Development of a Database to Support a Multi-Scale Analysis of the Distribution of Westslope Cutthroat Trout

Final Report

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Bruce Rieman, Jason Dunham, and Jim Peterson

U.S.D.A. Forest Service
Rocky Mountain Research Station
316 E. Myrtle
Boise, Idaho 83702

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Introduction

Westslope cutthroat trout (*Oncorhynchus clarki lewisi*) are part of a declining complex of subspecies in the inland United States (Allendorf and Leary 1988; Gresswell 1988; Young 1995; Duff 1996; Thurow et al. 1997). Many factors, including habitat loss and degradation, interactions with non-native salmonid fishes, and angler harvest have been identified as contributing to declines in westslope cutthroat trout populations (Rieman and Apperson 1989; McIntyre and Rieman 1995). Westslope cutthroat trout (WCT) occupy a geographically broad range that straddles the Continental Divide extending north from the Salmon and Clearwater drainages of central Idaho to the Saskatchewan River in southern Alberta, Canada (Behnke 1992). Recent estimates based on observed and modeled distributions, with a resolution of large (approx. 8,000 ha) watersheds, indicate WCT occupy about 85% of this potential range within the United States, but that strong populations (stable with moderate to high abundance, full expression of life history, and no hybridization) comprise only 22% of this total (Thurow et al. 1997). Regional estimates with finer resolution (stream reaches) are more pessimistic and suggest that such strong populations may be limited to less than 2.5% of the historical range in Montana (Liknes and Graham 1988) and 4 to 11% in Idaho (Rieman and Apperson 1989). WCT is recognized as a species of special concern throughout its range and is considered a sensitive species by the U.S. Forest Service. Recently a petition was filed with U.S. Fish and Wildlife Service to list WCT as threatened under the Endangered Species Act. Because they have a large geographic range, a listing would have wide-ranging management implications. Therefore, research is needed to identify opportunities for proactive measures to conserve and restore WCT habitats and populations. A variety of research needs have been identified for inland cutthroat trout (Young 1995). For WCT, these needs include the development of better distribution and life history information, habitat relations, and an understanding of the magnitude of displacement and risks posed by non-native salmonids (McIntyre and Rieman 1995).

Perhaps the most fundamental research need is to identify the primary elements that influence WCT distribution and produce the spatial structuring of populations at local and regional scales. Aquatic habitats are organized by processes that can ultimately be traced to landscape-scale influences on stream catchments or watersheds (e.g., Hynes 1975; Frissell et al.

1986; Schlosser 1991). A growing body of work confirms that both physical and biological processes that operate at landscape or even larger scales may influence both the availability of habitats and the dynamics of populations. Failure to recognize the fundamental processes structuring both local and regional populations may confound attempts to understand general fish-habitat relationships at finer scales (Dunham et al. In review) as well as our ability to define fundamental units for conservation (Ray In press). Failure to account for large-scale constraints may explain the lack of generality in fine-scale, habitat-based models (e.g., Fausch et al. 1988; Dunham et al. In review). Recent attempts to explain and model fish distributions based on geological, geomorphic and landform, and climate characteristics have met with some success (Lanka et al. 1987; Bozek and Hubert 1992; Nelson et al. 1992; Lee et al. 1997). Other work suggests that the size, quality, distribution, and independence of habitats may also affect the distribution and persistence of some populations (Rieman and McIntyre 1995; Dunham et al. 1997; Dunham and Rieman 1999; Rieman and Dunham In press). Without some understanding of the physical and biological processes that control the creation and maintenance of potential habitats, and the dynamics and distribution of populations, fine-scale studies will always be vulnerable to the confounding effects of larger scale processes (e.g., Dunham and Vinyard 1997).

Technological advances in methods to acquire and analyze information have dramatically increased the ability of aquatic ecologists to study large-scale patterns. A particular problem, however, has been the lack of consistent, reliable data collected across broad gradients of environmental characteristics. The ability to accurately estimate fish density and species presence/ absence is influenced by sampling method, the fish species and individual sizes, and the habitat characteristics of the area sampled (Bayley and Dowling 1993; Peterson and Rabeni In review). Further, few research projects or management programs have the resources to support surveys over large regions. Combining information among projects is a potential alternative, but may be frustrated by inconsistent or poorly supported methods and the lack of a common experimental design. The potential efficiency of using existing data, however, makes it important to explore the option. Thus, our objective was to develop a database that could be used to examine regional and landscape-scale patterns and their influence on WCT distribution. It is not clear, however, whether data from disparate sources can be useful to that end. We had three primary objectives.

First, was the development of the database. We obtained, summarized, and spatially located site scale data on the occurrence and/or abundance of WCT and other species including brook trout, across a major portion of the WCT range. We specifically sought observations over a broad geographic and topographic range with the hope of representing important environmental gradients, particularly those related to climate and presumably stream temperatures. As part of the data development we summarized existing landscape coverages including landform, climate, and relative degree of human disturbance for the watersheds linked to streams and sites included in the database.

Second, was an evaluation of the quality and utility of the data for the analysis we envisioned. We considered the sample consistency, sampling efficiency, and detectability for WCT based on the methods employed in the data sets we obtained. We also considered the representativeness of the resulting collection of observations. We attempted to identify potential biases and limitations that might confound our analysis and guide the development of more suitable information.

Data consistency and quality were examined by comparing observations of variables that should be relatively stable (i.e., channel gradient and width) at sites sampled across multiple years. Our analyses of sampling efficiency were based on models created with relative sampling efficiency data collected by personnel at the Rocky Mountain Research Station (RMRS). The primary objective was to provide a first approximation of sampling efficiencies, detectability, and *post hoc* estimates of the probability of occurrence for WCT and other fishes in the database. Data representativeness was addressed by comparing the distributions of landscape characteristics associated with streams in the data set and those representing the region as a whole.

Third, was an analysis of patterns in occurrence and abundance. We were particularly interested in geographic scale patterns that might be associated with the role of climate and stream temperature and local scale effects of stream size and gradient as potential landscape characteristics that may constrain the distribution of potential habitat for WCT. Originally we also anticipated an analysis including management related disturbance and introduced fishes as second order variables potentially influencing the abundance and occurrence of WCT. Concerns about limitations of the data and our ability to accurately represent the higher level effects, as well as our ability to collapse data to individual watersheds lead us to abandon that analysis.

