gradient comprising the best models (Table 4). These two models resulted in similar AIC estimates and similar $\check{R}^2$ values and together carried nearly all of the weight of evidence for both sexes based on w_i. However, based on the small range in $\check{R}^2$ values and the high successful classification rates, a number of these models could be used to estimate maturity status for desert redband trout collected in Idaho streams.

Recently, several of these models were used to estimate the number of mature redband trout present in numerous Idaho streams, and results subsequently were used in concert with additional abundance and demographic data to approximate effective population sizes across southwestern Idaho populations (Schill 2009). Fishery managers now have a tool that can assist in estimation of redband trout spawner abundance across arid landscapes, which will hopefully lead to improved management of a rarely studied salmonid.

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