

Length Variation in Age-0 Westslope Cutthroat Trout at Multiple Spatial Scales

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Abstract.—Phenotypic diversity provides ecological and evolutionary functions, stabilizing populations in variable environments. Although benefits of larger body size in juvenile fishes are well documented, size variation may have value as well. We explored the distribution of length and length variation in age-0 westslope cutthroat trout *Oncorhynchus clarkii lewisi* at three spatial scales: area (10² km²), stream (10¹ km²), and site (10⁰ km²). In addition, we examined relationships between length variables (mean length and interquartile range of length) and instream (temperature and conductivity) and landscape (aspect, elevation, headwater distance, and valley width) variables that were expected to be associated with fish size. Conductivity was included as a surrogate for productivity. Most variation in mean length and interquartile range of fish length was found among areas (62.2% and 62.6%, respectively). Mean length also varied among streams and sites (21.9% and 15.8%, respectively). Similarly, interquartile range of fish length varied among streams and sites (19.1% and 18.3%, respectively). Both length variables were associated with temperature and elevation. Mean fish length was also associated with conductivity, but the association between interquartile length range and conductivity was weak. We conclude that the conservation of variation in phenotypic attributes, such as length, in westslope cutthroat trout may require conservation of viable populations across broad areas and across environmental gradients that are associated with growth.

Phenotypic variation—the intraspecific variation in life history, morphology, and behavior—plays a critical part in many evolutionarily and ecologically essential functions (Skulason and Smith 1995) and therefore may be important to conserve. Processes driven by phenotypic variation include the ability to adapt to local conditions and disturbance regimes, population differentiation that may lead to speciation, and the ability to reduce intra- and interspecific competition through niche differentiation (e.g., Utter 1981; Skulason and Smith 1995). Diversity in some traits may allow adjustment to variable environments and compensation in processes that are closely linked to survival and fitness (Caswell 1983; Hilborn et al. 2003). Demographic modeling suggests that variation among individuals reduces extinction risk for small populations (Kendall and Fox 2002); variation among populations may contribute to the persistence of larger systems (Hilborn et al. 2003). Causes, consequences,

and evolutionary potential of phenotypic variation are important questions in the ecology and conservation of organisms in variable environments (Schlichting 1989). The processes responsible for generating phenotypic variation in cutthroat trout *Oncorhynchus clarkii* and other migratory salmonids (Gresswell et al. 1994) and the extent and spatial distribution of variables associated with those processes are poorly understood. Successful fish conservation and management may require recognition and understanding of phenotypic variation and processes generating that variation (Gresswell et al. 1994; Beechie et al. 2006).

Organism size has been well recognized as an important phenotypic characteristic that mediates various biological processes, including metabolism, growth, production rate, reproductive condition and commitment, and constraints on body function (Peters 1983). Through these relationships, body size has important effects on organism fitness. The benefits of large juvenile size may include increased first-year survival, intraspecific competitive advantage, and reduced vulnerability to predation (Sogard 1997). However, there are also advantages to small size and associated feeding behaviors. Predators have been shown to prefer larger prey (Litvak and Leggett 1992). Actively feeding and satiated individuals may

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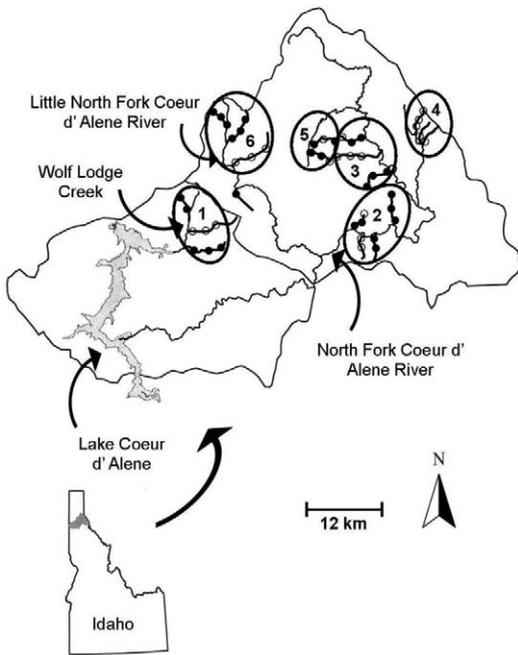


FIGURE 1.—Study area and sites sampled (solid circles = thermograph sites; open circles = sites that did not receive thermographs) for an examination of length variation in westslope cutthroat trout within six areas (ovals; see Table 1) of the Lake Coeur d'Alene watershed, northern Idaho, 2000–2001.

have a higher risk of predation (Lankford et al. 2001). Large individuals may self-limit future growth potential through adoption of low-risk feeding behaviors (Reinhardt and Healey 1999). In some circumstances, there may be no single “best” size. Size-based ontogenetic niche shifts may serve to reduce intraspecific competition within a population through morphological differentiation and niche separation (e.g., Skulason and Smith 1995). If size variation leads to life history variation, it may also contribute to recruitment stability and long-term survival in temporally variable environments (den Boer 1968).

Relationships among fish growth, size, water temperature, and food availability have been well documented (e.g., Donald et al. 1980; Nicieza et al. 1994; Sloat et al. 2005). Smith-Gill (1983) proposed that the linkage between temperature variation and significant phenotypic variation may be universal among ectotherms.