Occurrence and abundance of WCT and brook trout were considered as responses to environmental gradients important at geographic and local (site) scales. Geographic patterns in the distribution of WCT were explored in an effort to define critical landscape characteristics to delineate suitable habitats. We analyzed factors that may play an important role in terms of limiting abundance or population density of WCT within suitable habitats. These included stream width, gradient, and density of nonnative brook trout. We focused our analyses on occurrence and abundance of small, presumably juvenile fish. The distribution of juveniles should correspond more closely to spawning and rearing areas (than that of all fish), which are key to the persistence of local populations (Rieman and Dunham In press).

We view this work as a preliminary and exploratory analysis. Data consistency, sampling efficiency and detectability, and representativeness, all emerged as important issues. Both the lack of and the presence of patterns may result from confounding effects associated with the nature of the data. We cannot offer any definitive result regarding important environmental gradients influencing the distribution of WCT. Documentation and consideration of the issues as well as the patterns emerging in our results, however, should provide important guidance for further work.

Methods

Database Development

Our primary objective was to develop a consistent database of site-specific information on WCT occurrence and abundance and environmental characteristics that potentially influence their distribution and abundance. We sought to develop a broad representation of sites across a substantial portion of the species' range along three major environmental gradients: elevation and longitude/latitude (as a surrogates of climate and stream temperature), stream size (width), and stream gradient. We also incorporated ancillary information on habitat characteristics, sampling conditions, and biota (i.e., occurrence of other species), when possible. Our efforts were focused on the identification, verification, and summarization of appropriate data sources.

Potential data sources were identified through a review of gray and published literature and through direct contact with biologists working throughout the region. We made a particular effort to locate data that provided a broad geographic representation within the known range of WCT as identified by Lee et al. (1997). Observations were included in the database only when they met several criteria: (1) sampling methods were documented either through written work or direct correspondence with the principal source; (2) multiple sites were sampled within individual streams and multiple streams were sampled within at least one larger river subbasin; (3) the length of each sample site was recorded; (4) sample sites represented a minimum of 30 m of continuously sampled stream or multiple smaller sites were sampled in close proximity that could reasonably be pooled to represent at least 30 m of stream within a single geomorphic reach type (defined by gradient and confinement); (5) width was recorded in a fashion that represented a reasonable mean of the sample site; (6) the site could be spatially located either with direct geographic coordinates or by designation on a typical 1:24,000 topographic quad; (7) the sampling date was recorded; and (8) WCT were a principal species targeted and recorded in sampling. We required only designation of occurrence for WCT, but many observations included an estimate of abundance, occasionally by size class. Ancillary information included streambed gradient when measured on the site, temperature and visibility at time of sample, mean depth, and occurrence and abundance of other salmonids, notably brook trout (Appendix A).

Data sources.- We used two primary sources of data: (1) a compilation of observations from multiple, relatively small studies scattered throughout the range; and (2) the Idaho Department of Fish and Game (IDFG) General Parr Monitoring database (GPM). A potential third source, collected by the Montana Department of Fish Wildlife and Parks, was not incorporated because sampling sites could not be spatially located with a precision of better than several kilometers, which represented potentially substantial error in the estimation of site elevations. Because the relationship between WCT occurrence and climate (represented by elevation, latitude and longitude) was of primary interest, these sites were of limited value. Summary of several studies noted above, however, did provide substantial coverage of the range of WCT in Montana.

The compilation of small studies included 909 sites in Idaho and Montana (Figure 1). These data were obtained directly from state and federal agencies as unpublished or archived data and from published reports (Table 1). Two data sets, one for the Coeur d=Alene basin in Idaho (Dunnigan 1997) and the second for the Bitterroot basin in Montana (Rich 1996) were from Master=s research projects supported directly by the RMRS. All sites were sampled either by electrofishing (16.2% of observations), snorkeling (82.4%), or prima cord (1.4%). All sites had documented sampling protocols that identified cutthroat trout as primary target species.

