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What Limits Tailed Frog Tadpole Density and Distribution in Western Montana Streams?

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WHAT LIMITS TAILED FROG TADPOLE DENSITY AND DISTRIBUTION IN WESTERN MONTANA STREAMS?

by

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Abstract We explored the possible limitation of temperature and other habitat features on tailed frog tadpole populations in northwestern Montana. We sampled densities and habitat features in two regions with different climatic regimes and in streams with and without tadpoles, expecting larger density and size in the warmer region. We also expected habitat conditons to be more optimal (higher gradient, swifter velocity, and less canopy cover) in streams with tadpoles. Temperature appeared to positively influence tadpole size, though both tadpole size and density were strongly correlated with other variables. Density was correlated with gradient, canopy, depth, and elevation, whereas length was correlated with width and density. Contrary to expectations, we found lower densities in the warmer region. Streams in the warmer region were lower in elevation and gradient than the colder region streams. These lower gradient streams are optimal habitat for sculpin, which prey on tadpoles. The presence of sculpin in these warmer-region lower-gradient streams suggests predation could explain the lower densities. In comparing habitat features of streams with and without tadpoles, only gradient varied significantly, which also supports the idea of predation limiting densities.

Key words: *Ascaphus truei*, tadpoles, temperature, habitat, Montana, predation, densities, size

The tailed frog (Ascaphus truei) is found in swift, cold, perennial streams in forested areas (Metter 1968). Two disjunct populations of tailed frogs exist, one in the coastal and near coastal ranges of the Pacific Northwest and the other in the northern Rocky Mountains of Idaho and Montana (Metter 1968). Metter and Pauken (1969) suggest that the tailed frog population was continuous during the Miocene and Pleistocene when conditions were more humid and that the distribution contracted with climatic changes in the late Pleistocene. Populations are now separated by the arid Columbia Plateau and the upper Great Basin (Metter and Pauken 1969). Due to the influence of moist maritime air masses, the climate in some parts of Idaho and Montana is similar to that of the coastal ranges, and thus can sustain tailed frog populations (Arno 1979). Franz and Lee (1970) suggest that the presence of hemlocks or other coastal species such as alders might be correlated with suitable conditions for tailed frog tadpoles in Montana drainages.

Most research on the tailed frog has focused on Pacific Northwest populations and relatively little is known about the Rocky Mountain populations. However, anecdotal evidence suggests that population densities around the Flathead Lake region of western Montana are smaller and more patchily distributed than populations in the Northwest (Chris Frissel, Flathead Lake Biological Station, pers. comm.). Though no research has demonstrated this pattern to my knowledge, these observations suggest that one or more habitat factors may be suboptimal in this region.

One possible limiting factor is cold temperature. Though the climate in areas occupied by the Rocky Mountain population is modified maritime, cold arctic air masses often pass through the Flathead Valley of Montana. Other species that typically occur in maritime climates, e.g. the trees Tsuga (hemlock), Thuja (cedar), and Alnus (alder), are patchily distributed in this region. Both hemlocks and cedars are limited to sites where the climate is moderated by the presence of a large lake such as Flathead Lake or MacDonald Lake (Arno 1979). The distribution of these species implies that other coastal species, like the tailed frog, may also be affected by the colder climate. Progressing westward to areas like the Kootenai drainage, the climate is not affected by cold air masses. Thus, the climate and vegetation in the Kootenai region more closely resembles that of the Pacific coast.

Temperature may limit tailed frog abundance by affecting the developmental rate and survival of tadpoles. The larval period varies from one to four years and appears to be inversely related to temperature. Metamorphosis typically occurs at age two in the Pacific Northwest (Nussbaum et al. 1983). In Montana, tailed frogs spend three full years in the embryonic and tadpole stage, with metamorphosis occurring near summer's end of their fourth year (Daugherty & Sheldon 1982). The longer a tadpole spends in a stream, the greater its chance of mortality from predation or catastrophic floods. Slow larval development could therefore act to limit adult populations, which in turn would produce fewer eggs and tadpoles.

The objectives of this research were twofold. One objective was to compare tailed frog densities between a colder and warmer region within the Northern Rocky Mountains. I worked under the hypothesis that densities would be lower in the colder region, refelcting the influence of cold arctic air masses. In addition, I hypothesized that larger tadpoles would be associated with warmer streams. The other objective was to determine if streams with and without tadpoles differed in physical characteristics. My hypothesese were (1) streams lacking tailed frogs would be colder, have more canopy cover, lower gradients, smaller substrates, and slower velocities than frog streams and (2) tadpole densities would be positively correlated with stream tempertature, substrate size, current velocities, stream gradient, and negatively correlated with canopy cover.