Instream variables that are important for aquatic organisms vary across spatial scales in response to important habitat and landscape controls. Relationships between the spatial scales at which biotic variation and

causal processes occur are not well understood; causal physical processes and biological responses may occur at the same (Horne and Schneider 1995) or at different scales (Frissell et al. 1986; Levin 1992). Variation in organism life history may occur at multiple scales in response to the scale dependency of habitat (Healey and Prince 1995; Cooper et al. 1998).

We examined the distribution of fish length variation and characterized relationships between fish length and instream and landscape characteristics. Our objectives were to (1) describe the distribution of length variation in age-0 westslope cutthroat trout *O. clarkii lewisi* at three scales (area, stream, and site), (2) identify instream and landscape factors associated with length variation, and (3) examine the patterns of spatial variation between fish length and potential causal (instream and landscape) variables for clues to the relationship between scale and length variation.

Study Area

The study was conducted in the Coeur d'Alene River watershed of northern Idaho (Figure 1), a region of low mountains vegetated by coniferous forest. The forest is dominated primarily by Douglas-fir *Pseudotsuga menziesii*, western redcedar *Thuja plicata*, and western hemlock *Tsuga heterophylla* (Bailey 1995). Elevation ranges from 600 to 1,850 m. Climate includes winters characterized by snow, rain on snow, and rain; annual precipitation is 50–100 mm (about 20–40 in; NOAA 2003). Geology is dominated by Precambrian Belt sedimentary rock containing basalt sills and granite sheets (Johnson and Raines 1996). The majority of the basin is managed by the U.S. Department of Agriculture (USDA) Forest Service (Idaho Panhandle National Forest). Fish fauna of study streams includes native westslope cutthroat trout, torrent sculpin *Cottus rhotheus*, and shorthead sculpin *C. confusus* and nonnative brook trout *Salvelinus fontinalis* and rainbow trout *O. mykiss*. Bull trout *S. confluentus* are native to the system but are believed to be extirpated. Anadromous species do not have access to this system because of natural migration barriers below Lake Coeur d'Alene.

Study sites were selected on 19 streams; of these, 12 drain to the North Fork of the Coeur d'Alene River, 4 drain to the Little North Fork of the Coeur d'Alene River, and 3 drain to Wolf Lodge Creek. All ultimately drain to Lake Coeur d'Alene and the Columbia River. Study streams are second or third order and have moderate gradient (2–6%), gravel or cobble substrate, low turbidity, and relatively cool water temperature. Abundances in some streams were low, possibly due to habitat disruption from historic logging and mining; therefore, we selected streams in which westslope

TABLE 1.—Mean corrected total length (CLen; corrected for differences in sample date) of westslope cutthroat trout; corrected interquartile range of length (CIQR); instream variables (Temp = mean temperature; Cond = mean conductivity); and landscape characteristics (Asp = aspect, reversed Day scale from 1 [northeastern] to 16 [southwestern]; Elev = elevation; HDist = headwater distance; VWidth = mean valley width) measured at the area scale (Figure 1), stream scale, and site scale (L = lower site within a stream; M = middle site; U = upper site) in the Lake Coeur d'Alene watershed, Idaho, 2000–2001 (data are pooled across years).

Area	Stream	Site	CLen (mm)	CIQR (mm)	Temp (°C)	Cond (µmho)	Aspect	Elev (m)	HDist (m)	VWidth (m)
1	Cedar	L	47.8	8.0	13.9	78	11	585	8,394	51
		M	39.8	11.5	13.7	123	11	792	3,880	18
		U	41.7	6.7	11.9	45	11	829	2,684	28
	Lonesome	L	37.2	5.5	12.1	20	14	732	3,587	68
		U	36.1	7.0	11.4	22	12	805	2,611	19
		M	37.4	5.7		19	13	683	13,957	188
	Marie	L	37.9	5.9		17	7	738	11,419	65
		M	38.2	5.4		18	5	777	9,467	59
		U	40.8	9.0	11.3	72	16	722	5,563	65
2	Brown	L	40.5	7.9	10.6	61	14	786	3,453	37
		M	32.8	5.3	9.9	63	14	878	1,708	11
		U	35.0	7.2	9.8	6	4	661	5,636	32
	Coal	L	29.7	5.4	9.1	6	1	774	4,782	15
		M	32.7	5.4		19	1	707	7,003	101
		U	31.6	5.5		26	3	780	4,929	75
	Graham	L	36.9	11.6	10.7	57	16	671	4,148	25
		M	38.2	6.1	10.0	57	13	744	3,294	13
		U	37.3	4.1		61	16	817	2,562	5
3	Flat	L	33.6	7.2		52	8	914	7,125	34
		M	36.1	3.4		47	6	975	5,539	12
		U	36.0	3.1		69	8	1,036	3,928	15
	Miners	L	42.1	4.2	9.4	102	6	841	5,173	31
		M	39.1	4.4	9.0	106	2	914	3,782	24
		U	34.3	4.0		118	8	1,000	2,318	16
	Yellowdog	L	36.2	5.3	12.0	14	2	808	7,466	6
		M	34.6	5.7	11.0	17	6	878	5,026	74
		U	27.8	4.3	9.4	16	7	963	3,367	36
4	Cabin	L	35.8	7.8		41	16	884	4,758	15
		M	36.6	3.7		36	16	927	5,441	125
		U	44.2	3.3		39	14	890	5,954	45
	Clinton	L	38.0	0.8		34	16	975	4,148	24
		M	26.2	2.6		28	15	1,097	2,440	15
		U	38.7	6.0	10.5	78	5	939	6,783	54
5	Halsey	L	33.9	6.3		75	15	988	4,782	75
		M	38.3	3.4	9.3	75	7	1,036	3,440	15
		U	36.5	6.4	9.6	102	11	951	7,320	30
	Little Elk	L	31.7	3.3	8.8	115	9	1,000	3,172	84
		M	29.9	2.3		120	11	1,024	2,196	26
		U	35.6	4.3		39	15	863	7,149	68
6	Cascade	L	31.3	3.2		37	11	924	4,587	15
		M	26.9	4.5		28	15	1,021	2,074	35
		U	36.2	6.0	10.4	63	13	930	8,491	223
	Iron	L	36.3	6.2	9.5	57	16	951	6,905	86
		M	31.6	2.1	9.6	53	16	1,015	5,246	14
		U	26.8	3.4		15	3	835	4,734	66
	Skookum	L	32.4	7.0	9.7	12	11	1,000	4,612	36
		M	30.3	3.0	9.5	12	12	1,015	3,318	32
		U	27.7	2.4	8.9	13	10	1,109	2,342	19