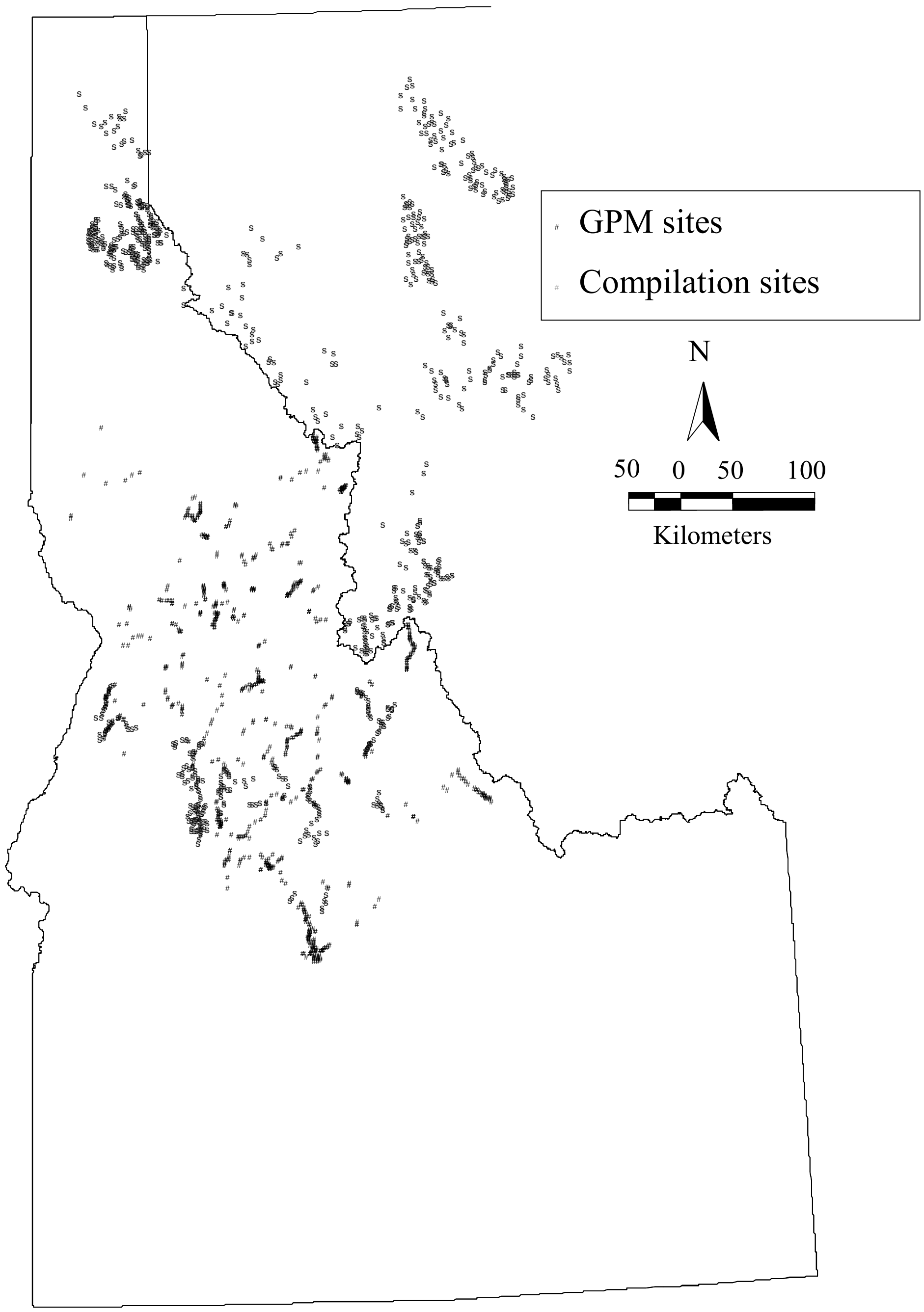

Figure 1. Distribution of sites included in the westslope cutthroat trout database.

Table 1. Number of sites and source of data by basin for observations obtained directly from state and federal agencies as unpublished or archived data, and from published reports.

Number Of Sites	Sites with Cutthroat Present	Basin	Source
124	45	Middle Fork Salmon R.	Unpublished data[1]
92	7	South Fork Salmon R.	Platts 1974, 1979, Unpublished data[2]
28	22	Pend Oreille Lake	Hoelscher and Bjornn 1988
66	62	Clark Fork R.	Unpublished data[3]
57	35	Swan R.	Leathe et al. 1985
87	79	Middle Fork Flathead R.	Weaver et al. 1983
39	4	Payette R.	Unpublished data[4]
63	35	Blackfoot R.	Peters 1990
122	119	Bitterroot R.	Unpublished data[5] Clancy 1993
231	225	Coeur d' Alene R.	Unpublished data[6]

[1] USFS R1/R4 fish survey. K. Overton. USFS Rocky Mountain Research Station, Boise, Idaho.
[2] W. Platts, USFS Rocky Mountain Research Station, Boise, Idaho.
[3] D. Kramer and B. Riggers, USFS Lolo National Forest, Missoula, Montana.
[4] D. Olson, USFS Cascade Ranger District, Cascade, Idaho.
[5] Unpublished data from C. Rich 1996.
[6] Unpublished data from J. Dunnigan 1997.

The remaining data, 822 sites, was from the IDFG salmon and steelhead GPM database. GPM sites were sampled by IDFG, U.S. Forest Service, Nez Perce Tribe and Shoshone-Bannock Tribe biologists between 1984 and 1997. Sites were distributed across the Salmon and Clearwater River basins in Central Idaho (Figure 1) and many were sampled in multiple years.

All sampling was conducted via snorkeling at established stream sites (approx. 100 m long) throughout the known range of salmon and steelhead. Methods were well documented, and were generally consistent with established protocols (Thurow 1994). Although there were nearly 1,400 sites in the GPM database, we were unable to use many sites because they could not be spatially located or site/habitat measurement data (site length, width, gradient, etc.) were either missing or key identifiers, such as site name, had been recorded inconsistently. This may have been the result of several years of monitoring by different biologists and crews with differing protocols.

Site location.- The locations of sites from the small studies were either noted in publications, on maps provided by the biologists responsible for collection of the data, or in the form of geographic positioning system (GPS) coordinates. For the 822 GPM sites, the geographic location of each was determined from descriptions or directions in field notes, IDFG annual reports, or direct contact with the biologist responsible for the data. As a quality control check, the locations of the sites were recorded on 1:24,000 topographic maps, given a unique site-ID, and shown to the biologists responsible for verification. These locations were then digitized from the topographic maps to a GIS coverage. Using an overlay process, we annotated each site with the name of the topographic map where it was located and generated a table of site-ID and quad name. Each observation was then checked against the points marked on the topographic maps to validate the accuracy of the GIS coverages. Some sites were located in the field by biologists using a geographic positioning system (GPS). These locations were converted directly into a GIS coverage. The final coordinates for all observations were reported in a customized UTM zone (termed “ITM” units) where the central meridian is shifted 3 degrees east to include all observations in the database. The origin for this customized zone is the equator and -114 degrees longitude. The same false northing and easting used by standard UTM to eliminate negative coordinates were applied here.

Elevation.- Elevation was estimated for each site in the GPM database and Coeur d=Alene data by overlaying point coverage of site locations on a USGS digital elevation model (DEM) with a grid resolution of 30 m. Results of a scatter plot of DEM generated elevations with elevations read from a topographic map for 89 random points, showed no meaningful difference between methods (Figure 2). All other sites had elevations reported and were not overlaid to generate an elevation for the database.