Study design

To test my hypothesis that tadpole density and size were positively correlated with temperature, I needed data on tadpole densities from regions with different climate regimes. To obtain this information, I sampled tadpole density in streams from the colder Flathead region and warmer Kootenai region. To test my hypothesis about the relation of tadpole density and distribution to habitat features, I sampled physical characteristics in streams with and without tadpoles (frog and non-frog streams).

Throughout this paper I refer to streams with and without tadpoles as "frog streams" and "non-frog" streams. I define frog streams as those with documented tailed frog tadpole populations, whereas non-frog streams are those previously reported to contain no tadpoles. I point out, however, that tadpoles may have been present in low abundances in designated non-frog streams.

For the Flathead region, designation of frog and non-frog streams was based on Franz and Lee's 1970 study. In this study, Franz and Lee (1970) reported tadpole presence in 26 of the 74 streams they sampled. In making designations for Kootenai region streams, I consulted the fish biologist, Dave Dorman, of the Libby Ranger District, Kootenai National Forest (Dave Dorman, U.S.F.S., Libby Ranger District, pers. comm.). Using information from Forest Service records and personal observation, Dorman (pers. comm.) provided information on streams where tadpoles were present and absent.

Originally, I planned to sample ten frog streams in both the Flathead and Kootenai regions to examine climatic influences on density. In each region, I also planned to sample physical characteristics of ten non-frog streams to determine any relationship between habitat and tadpole density and distribution. I was able to sample ten frog and ten non-frog streams in the Flathead region as planned. However, due to limited site accessibility, I only sampled four frog and seven non-frog streams in the Kootenai region. Sampling occurred from late June to early August, 1995. To determine the effect of various habitat features on tadpole density and distribution, I sampled streams with a variety of environmental conditions (Table 1).

Study Area

I conducted my study in 1st- and 2nd-order perennial tributaries of the Flathead River (Swan and Flathead Ranges) and the Kootenai River (Cabinet and Purcell Mountains). Vegetation in the Flathead and Kootenai regions reflects the influence of moist maritime air masses (Arno 1979). However, cold arctic air masses pass through the Flathead Valley, limiting tree species such as Thuja and Tsuga to areas where large lakes mediate the local climate. Average summer temperatures of streams in the Flathead are less than 10 °C (Aagaard 1969). The mildest climatic conditions in northwestern Montana exist in the Kootenai region. Here vegetation more closely resembles that in Northern Idaho, indicative of a warmer and moister coastal climate (Arno 1979). In Kootenai streams, average summer temperatures are about 11 °C (Aagard 1969). Average annual precipitation in subalpine forests of northwestern Montana ranges from 101 to 165 cm (Arno 1979).

Methods

Sampling

In each frog stream, I sampled ten riffles, 20 m apart, for tadpole densities and physical characteristics. In non-frog streams, I sampled physical characteristics in five riffles, also spaced 20 m apart. I did not sample tadpoles in non-frog streams

To collect tadpoles I placed the leading flat edge of a D-frame net perpendicular to flow (Hawkins et al. 1988). In a 0.1 m^2 area in front of the net I lifted and examined rocks for tadpoles. At each riffle I took five tadpole samples spaced evenly along a transect perpendicular to flow. After capturing them in the net, I placed tadpoles in a holding bucket, then measured their length to the nearest mm and returned them to the stream.

I used the following procedures to quantify physical features in all streams. At each stream I took water temperature measurements with a minimum-maximum thermometer that was left in place for a minimum of five days. Upon removing the thermometer, I recorded minimum (Tmin) and maximum (Tmax) temperatures. Using a canopy densiometer, I estimated riparian shading in the middle of each riffle, taking measurements in up- and downstream views and in both directions perpindicular to flow. For frog streams I measured physical characteristics along the same transect used to sample tadpoles. I measured width with a meter stick along a transect in the middle of each riffle. For depth I averaged measurements from three evenly spaced points along the transect. I estimated the current velocity of each riffle by recording the time a wood chip traveled a known distance of the stream. Using topographic maps I determined the aspect and elevation of each stream.