cutthroat trout abundances were sufficient to ensure adequate sample sizes and that represented a range of conditions for the variables of interest. Study streams were accessible by road or trail and generally supported good to excellent habitat conditions.

In general, three sites were selected per stream (site scale: 10^0 km²) in two to four adjacent streams (stream scale: 10^1 km²) that were distributed within six areas (area scale: 10^2 km²) throughout the study area (Figure

1; Table 1). Streams were also selected to represent a range of temperatures and conductivity levels. In each stream, an upper site was located near the upper extent of fish distribution. Lower sites were generally situated immediately above the confluence with a receiving stream; however, in a few cases where study streams were larger than average, the lower site was placed higher in the drainage to maintain comparable stream sizes across all study streams. Middle sites were

located approximately halfway between the lower and upper sites. Due to hydrologic barriers to upstream fish passage, difficult site access, or low fish abundance, three of the streams had only one sample site each and three additional streams had only two sample sites each.

Methods

Fish collection.—Age-0 westslope cutthroat trout were collected during July–August 2000 (41 sites sampled) and 2001 (30 sites). Of the total number of sites, 23 were sampled during both years, 18 were sampled only in 2000, and 7 were sampled only in 2001. A subset of sites was sampled multiple times between July and October of each year to estimate growth rates for standardization of two length variables. Within a site, all habitats with suitable characteristics were sampled. Habitats used by age-0 westslope cutthroat trout typically consist of isolated or partially isolated stream margins characterized by low water velocity and are often separated from main-channel flow by a sharp change in velocity or by physical obstructions (e.g., Moore and Gregory 1988; Lentz 1998).

Collection proceeded at each site until a minimum of 33 age-0 individuals was obtained. We used both backpack electrofishing (Smith-Root, Inc., Vancouver, Washington; Type VII electrofisher) and hand netting, because length of age-0 fish varied among sites and across the sampling period and because collection methods can be size selective (Nielsen and Johnson 1983). Voltage was varied by site to compensate for differences in conductivity. Captured westslope cutthroat trout were anesthetized, measured (total length, mm), and released. Individuals of uncertain age were retained for age confirmation from subsequent otolith analysis.

We used length frequencies to differentiate age-0 westslope cutthroat trout from older fish at each site. A 5–10-mm gap in length generally was observed between age-0 and age-1 fish. When age assignment based on length-groups was uncertain for a given individual, the fish was sacrificed and otoliths were removed. One otolith per fish was mounted on a glass slide with thermoplastic resin, ground on one side using 2,000- and 1,200-grit sandpaper and 9- and 3- μ m lapping paper, flipped, and ground on the second side until annual rings were clearly visible. Because annual rings are generated when growth ceases during the winter period, age-0 fish lack annual rings. The presence of annual rings was determined using the methods of Campana (2001). Of the 130 otoliths examined from fish ranging from 20 to 70 mm, none was incorrectly classified as belonging to an age-1 fish.

Instream and landscape variables.—Temperature was recorded using calibrated instream thermographs. Because of equipment limitations, some sites did not receive thermographs. Thermographs were used at 21 of 41 sites in 2000 and at 19 of 30 sites in 2001. In the combined data set (see below), 27 of the 48 sites had received thermographs. Thermographs were placed at each site as soon as possible after snowmelt and were retrieved in late September or October. Thermographs were anchored to the bottom of the stream and were shaded with cobbles in an eddy that was characteristic of age-0 fish habitat. Average water temperature was calculated for a common time period for all sites during both years.

Conductivity is positively correlated with primary production and geology in streams from the same basin (e.g., Chetelat et al. 1999), and this was also demonstrated for the Coeur d'Alene River (Wells et al. 2003). Conductivity was measured with a YSI Model 30 SCT meter at each site three times during each summer, and measurements were averaged for the analyses.

Data for three landscape variables—elevation, headwater distance, and aspect—were obtained from 1:24,000-scale topographic maps. Elevation was estimated to the nearest 3 m. Headwater distance was measured from the upstream source. Average aspect of the stream channel was estimated using a reversed Day scale (Day and Monk 1974) from 1 (northeastern) to 16 (southwestern). Valley floor width was estimated by pacing at each site.