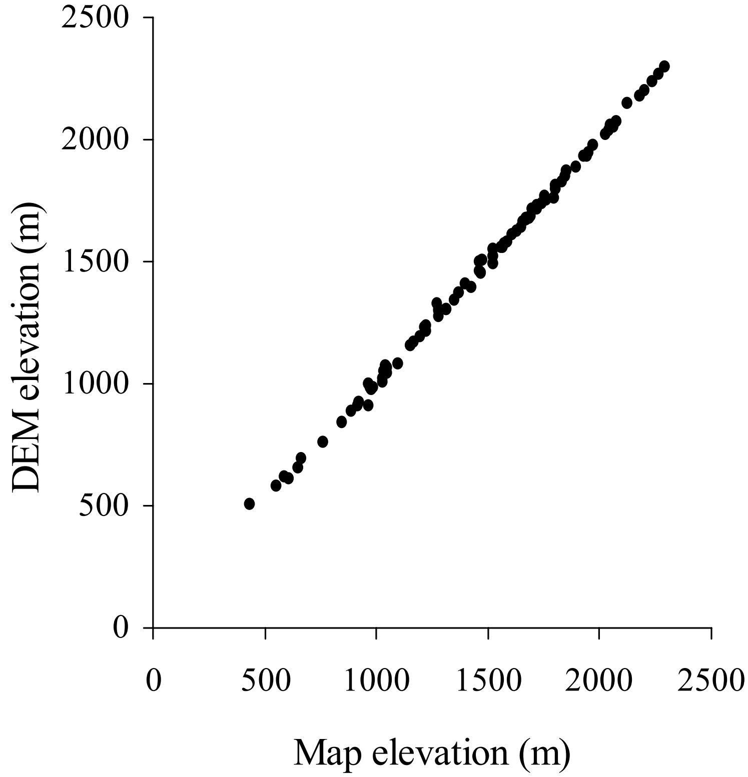

Figure 2. Comparison of site elevations derived from digital elevation models (DEM) with elevations derived from topographic map locations.

The final database is a composite of all sources, with fish and site measurement data (e.g., habitat) combined. Although the emphasis for this report is WCT, the database includes information on brook trout, bull trout, and other species and a variety of habitat measurements (Appendix A). The complete database has 1,731 sites with 4,970 observations when including multiple years. Approximately 650 sites had enough information to examine the influence of sampling efficiency and detection probability on data quality, as described below.

Data Quality and Utility

Consistency.- Although stream width and gradient may vary among years and seasons, extreme variation or large measurement error could confound analyses of underlying relationships with fish abundance or occurrence. Thus, we examined the consistency of physical habitat measurements by comparing repeated measurements of stream width and gradient. These characteristics should change little across time at sites that were sampled on multiple occasions.

Sampling Efficiency and Species Detection.- We define sampling efficiency as the proportion (or percentage) of fish, in a given area, that are captured or observed during sampling. To examine the potential influence of sampling efficiency on WCT data quality, we first modeled the efficiency of snorkeling and single pass electrofishing relative to removal estimates of WCT abundance. These data were collected by RMRS personnel as part of a sampling efficiency study (R. Thurow, unpublished data). The effects of individual predictor variables (e.g., depth, visibility) and combinations of uncorrelated predictor variables (Table 2) on sampling efficiency were estimated using logistic regression (Agresti 1990). Predictor variables were considered statistically significant at $\alpha = 0.05$ and residuals were inspected for outliers, constancy of variance, and independence.

Table 2. Predictors for day snorkeling and single pass backpack electrofishing relative efficiency models[1]. Sign preceding the predictor names indicate the direction of the influence. All predictors were statistically significant at $P < 0.05$.

Day snorkeling		
	+ Depth	+ Gradient
	+ Width	+ Water temperature
	+ Visibility	
Single pass electrofishing		
	+ Gradient	- Width
	+ Water temperature	

[1]Sampling efficiency was estimated relative to removal estimates of WCT abundance.

Predicted sampling efficiency was calculated following Bayley (1993) as:

$$\pi = \{1 + \exp(-(\beta_0 + \beta_i x_i ...))\}^{-1} \tag{1}$$

where π = predicted efficiency as a fraction, β_0 is the constant, β_i are the model coefficients, and x_i are the corresponding values for the independent variables. Using the efficiency models, we estimated the expected sampling efficiency for each observation in the WCT database that included the appropriate stream habitat data.

The probability of detecting the occurrence of WCT was estimated for sites where WCT were not detected following Bayley and Peterson (In review) as:

$$h = \sum_{i=1}^{\infty} [1 - (1-\pi)^i] \cdot \left[\frac{\Gamma(k+i)}{\Gamma(i+1) \cdot \Gamma(k)} \cdot \left[p^k \cdot (1+p)^{(-k-i)} \right] \right] \tag{2}$$

where *h* is the probability of detecting WCT in the sampled site, π is the sampling efficiency (from above), and *k* and *p* are the parameters (as described in Pielou 1977) from a negative binomial estimate of fish abundance. These estimates were computed using site specific stream habitat data (Table 3) and a negative binomial regression model fit with the WCT removal estimates from the sampling efficiency study (above).

Table 3. Predictors used to estimate fish abundance with negative binomial regression model (top), and fish occurrence with an extended K-nearest neighbor landscape model (bottom) during cross validation of probability of detection estimates. Sign preceding the fish abundance model predictor names indicate the direction of the influence.

Fish Abundance Model
+ Size of the area sampled
+ Site elevation and (-) quadratic term
- Mean depth
- Gradient
Probability of Subwatershed Occurrence Model
Streambank erosion hazard
Base erosion index
Drainage density (km/km^2)
Mean elevation (m)
Soil texture coefficient
Number of contributing upstream sub-watersheds
Mean annual temperature (C)
Mean annual precipitation (mm)
Mean road density (km/km^2)
Area weighted average midslope (degrees)
(Langley's) mean annual solar radiation loading

The removal estimates (used to fit the negative binomial regression model) are generally biased low (Buttiker 1992; Riley et al. 1993) and, as such, our estimates of relative sampling efficiency and probability of detection are most likely biased high. Unfortunately, we have no means to evaluate the ‘true’ accuracy of our probability of detection estimates without knowledge of the true distribution and abundance of WCT (i.e., a baseline). However, assuming that occupied sites are always occupied (i.e., during sampling, across years), the proportion of sampling occasions in which WCT were detected at multiply sampled sites could provide a baseline for an examination of *relative* accuracy. Therefore, we examined the *relative* accuracy of our probability of detection estimates using data for occupied sites that were sampled on three or more occasions. In this analysis, habitat measurements and sampling efficiency estimates for individual sites were averaged across sampling occasions. The "average" probability of detection was then estimated using average values of stream habitat characteristics and the negative binomial regression models (above) and average sampling efficiency estimates. Note that our baseline was probably optimistic (i.e., biased high) because we considered only sites where WCT were actually detected.