Analysis

We used stepwise regression to determine how much variation in tadpole size and abundance was associated with temperature and other habitat features. To determine which habitat features differed between the Flathead and Kootenai regions, we conducted discriminant analysis. We also used discriminant analysis to determine if differences in physical characteristics existed between frog and non-frog streams.

Results

Flathead and Kootenai Comparison

Tadpole density was almost an order of magnitude lower in the Kootenai than in the Flathead (Table 2). In contrast, average tadpole length (mm) was 1.4 times longer in the Kootenai than in the Flathead. In both regions combined, density correlated most highly with gradient, but also with canopy, depth, and elevation (Table 3). Tadpole length was most strongly correlated with density, but was also correlated with width (Table 4). Plots showing the relationship of temperature and habitat characteristics with tadpole size and density are shown in Figure 1. For Flathead streams, regression analysis showed that 60% of the variation in tadpole density was associated with Tmax, whereas length was not correlated with any variable.

Regressing temperature and physical characteristics on density and length was not feasible for Kootenai streams due to small sample size.

Three physical characteristics appeared to differ between the two regions (Table 2). Minimum temperature was about 2 C lower in Flathead streams than in Kootenai streams. Flathead streams were about 150 m higher in elevation and 2.5 times steeper in gradient than Kootenai streams.

Frog and Non-frog Comparison

Only gradient appeared to differ between frog and non-frog streams (Table 5). For streams in both regions combined, gradient was about 1.6 times higher in frog streams than in non-frog streams. We found similar results in comparing frog and non-frog streams in the Flathead region only, with gradients nearly two times higher in frog streams. Small sample size precluded similar analyses for Kootenai streams.

Discussion

Regional Comparison

Our analyses showed a significant difference in Tmin between the two regions, about 2 C colder in the Flathead. Tmax, also colder in the Flathead by about 1.5 C, did not differ significantly between the two regions. Minimum-maximum thermometers were left at a site for 5-14 days, and were in place at different times throughout the summer. Due to the influence of snowmelt in early summer, maximum temperatures do not occur until mid to late August. Given the seasonal variation and limited duration of temperature measurements, elevation is probably a better indicator of overall differences in temperature regimes among sites. This variability in temperature measurements could also account for the lack of significant difference in Tmax between the two regions.

In their sampling of over 70 streams in the Flathead River drainage, Franz and Lee (1970) found no tadpoles in streams with temperatures above 16° C. However, this temperature is considered optimal temperature for tadpoles in the Pacific Northwest (Hawkins et al. 1988) and Brown (1975) observed abnormal development of tadpoles at temperatures below 7.6° C. I therefore expected a positive relationship between temperature and both tadpole density and size, as temperatures approach 16° C in the warmest streams in this region.

Because climatic conditions were colder in the Flathead, we expected that tadpole densities and lengths would be smaller than in the Kootenai. Although length followed this pattern, the reverse was true for density. Density was associated with Tmax in the Flathead region. However, our regression analyses for both regions combined showed that neither length nor density were correlated with temperature as expected, although density was correlated with elevation, possibly a better indicator of temperature as explained above. Nonetheless, this does not explain why densities were nearly an order of magnitude lower in Kootenai streams. If elevation did indeed serve as a surrogate for temperature, we would still expect to see lower densities in the Flathead region.

The unexpected difference in tadpole densities between the two regions could be linked to other environmental variables. Tadpoles were more abundant and smaller in the Flathead, where stream gradients were significantly higher than in the Kootenai, which probably corresponds to the elevational difference between the regions (Table 2). In addition, sculpin were observed in the Kootenai region and are known to prey on tailed frog tadpoles (Feminella and Hawkins 1994). Feminella and Hawkins (1994) observed reduced activity of tadpoles in the presence of trout and gaint salamanders but not sculpin. The authors hypothesize that tadpoles have not evolved an effective mechanism for detecting sculpin. At their study site, tadpoles were scarce in the mainstem and lower-gradient tributaries where sculpin were abundant, even though physical habitat appeared to be near optimal conditions. Where sculpin were excluded by barriers upstream, tadpoles were abundant. Our observations from Flathead and Kootenai streams are consistent with this idea.