Data analysis.—We selected mean fish length (CLen, corrected as described below) and the interquartile range of fish length (CIQR, also corrected) to represent two different aspects of fish size. We used CIQR as a measure of length variability because it should be insensitive to outliers that might be produced by incorrect aging (MathWorks 2005).

To compensate for possible fish length and length variation differences related to date of sampling, a correction based on sampling date and average growth rate through the sampling season was applied to total length for each sample using an approach similar to that described by Rieman and Myers (1992). Average growth rate (slope of the length–date linear regression) was obtained by sampling 13 representative sites two to four times in 2000 and 11 representative sites three to four times in 2001. Growth rates for all sites were averaged for each year, and each length was subsequently standardized to the midpoint of the sampling period for the 2 years combined (day 221: August 8, 2000, or August 9, 2001). The CIQR was calculated using raw data, and a correction factor was calculated by use of the same procedure. The CLen and CIQR

were used in all analyses. Coefficients of determination (r^2) for growth rate regression parameters at sites sampled more than twice were generally 0.9 or higher, suggesting good linear model fit. Mean change from nonstandardized values was 14.1% for CLen and 32.3% for CIQR. To determine whether our standardization method introduced a systematic bias into the data, we examined correlations between date of collection and all independent variables. All values were low ($r \leq 0.40$).

We used the Wilcoxon paired-sample test to examine between-year differences in CLen, CIQR, and water temperature based on all sites with 2000 and 2001 data. Other instream and landscape variables were unlikely to vary during the study. No significant difference between 2000 and 2001 was observed for CLen ($N = 23$, $P < 0.09$) or CIQR ($N = 23$, $P < 0.16$). We therefore combined data for those sites sampled in both years. Mean water temperature was $1.2 \pm 0.3^\circ\text{C}$ (mean \pm 2SE) warmer in 2000 than in 2001 ($N = 13$, $P < 0.001$). We adjusted 2001 temperatures upward by 1.2°C and averaged 2000 and 2001 temperatures when data existed for both years. The combined data set (both 2000 and 2001) used in analyses included 48 sites within 19 streams and 6 areas.

To examine the distribution of variation in CLen and CIQR among spatial scales (objective 1), we conducted a nested, mixed-model analysis of variance (ANOVA) on each variable and used area, stream (nested within area), and site (nested within stream within area) as independent variables. This approach partitions variation among spatial scales by calculating the percentage of the total mean square error attributable to each scale (Larsen et al. 2004). Analyses were conducted on CLen per site rather than individual fish length to allow comparison with CIQR and instream and landscape variables, which did not vary within sites. We used the same approach to examine the distribution of variation in instream and landscape variables among scales, and we visually compared the distribution of CLen and CIQR with the distributions of instream and habitat variables. Appropriate residual plots were analyzed to verify that assumptions of normality were not violated.

Relationships between fish length and instream and landscape variables were examined through linear regression of all possible subsets (Burnham and Anderson 2002); site-scale data were used in these analyses, since we did not have the observations necessary to use more complex hierarchical models (Snijders and Bosker 1999). Pairwise Pearson's product-moment correlations (Hair et al. 1998) were examined to identify redundant variables. Of the 15 variable pairs, 3 pairs were significantly correlated: elevation and headwater distance ($N = 48$, $r = -0.435$,

$P < 0.002$), elevation and temperature ($N = 27$, $r = -0.632$, $P < 0.0004$), and headwater distance and valley width ($N = 48$, $r = 0.598$, $P < 0.0001$). Because we were interested in both temperature and elevation, we chose to examine two global models that each contained aspect, conductivity, and valley width and either elevation or temperature. Within each global model, we considered the best model to have the lowest corrected value of Akaike's information criterion (AIC_c ; Burnham and Anderson 2002). Among models with different data sets (temperature versus elevation), the best model had the highest r^2 value.

To evaluate whether length variation not accounted for by our instream and landscape variables could be associated with the spatial distribution of our sample sites, we conducted a Mantel test at the site scale on the residuals from the best regression models identified for CLen and CIQR. Euclidean distance was used in the Mantel test instead of length distance, because the spatial patterns in environmental characteristics influencing individual growth and size are likely to depend on geology, landform, and biophysical setting, which will affect local habitats that vary in two-dimensional space rather in one dimension (i.e., along the stream corridor). We also visually examined residual plots of CLen and CIQR for spatial autocorrelation at the area and stream scales.

Most analyses were conducted in JMP version 6.0.0 (SAS Institute, Inc., Cary, North Carolina). The ANOVA was conducted in the Statistical Analysis System version 9.1 (SAS Institute), and the Mantel test was conducted in XLSTAT version 2007.4 (Addinsoft USA, New York, New York). The significance level for all analyses was 0.05.

Results

The CLen ranged from 31.5 to 39.5 mm at the area scale (Figure 2a), from 26.8 to 43.1 mm at the stream scale (Figure 2b), and from 26.2 to 47.8 mm at the site scale (Figure 2c). The CIQR ranged from 3.6 to 6.9 mm at the area scale, from 2.2 to 8.7 mm at the stream scale, and from 0.8 to 11.6 mm at the site scale. Variation in CLen was distributed as follows: 50.3% at the area scale, 20.1% at the stream scale, 12.6% at the site scale, 15.5% between years, and 0.5% within sites. Variation in CIQR was distributed with 39.2% at the area scale, 13.6% at the stream scale, 12.0% at the site scale, and 26.1% between years. When only variation at the three primary scales of interest (site, stream, and area) was estimated (excluding within-site and between-year variation), 62.2% of the variation in CLen was among areas, 21.9% was among streams, and 15.8% was among sites. Similarly, 62.6% of the variation in CIQR