At many of the non-detection sites, WCT absence may have been due to inadequate sampling effort (e.g., small sites) or difficult sampling conditions (e.g., deep, turbid streams). Thus, there remained the possibility that these sites were truly occupied. To quantify this, we estimated Bayes' posterior probabilities of occurrence for non-detection sites following Bayley and Peterson (In review) as:

$$P(F \mid Co) = \frac{P(Co \mid F) \quad P(F)}{P(Co \mid F) \quad P(F) + P(Co \mid \sim F) \quad P(\sim F)} \tag{3}$$

where *P(F)* is the prior estimate of probability of occurrence using the abundance estimate from the negative binomial model, *P(Co|F)* is the probability of not capturing WCT when present (i.e., one minus the probability of detection from above), *P(Co|~F)* is the probability of not capturing WCT when absent (i.e., 1), and *P(~F)* is the probability of WCT absence.

Representativeness.- To assess the representativeness of the sampled streams, we assumed that watershed-scale features (e.g., valley physiography and land use) influenced stream habitat characteristics. Thus, the representativeness of sampled streams was indirectly assessed by comparing the landscape characteristics of 6^{th} code U.S. Geological Survey hydrologic units (subwatersheds) containing sampled streams to those with known populations of WCT or at least a 50% probability of containing WCT in the Interior Columbia River Basin. Landscape data were obtained from the U.S. Forest Service Interior Columbia Basin Ecosystem Management Project (ICBEMP; Quigley and Arbelbide 1997) and estimates of the probability of WCT occurrence were as described in Lee et al. (1997).

Patterns in Distribution

Geographic variation.- Elevation is generally correlated with climatic and geomorphic characteristics that may be important in determining distribution limits of fish within watersheds (Rieman and McIntyre 1995; Dunham and Rieman 1999; Dunham et al. 1999). Previous studies of closely related species, such as Lahontan cutthroat trout (*O. c. henshawi*), reported geographic variation in the elevation of distribution limits to regional climatic gradients (Dunham et al. 1999). Presumably, similar gradients would be apparent for WCT, particularly near the southern edge of the species= range, where temperature may be an important limiting factor. Thus, we hypothesized that, at a geographic scale, elevation of WCT downstream distribution limits would change as a function of latitude and longitude.

We used logistic regression to relate occurrence of small (total length < 100 mm) or any (all sizes) WCT to latitude (indexed by ITM northings), longitude (ITM eastings), elevation, density of nonnative brook trout, stream width and gradient, and maximum summer air temperatures (see Lee et al. 1997). We examined only the signs of the coefficients and their statistical significance (Ramsey and Schafer 1996). Given questions regarding data quality (see below), we did not feel it was appropriate to report specific estimates of model parameters.

Local variation.- Variables related to density of WCT within sites included stream gradient, stream size (as indexed by stream width), and occurrence of nonnative brook trout. Previous work on Yellowstone cutthroat trout (*O. c. bouvieri*) indicates cutthroat trout may avoid stream habitats with gradients exceeding about 10% (Kruse et al. 1997), but this pattern is not universal (Dunham et al. 1999). Stream width may have important effects on fish density due to the fact that stream-living salmonids defend two-dimensional feeding territories (Grant et al. 1998). Therefore, stream width may impose an upper limit on the density of WCT. The effects of these two factors may be modified by interactions with native and nonnative salmonids, particularly nonnative brook trout (Fausch 1989; Bozek and Hubert 1992; Shepard and White 1998; Dunham et al. 1999). Densities of cutthroat trout and brook trout were summarized for each data source in terms of fish per meter and area. To examine the response of small WCT and small brook trout in greater detail, we modeled relationships between density and stream width and gradient for both species. Interaction terms and quadratic effects were included in the models.

We used regression quantiles (Terrell et al. 1996; Scharf et al. 1998; Cade et al. 1999) to model fish-habitat relationships. In contrast to more conventional regression models, which attempt to model mean responses, regression quantiles allow an exploration of a range of limiting relationships. Most importantly, regression quantiles can model the upper bound of the relationship between density and explanatory variables (e.g., stream width and gradient). The upper bound is of particular interest if explanatory factors are thought to act as Alimiting@ factors (see Terrell et al. 1996; Cade et al. 1999 for details).

There are a number of alternative approaches to analyzing fish-habitat relationships. In this section, we used regression quantiles because we believed the approach more truly represented the form of the biological response to be modeled (i.e., a Alimiting factors@ model). One issue with use of regression quantiles is that many models are generated and selection among them may be difficult. Model selection as applied to more conventional approaches (e.g., Burnham and Anderson 1998) has not been explored for regression quantiles (B. Cade, USGS Midcontinent Ecological Sciences Center, Fort Collins, CO, personal communication). Here we used regression quantiles in what we consider to be an exploratory analysis of the data. We place emphasis on general, qualitative patterns rather than specific and (perhaps misleadingly) precise predictions of fish density.

Results

Data Quality and Utility

Consistency.- Plots of multiple year samples of stream width and gradient show substantial variation (up to 2 to 3 fold) among observations at the same site (Figure 3). Although paired observations were positively correlated, the data suggest there was substantial error in the physical habitat measurement at many sites. Widths and gradients can change with seasonal variation in stream flow and channel conditions (Gordon et al. 1992; Herger et al. 1996), but without far more detailed sampling within and among years, it is impossible to determine whether the variation is related to inherent variation in stream characteristics or sampling error.

The large variation in gradient measurements (that presumably should change least) suggests the latter is important.