Predation by sculpin could explain the reduced densities and larger sizes in the Kootenai region. As densities were depressed by predation, any remaining tadpoles would have access to more food and thus would increase in size. The larger tadpoles would then be less susceptible to predation as they exceeded the gape size of sculpin. The largest Kootenai tadpole was 15 mm longer than the largest

Flathead tadpole. This size difference reflects the influence of predation. However, given the magnitude of the difference, it seems that temperature is still an important factor, though overwhelmed by the effects of predation in the Kootenai. If predation were not occurring in the Kootenai, we would expect tadpole sizes as well as densities to be larger than those in the Flathead.

Frog and Non-frog Stream Comparison

Gradient differed significantly between frog and non-frog streams, which is consistent with the idea of predation. However, no other enviornmental variables differed between the two stream types. Two possibilities exist for this lack of difference in variables besides gradient. One possibility is that variables I measured were not the most important to tadpoles. This idea is supported by Franz and Lee's (1970) assertion that tadpole density and distribution is highly correlated with naturally varying water quality factors such as pH, alkalinity, and dissolved oxygen (Franz, pers. comm.), factors that I did not measure. The other possibility is that my original assumptions about frog distributions (designation of frog and non-frog streams) were faulty. I found tadpoles in one Flathead stream originally designated as a non-frog stream, though densities were among the lowest of all Flathead frog streams. Thus it seems my original assumptions could be faulty. In summer 1994, Franz (pers. comm.) re-visited about 20% of the streams he sampled in the 1960's and found tadpoles at higher elevations in many streams originally reported as lacking tadpoles.

Conclusions

Temperature does appear to affect tadpoles as evidenced most strongly in size differences between the colder Flathead and warmer Kootenai regions. We expected a similar effect on density, though predation seems to mask the effect of temperature in the Kootenai region. Though I did not test for predation, our observations support this hypothesis, suggesting a need for further research. In addition, given the limited number of streams I was able to sample, there is need for additional research about the importance of temperature on tadpole density and distribution. Furthermore, the lack of significant difference in habitat variables I measured suggests that more research on the importance of other variables is needed.

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Table 1. Comparison of range in various physical stream features and biological characteristics for the Kootenai and Flathead regions. Tmin and Tmax are low and high temperatures recorded by minimum-maximum thermometers.

Region	Variable									
	Elevation (m)	Gradient	Tmin (C)	Tmax (C)	Velocity (m/s)	Canopy Cover (%)	Width (m)	Depth (m)	Tadpole Density (#/m²)	Tadpole Length (mm)
Flathead	976 - 1646	0.01 - 0.20	4 - 11	8 -18	0.29 -1.59	11.2 -84.6	1.7 -13.6	0.06 - 0.37	0.4 - 4.6	27 - 45
Kootenai	768 -1159	0.01 - .012	6 - 11	9 -16	0.40 -1.26	37.9 -74.6	1.9 - 6.8	0.05 - 0.21	0.2 - 0.5	29 - 63

Table 2. Comparison of mean physical and biological characteristics of streams in the Flathead and Kootenai regions. Standard error of means given in parentheses. Tmin and Tmax are low and high temperatures recorded by minimum-maximum thermometers.

** indicates significance at the 0.10 level, * at the 0.05 level

Region	Variable									
	Elevation (m)	Gradient	Tmin (C)	Tmax (C)	Velocity (m/s)	Canopy Cover (%)	Width (m)	Depth (m)	Tadpole Density (#/m²)	Tadpole Length (mm)
Flathead	1176 (42) *	0.07 (0.01) **	6.8 (0.4) *	11.8 (0.6)	0.92(0.07)	47.9 (4.3)	4.4 (0.6)	0.16 (0.02)	2.2 (1.4)	37 (7)
Kootenai	976 (57)	0.04 (0.01)	8.9 (0.5)	13.3 (0.8)	0.82 (0.10)	56.9 (5.6)	4.0 (0.7)	0.12 (0.02)	0.4 (0.1)	56 (14)

Table 3. Stepwise regression of tadpole density on physical features. Standardized coefficients for all significant variables are given.

Variable	Standardized Coefficient
Gradient	0.682
Canopy	-0.388
Depth	0.402
Elevation	0.353

Table 4. Stepwise regression of tadpole length on physical and biological characteristics. Standardized coefficients for significant variables are given.