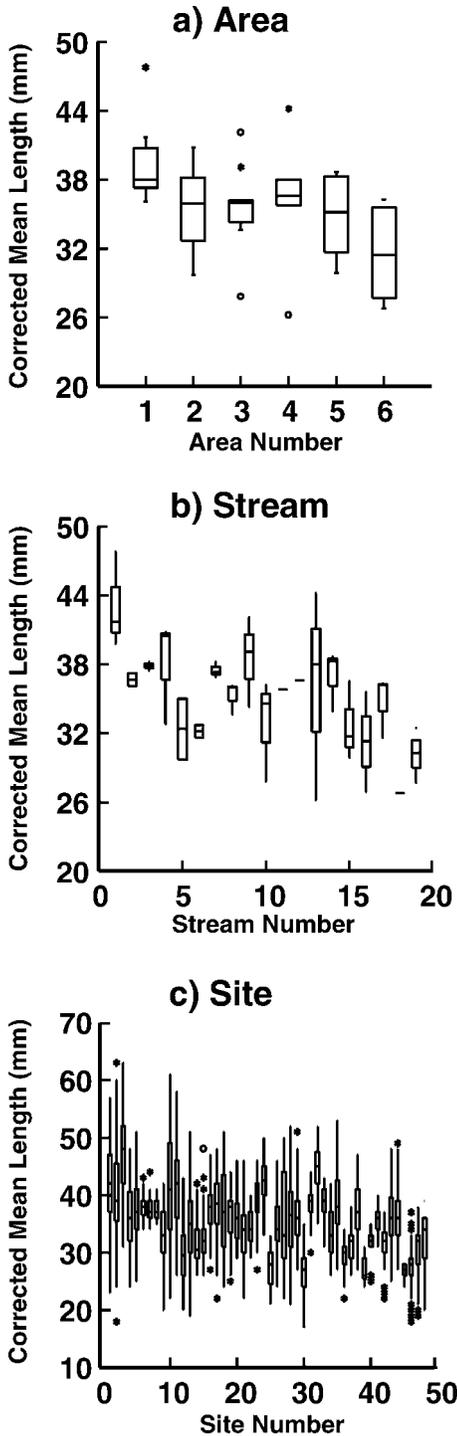


FIGURE 2.—Distribution of variation in corrected mean total length (mm) of westslope cutthroat trout among (a) areas, (b) streams, and (c) sites in the Lake Coeur d’Alene watershed, Idaho, 2000–2001.

TABLE 2.—Summary of regression results for a set of candidate models used to predict mean corrected total length (CLen, mm; corrected for differences in sample date) and corrected interquartile length range (CIQR) of westslope cutthroat trout based on instream (Temp = temperature, °C; Cond = conductivity, μ mho) and landscape (Elev = elevation, m) variables in the Lake Coeur d’Alene watershed, Idaho, 2000–2001 ($N = 48$ sites represented in models containing Elev; $N = 27$ sites represented in models containing Temp; r^2 = adjusted coefficient of determination; RMSE = root mean square error; AIC_c = Akaike’s information criterion corrected for small sample size).

Candidate model	r^2	RMSE	AIC_c
CLen with Temp			
Temp, Cond	0.581	3.027	64.10
Temp	0.366	3.721	73.67
Cond	0.248	4.054	78.30
CLen with Elev			
Elev, Cond	0.420	3.509	124.16
Elev	0.240	4.017	135.86
Cond	0.094	4.387	144.32
CIQR with Temp			
Temp	0.372	1.867	
CIQR with Elev			
Elev, Cond	0.418	1.693	54.19
Elev	0.378	1.750	56.09

was among areas, 19.1% was among streams, and 18.3% was among sites.

In CLen models containing temperature, the model consisting of conductivity and temperature provided the best fit to the data ($AIC_c = 64.10$; $r^2 = 0.581$; Table 2). Single-variable models based on temperature ($AIC_c = 73.67$; $r^2 = 0.366$) or conductivity ($AIC_c = 78.30$; $r^2 = 0.248$) were also significant. Among models containing elevation as a factor, the model with elevation and conductivity provided the best fit ($AIC_c = 124.16$; $r^2 = 0.420$; Table 2). The other significant models were univariate and were based on either elevation ($AIC_c = 135.86$; $r^2 = 0.240$) or conductivity ($AIC_c = 144.32$; $r^2 = 0.094$). The CLen was positively associated with conductivity and temperature and negatively associated with elevation (Figure 3). Aspect and valley width were not significant in any models of CLen.

In CIQR models containing temperature, the only significant model was the univariate model based on temperature ($r^2 = 0.372$; Table 2). Among models based on elevation, the model containing both elevation and conductivity yielded the best fit to the data ($AIC_c = 54.19$; $r^2 = 0.418$; Table 2) and the elevation-only model was also significant ($AIC_c = 56.09$; $r^2 = 0.378$). As was observed for CLen, CIQR was positively associated with conductivity and temperature and was negatively associated with elevation (Figure 3). Aspect and valley width were not significantly associated with CIQR in any model.