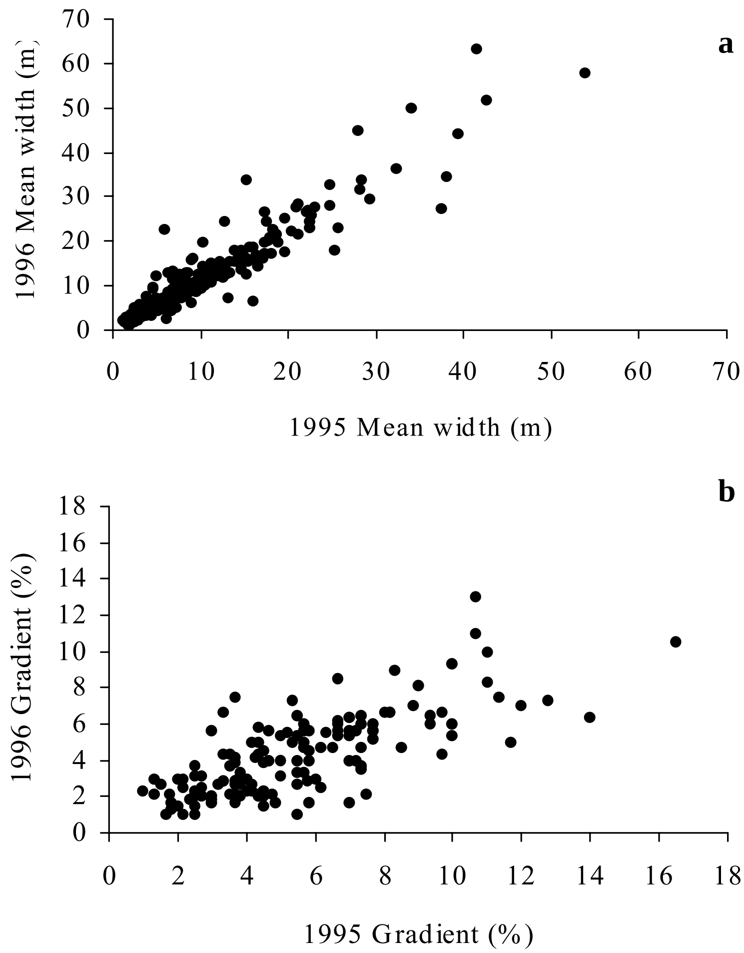

Figure 3. Comparison of (a) mean widths and (b) gradients sampled on successive occasions for sites with multiple observations in the westslope cutthroat trout database.

Sampling Efficiency and Species Detection.- An examination of the sampling efficiency model residuals and the dispersion parameter indicated that the data were overdispersed (i.e., the variance exceeded the presumed binomial). Overdispersion is often associated with modeling fish sampling efficiency due to the non-independence of fish responses and/or unmeasured factors affecting efficiency. Because this source of variance could also affect estimates of detection probabilities, we modeled sampling efficiency with two different methods, quasi-likelihood and beta-binomial regression. Quasi-likelihood and beta-binomial regression are similar to logistic regression in that they use dichotomous dependent variables. However, quasi-likelihood regression contains an additional element, the extrabinomial variance, to account for error variances in excess of assumed distributions (Williams 1982), whereas beta-binomial regression accounts for overdispersion by modeling the variance as a beta distribution (Prentice 1986). To choose the best fitting of these two methods, we used Akaike's information criteria with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989). AIC_c is an entropy-based measure used to compare candidate models for the same data (Burnham and Anderson 1998), with the best fitting model having the lowest AIC_c.

The beta-binomial model fit the relative sampling efficiency data better than quasi-likelihood (AIC_c: beta-binomial- 544.8 and quasi-likelihood- 632.7). Among the variables considered, water temperature, visibility, and stream gradient positively influenced snorkeling efficiency (Table 2). In contrast, mean stream wetted width negatively influenced the relative efficiency of single pass backpack electrofishing (Table 2). An examination of the distribution of estimated relative sampling efficiency under average sampling conditions (e.g., visibility, temperature) also suggested that snorkeling efficiency was, on average, less efficient and more variable than single pass electrofishing (Figure 4). Across gear-types, our estimates of relative sampling efficiency averaged 34%, but were highly variable among sites and sampling occasions (Figure 5).

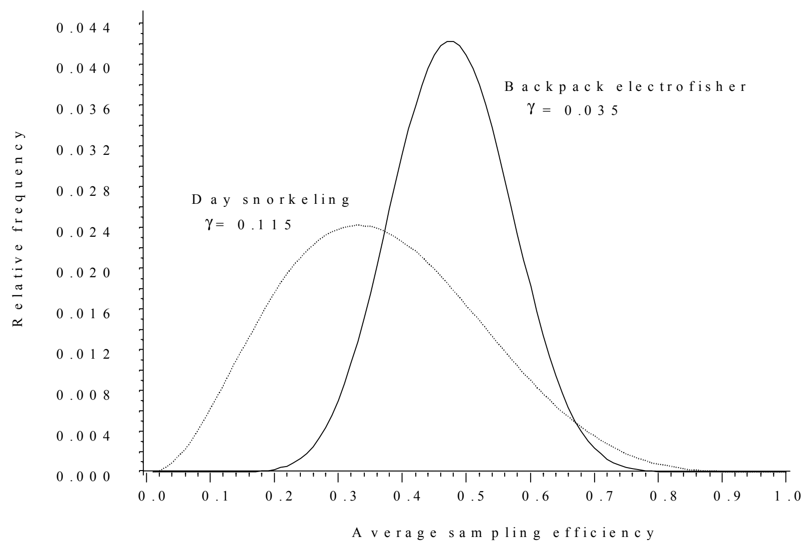

Figure 4. The estimated variablility of relative sampling efficiency for backpack electrofishing and day snorkeling under average sampling conditions for sites in the westslope cutthroat trout database. Estimates are based on average habitat characteristics during sampling, by method, and beta-binomial regression models with dispersion parameters, γ, also referred to as intraclass correlation coefficients. Note that sampling efficiency estimates are relative to removal estimates and are likely biased high.

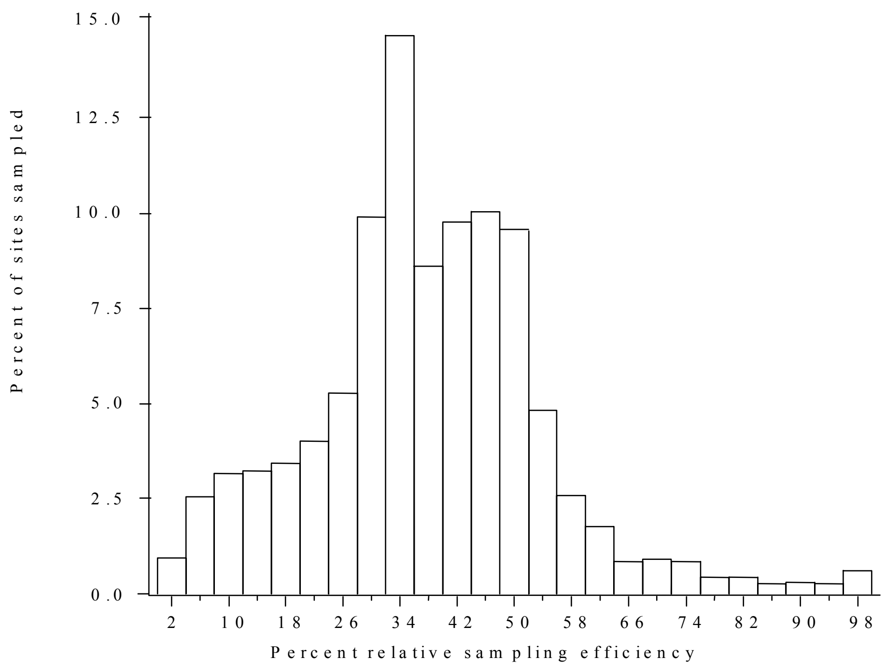

Figure 5. The distribution of relative sampling efficiency for sites in the westslope cutthroat trout database. Note that sampling efficiency estimates are relative to removal estimates and are biased high.