Variable	Standardized Coefficient
Width	0.480
Density	-0.562

Table 5. Comparison of mean physical characteristics of Frog and Non-Frog streams. Standard errors are within parentheses. Tmin and Tmax are low and high temperatures recorded by minimum-maximum thermometers. ** indicates significance at the 0.10 level, * at the 0.05 level

Region	Variable									
	Elevation (m)	Gradient	Tmin (C)	Tmax (C)	Velocity (m/s)	Canopy Cover (%)	Width (m)	Depth (m)	Tadpole Density (#/m²)	Tadpole Length (mm)
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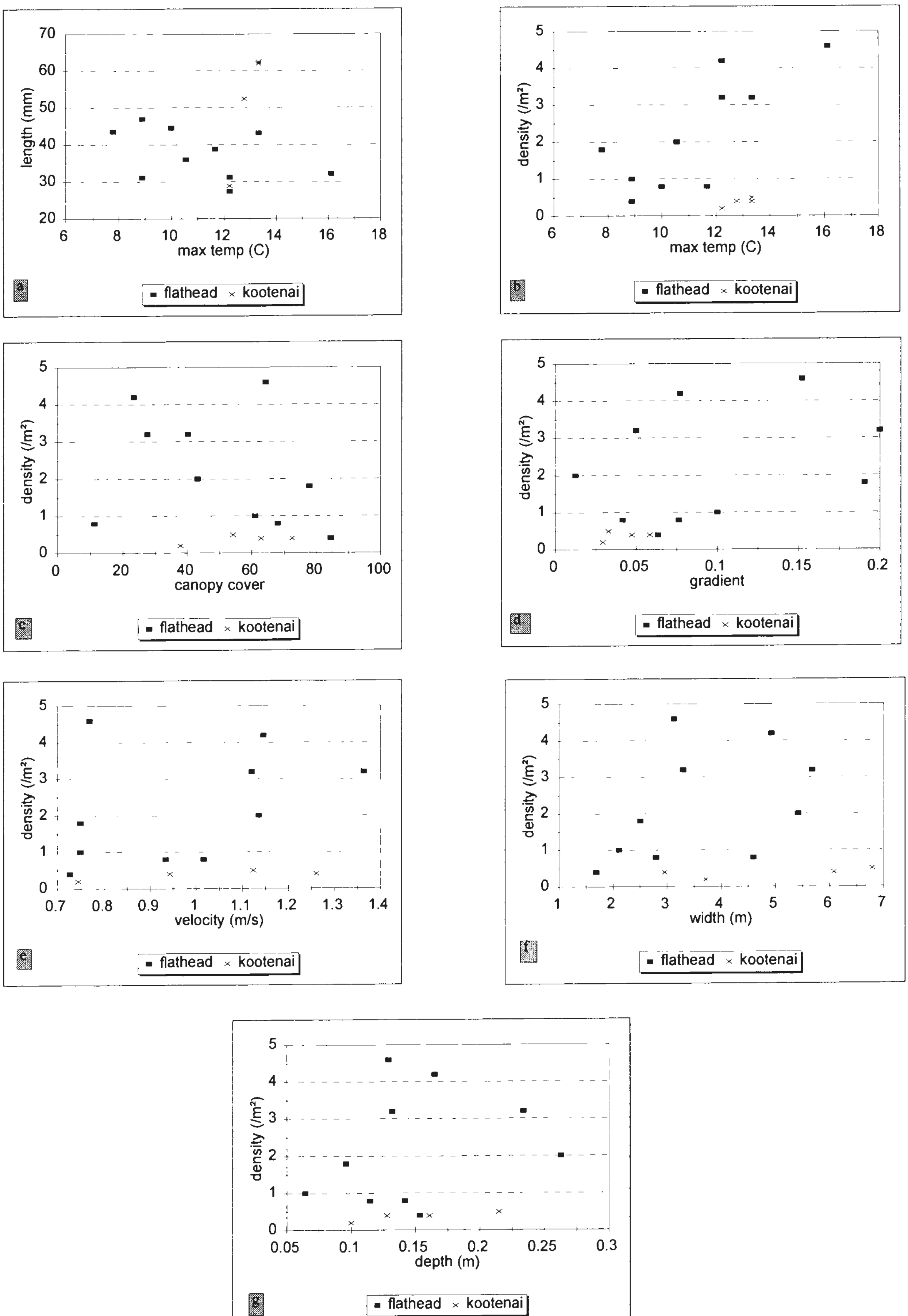

Figure 1. Plots of (a) length versus maximum temperature and density versus (b) maximum temperature, (c) canopy cover, (d) gradient, (e) velocity, (f) width, and (g) depth for individual streams in the Flathead and Kootenai regions.