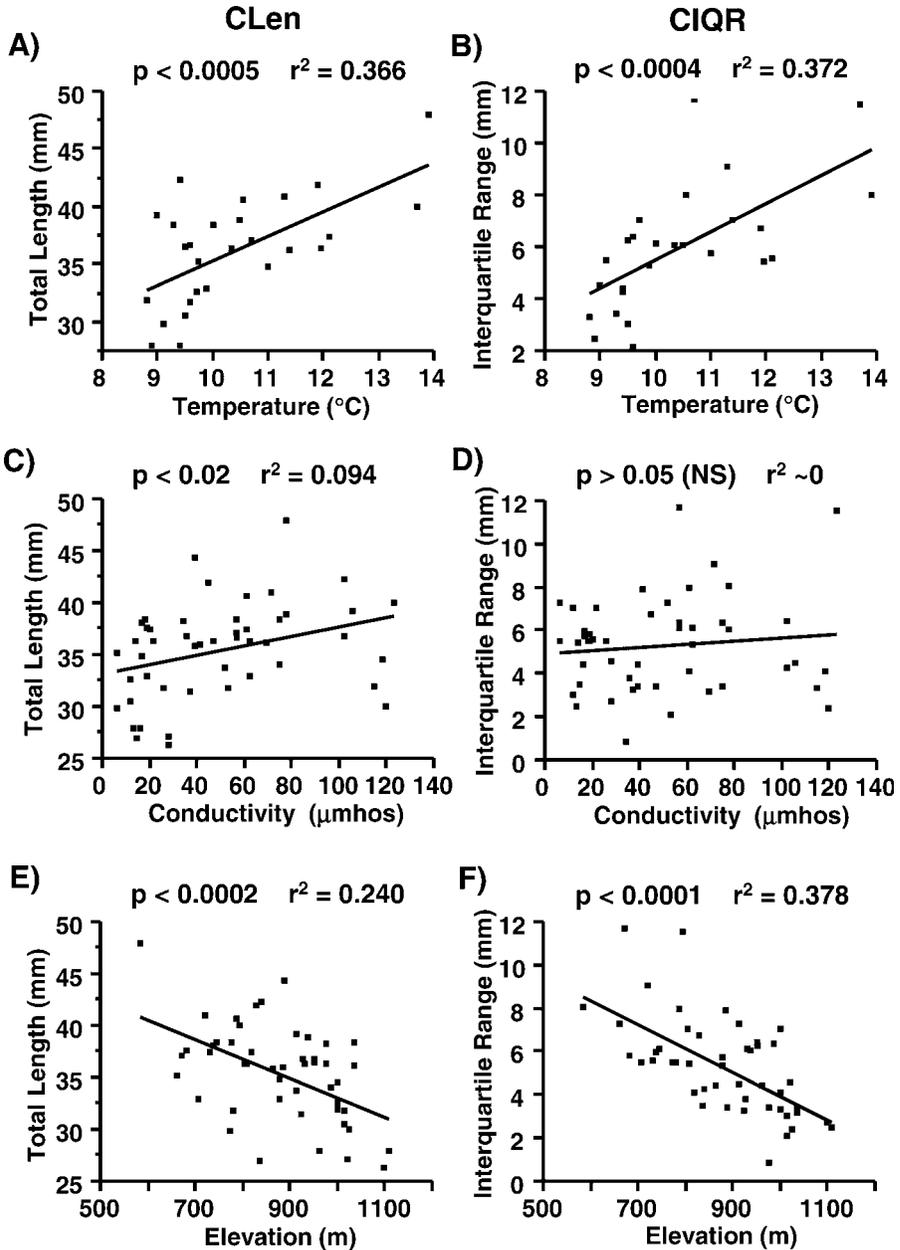


FIGURE 3.—Single-variable regression relationships between (A) temperature ($^{\circ}\text{C}$) and corrected mean total length (CLen, mm); (B) temperature and corrected interquartile range of total length (CIQR); (C) conductivity (μmho) and CLen; (D) conductivity and CIQR (NS = not significant); (E) elevation (m) and CLen; and (F) elevation and CIQR of westslope cutthroat trout in the Lake Coeur d'Alene watershed, Idaho, 2000–2001.

Distribution of variation among scales differed among fish length, instream, and landscape variables (Figure 4). Both CLen and CIQR exhibited the most variation at the area scale. Most of the variation for instream variables (conductivity and temperature) and for two of the landscape variables (aspect and

elevation) also occurred at the area scale (57.7–89.6%). Of these variables, conductivity and aspect were similar to the length variables in having most of the variation at the area scale and also having considerable variation at the stream scale. In contrast, relatively little variation in temperature and elevation

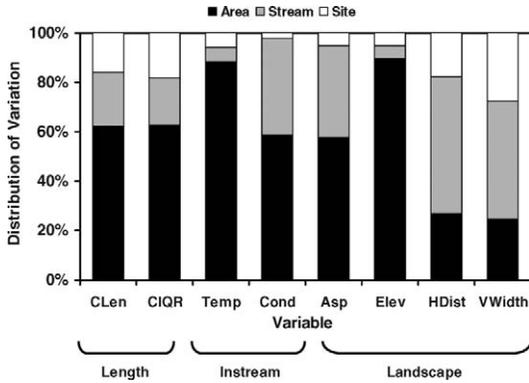


FIGURE 4.—Distribution of variation in mean corrected total length (CLen, mm) of westslope cutthroat trout, corrected interquartile range of fish length (CIQR), instream variables (Temp = temperature, °C; Cond = conductivity, µmho), and landscape variables (Asp = aspect, reversed Day scale from 1 [northeastern] to 16 [southwestern]; Elev = elevation, m; HDist = headwater distance, m; VWidth = valley width, m) in the Lake Coeur d’Alene watershed, Idaho.

occurred at either the stream or site scale. Headwater distance and valley width differed from all other variables, displaying most of the variation at the stream scale (55.2% and 47.8%, respectively), and the remaining variation was distributed approximately equally among sites and among areas.