An examination of the detection probability baseline indicated that WCT were detected at multiple-sampled, occupied sites 41% of the time, but varied substantially among sites (Figure 6). Preliminary comparison of the relative accuracy of probability of detection estimates to this baseline suggested that our initial models tended to overestimate detection probabilities 28%, on average (Figure 6). This was likely the result of the low predictive ability of the negative binomial model due to model-fitting abundance data that contain large numbers of zeros (Welsh et al. 1996). In an effort to improve accuracy, we fit conditional models of WCT occurrence. These models differ from more familiar unconditional models by consisting of two parts: (1) a model of the probability of species' occurrence and (2) a model of species' abundance, given that it is present (Welsh et al. 1996). We estimated the probability of WCT occurrence for individual subwatersheds using landscape (Table 3) and large-scale WCT distribution data for the Interior Columbia River Basin (Lee et al. 1997) via an extended K-nearest neighbor classification technique (Peterson et al. 1998). Negative binomial models were then fit using data from streams in known occupied subwatersheds (i.e., conditional abundance data). The probability of species detection was estimated as the product of probability of subwatershed occupancy and the probability of detection (using the conditional abundance estimates), given subwatershed occupancy. An examination of the relative accuracy of the conditional model suggested that it was more accurate than the unconditional model (Figure 6). Consequently, the conditional model was used to estimate the relative detection probabilities for non-detection sites.

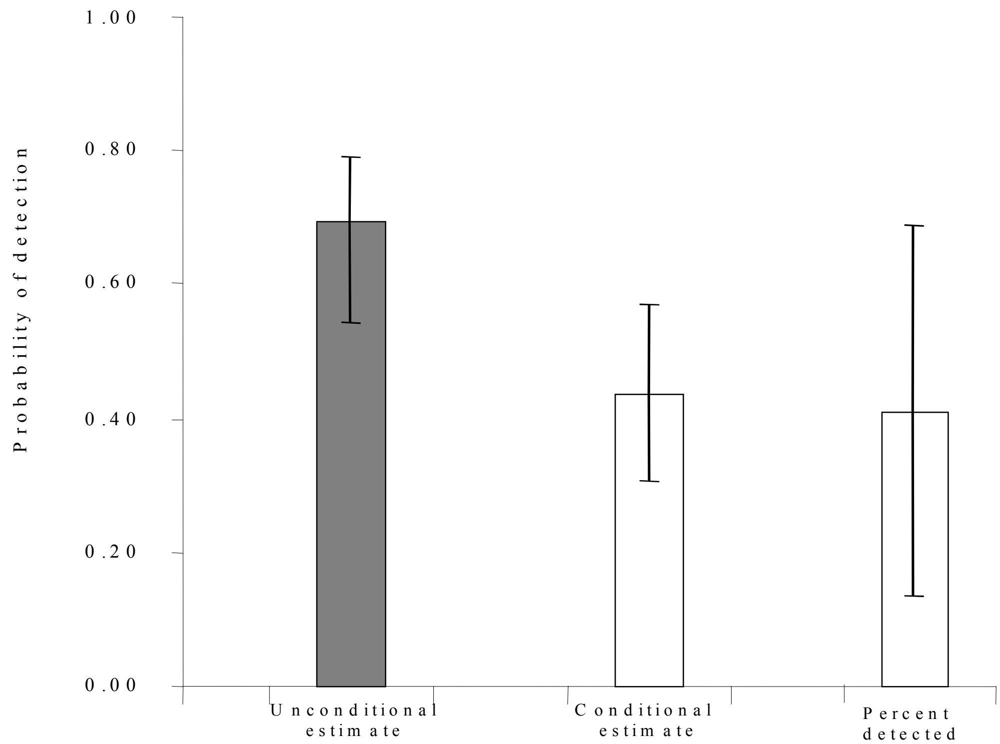

Figure 6. Comparison of unconditional and conditional estimates of the probability of detection for multiple-sampled occupied sites and the percent of sampling occasions that westslope cutthroat were detected (percent detected). Bars represent bootstrapped 95% confidence interbals.

On average, the relative detection probabilities for sites where WCT were not observed was 17% and exceeded 50% for only 22% of the sites (Figure 7). The very low relative detection probabilities suggested that sampling effort at these sites was probably inadequate. This is further reflected in the relatively high estimates of probabilities of occurrence for these sites (Figure 8).

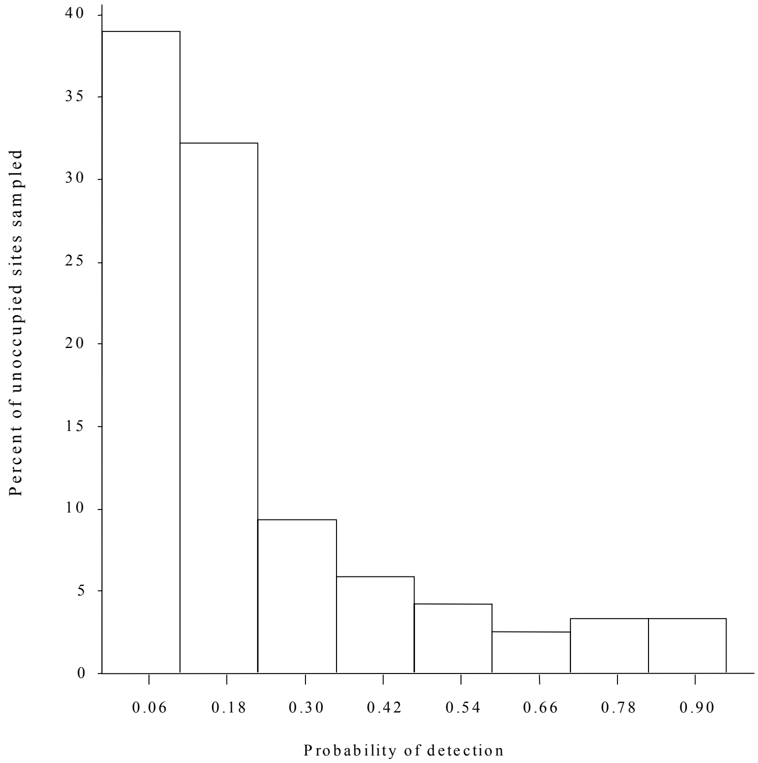

Figure 7. The distribution of probability of detection estimates for sites where WCT were not observed in the westslope cutthroat trout database.