The Mantel test was nonsignificant for CLen ($N = 351, r = -0.097, P = 0.07$) and CIQR ($N = 351, r = -0.008, P = 0.88$), indicating that no spatial autocorrelation was present among sites other than that accounted for by the instream and landscape variables used in the best-fitting models. Examination of residual plots at stream and area scales also indicated that spatial autocorrelation was not present at these scales.

Discussion

Most of the variation in westslope cutthroat trout CLen and CIQR occurred among areas, the broadest scale studied here. This result is contrary to that of Shepard et al. (1984), who found that size of age-0 westslope cutthroat trout was similar among tributaries (area scale) of the Flathead River, Montana. Differences in findings between the two studies can be explained by (1) the higher resolution of size variation in our study or (2) the greater heterogeneity of the Lake Coeur d’Alene watershed relative to the Flathead River system. Geology and apparent productivity in the Lake Coeur d’Alene watershed vary dramatically across the basin (e.g., Wells et al. 2003), and the range of productivity among streams may be substantially greater than that in other systems, thus contributing to greater length ranges in westslope cutthroat trout.

Regardless, we believe the observation of significant variation across scales in the Lake Coeur d’Alene watershed holds important clues to the processes driving phenotypic diversity and has important implications for conservation management.

Causes of Variation

Age-0 westslope cutthroat trout were larger on average at lower-elevation and higher-temperature sites. At least three mechanisms may contribute to this pattern. First, associations between higher growth rate and higher temperature have been well documented for many fish species (including westslope cutthroat trout: Sloat et al. 2005) and at many localities. Second, because the development rate of embryos in redds is a function of water temperature, warmer sites may have earlier emergence (Crisp 1990), extending the first-year growth period and producing larger individuals than are produced at colder sites. Fish at lower-elevation, warmer sites were probably older. Age-0 fish at lower-elevation sites within our study streams emerged 9–15 d earlier than those at upper-elevation sites within the same streams (K.E.M., unpublished data). Third, the spawning areas used by larger, migratory adults within individual streams may be lower than the areas used by smaller, resident adults (Averett and MacPhee 1971; Bohlin et al. 2001). Because larger females tend to have larger eggs, they are also likely to produce larger offspring (Einum and Fleming 1999).

An additional potential influence on westslope cutthroat trout growth (and therefore the observed pattern of larger fish at lower elevations within and among streams) is introgression with nonnative rainbow trout in the watershed. Rainbow trout may spawn and emerge earlier than westslope cutthroat trout, and introgression proceeds primarily from downstream to upstream, a pattern seen in tributaries to the Coeur d’Alene River (Hitt 2002; B. Rieman, unpublished data; P. Spruell, University of Montana, Missoula, unpublished data). However, hybridization between rainbow trout and cutthroat trout has been associated with reduced growth rather than increased growth. Allendorf and Leary (1988) demonstrated that age-0 F_1 hybrids grew more slowly than pure westslope cutthroat trout, and Hawkins and Foote (1998) found that coastal cutthroat trout *O. clarkii clarkii* × steelhead (anadromous rainbow trout) hybrids had lower early growth and survival than did fish of the parental stock. Rainbow trout also develop more slowly than do cutthroat trout; therefore, in spite of potentially earlier emergence, age-0 hybrids may not have a size advantage over pure cutthroat trout (Hawkins and Foote 1998). For these reasons, we believe it is unlikely that introgression with rainbow trout contrib-

uted significantly to the size patterns observed in our study, but we cannot exclude that possibility.

The CIQR was also associated with higher temperature and lower elevation. The differences in CIQR were due primarily to the presence of larger individuals at warmer sites. This suggests that increased growth rates or earlier emergence times were important for influencing CIQR in addition to CLen. Several researchers have observed the progressive development of bimodal size variation in age-0 salmonids, which indicates that differential growth through the season is important to size variation (Griffiths 1994; Nicieza et al. 1994). Dispersal of individuals from other natal sites might also be important. We think it unlikely that westslope cutthroat trout movement from upstream sites was sufficient to produce the greater length variation, because movement by small fish was not driving the result. Kahler (1999) also found that few age-0 cutthroat trout moved distances that were sufficient to influence size distributions at adjacent sites.

The CLen and CIQR may differ in the nature of their association with conductivity. We found that CLen was consistently associated with conductivity (and presumably productivity), whereas CIQR was associated with conductivity in models that also contained elevation but less so in models containing temperature. An association between fish length and productivity is common in the literature (e.g., O'Gorman and Burnett 2001), but our results suggest that the range of lengths within a site is more a function of life history characteristics (e.g., emergence timing influenced by temperature) than of growth rate associated with productivity. Many streams with suitable habitat that span substantial elevation and temperature ranges should produce substantial diversity in age-0 fish size, whereas differences in CLen among streams may be influenced by temperature and geology or other environmental characteristics that influence productivity.

We hypothesized that relationships between length variables and explanatory variables would be scale dependent such that the strongest relationships would coincide with the scales at which explanatory variables varied. We found that most of the variation in CLen occurred at the area scale. Two of the variables that were closely associated with CLen (temperature and elevation) also varied primarily at the area scale. A strong and potentially causal gradient clearly exists.

Our results provide clues to the nature of relationships between scale and pattern, but the relationships between the scales at which causal and response processes occur are complex. Causal physical processes and biological responses may occur at the same scale (Horne and Schneider 1995) or at different scales

(Levin 1992), and multiple factors can contribute to the ultimate pattern observed. When causal variables occur at different scales, patterns at finer scales may disrupt or mask relationships that are present at broader scales. Causal gradients occurring at the same scale may interact due to differences in their spatial patterns on the landscape. Important gradients that are offset in space may produce one or more relationships at finer scales; gradients with coinciding spatial patterns can produce multiple potential outcomes that depend on the nature of their effects on response variables. Patterns may be strengthened or neutralized; neutralization of a pattern can allow additional causal variables to be expressed. Finally, an organism's mobility may limit (1) the scales at which the organism is responsive to its environment and (2) the ranges of environmental gradients to which the organism is exposed. For example, age-0 salmonids integrate variation in environmental gradients occurring at scales finer than their ranging movements. Gradients at scales broader than ranging movements are more likely to produce length differences among populations.

Implications for Conservation Management

The size variation we observed in age-0 westslope cutthroat trout among sites, streams, and areas in the Lake Coeur d'Alene watershed may have important implications for the fitness of individual fish (Sogard 1997). More importantly, it may promote diversification of life history strategies within and among populations (Jonsson et al. 1988; Conover and Schultz 1995; Bohlin et al. 2001) and contribute to population stability and long-term survival in temporally variable environments (den Boer 1968; Chandler and Bjornn 1988; Good et al. 2001; Kendall and Fox 2002).

Size differences found at finer scales are likely to be ecologically significant as well. Our results suggest that mean size of age-0 fish in adjacent streams can be very different depending on the specifics of instream and landscape environments. Numerous ecological processes, such as survival, competition, and predation, are mediated by age-0 fish length differences of only 5–10 mm, as were observed among sites within streams in the present study. For example, smaller individuals within a population may be less successful at establishing territories (Keeley and McPhail 1998), and survival through the first winter may be dependent on length differences less than 10 mm (Smith and Griffith 1994). Age-0 individuals differing in length by as little as 5–10 mm may occupy habitats that differ in water depth, velocity, and distance to refuge habitat (Moore and Gregory 1988) and may respond differently to changes in environmental cues, such as temperature and light (Breau et al. 2007). Ultimately,

these differences in habitat use and behavior may lead to broader utilization of available cover and food resources and greater overall abundance and production in the population (Chandler and Bjornn 1988).

We believe our findings have important conservation management implications. To maintain phenotypic diversity in fishes, it is necessary to maintain the range of environments and habitats that support the expression of that diversity (Healey and Prince 1995). If length variation in age-0 fish leads to important diversity in life history, fuller exploitation of available habitats, and ultimately more-resilient and productive populations, then the maintenance of that variation across important gradients at appropriate scales will be an important goal for conservation and management. Much of the variation in length associated with instream and landscape variables cannot be represented by individual streams or even among streams within a drainage. Representation will require multiple streams and populations distributed across distinct portions of a given basin. This is consistent with the findings of Gresswell et al. (1997), who reported that life history in Yellowstone cutthroat trout *O. clarkii bouvieri* varied among streams in response to landscape characteristics.

Broad-scale environmental gradients, such as those in elevation and productivity, have been associated with salmonid life history characteristics other than juvenile growth. For example, resident and migratory life histories may arise from different growth environments (Jonsson and Jonsson 1993). Expression of the migratory life history in cutthroat trout and other species has been observed to vary along stream size and elevational gradients (Johnson 1963; Bohlin et al. 2001). Growth and maturation rate in Atlantic salmon *Salmo salar* have been associated with elevation differences within and among drainages (Baum et al. 2004). Multiple life history characteristics occurring throughout the life cycle of salmonids have been associated with broad-scale environmental gradients, indicating that life history diversity essential for population stability and persistence can be conserved only by conserving multiple salmonid populations at these broad scales.

The siting of human land use activities may be associated with the productivity gradients we examined and could result in habitat loss at the extremes of important growth gradients, eventually leading to overall habitat homogenization. For example, agriculture, timber harvest, urbanization, and other human development tend to occur first in lower-elevation, wider, flatter valleys, which are often more accessible to fish and more productive (Rieman et al. 2000). Invasion by nonnative brook trout and rainbow trout into lower-elevation cutthroat trout habitat may be

associated with habitat degradation and associated effects on temperature (Dunham et al. 2002; Bear et al. 2007). Habitat degradation may affect cutthroat trout populations, associated size variation, and phenotypic diversification at both extremes of the gradients associated with fish growth through the populations' differential vulnerability and sensitivity to anthropogenic effects. Conservation and management strategies should identify not only important gradients and processes that generate intraspecific diversity but also those populations that may be particularly sensitive to alteration or disturbance. Such populations may include those that are ecologically sensitive or marginal (Lesica and Allendorf 1995), including populations of homogeneously small fish that tend to occur within the headwaters of high-elevation streams. These populations may be vulnerable to catastrophic events or chronic habitat degradation that results in small population sizes. Populations at low elevations are more accessible to humans and invasive species (Dunham et al. 2002) and therefore are more vulnerable to disturbance. Both extremes of the temperature-elevation gradient may, for different reasons, present conservation challenges.

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