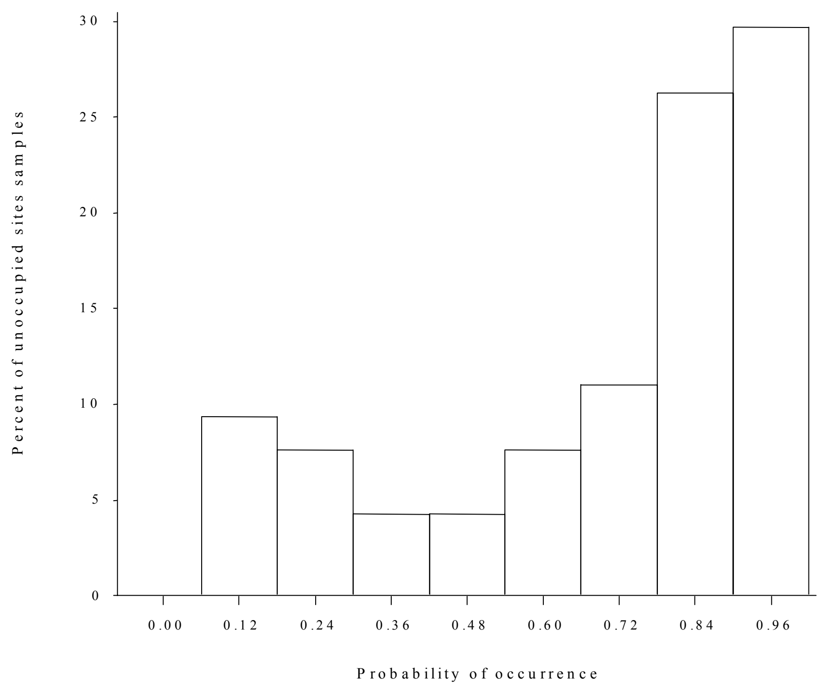

Figure 8. Empirical posterior Bayes' estimates of the probability that WCT actually occur at sites where they were not observed in the database.

Sampled streams were located in 451 6th code watersheds and represented, on average, 1.08% (range, 0.3-7.3%) of the total length of perennial streams per watershed. Comparisons of these watersheds to those in 2,689 6th code watersheds with a 50% or greater probability of containing WCT suggested a bias in site distribution. In general, sites included in the database were disproportionately located in flatter subwatersheds (Figure 9) with higher mean annual temperature and lower precipitation (Figure 10). These subwatersheds also tended to have higher management impacts and greater road densities compared to those within the Interior Columbia River Basin that were likely to contain WCT (Figure11).

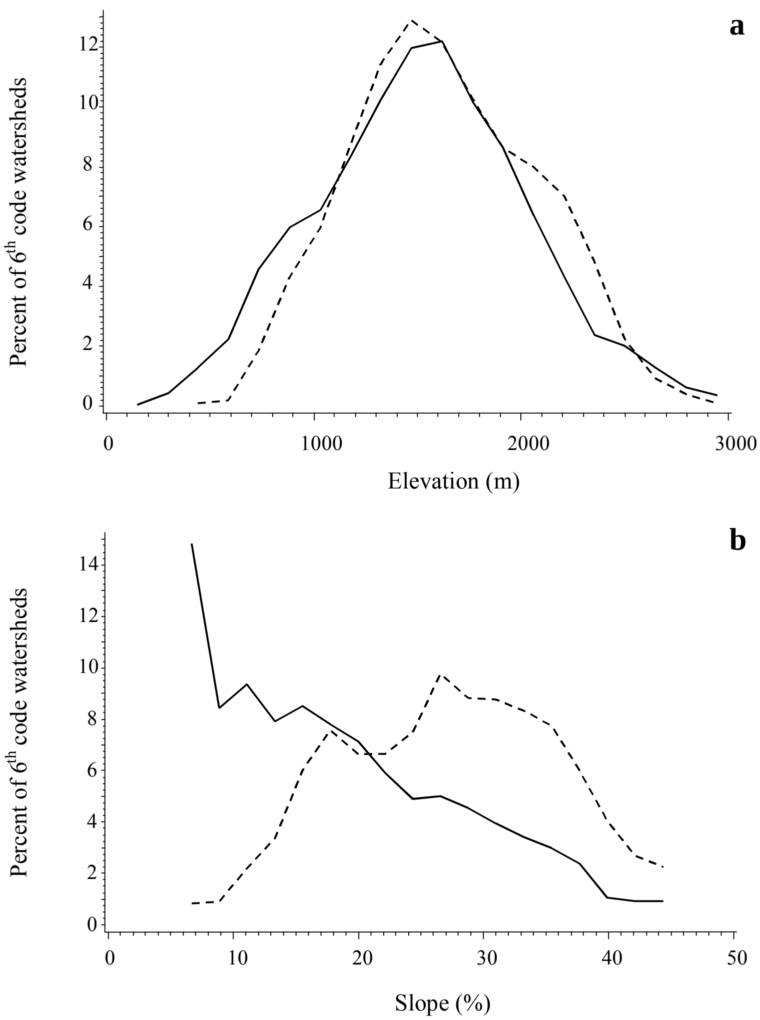

Figure 9. The frequency distributions of (a) elevation and (b) slope for 6th code watersheds in the Interior Columbia River Basin with $\geq$ 50% probability of westslope cutthroat trout presence (broken) and 6th code watersheds containing sampled streams (solid).

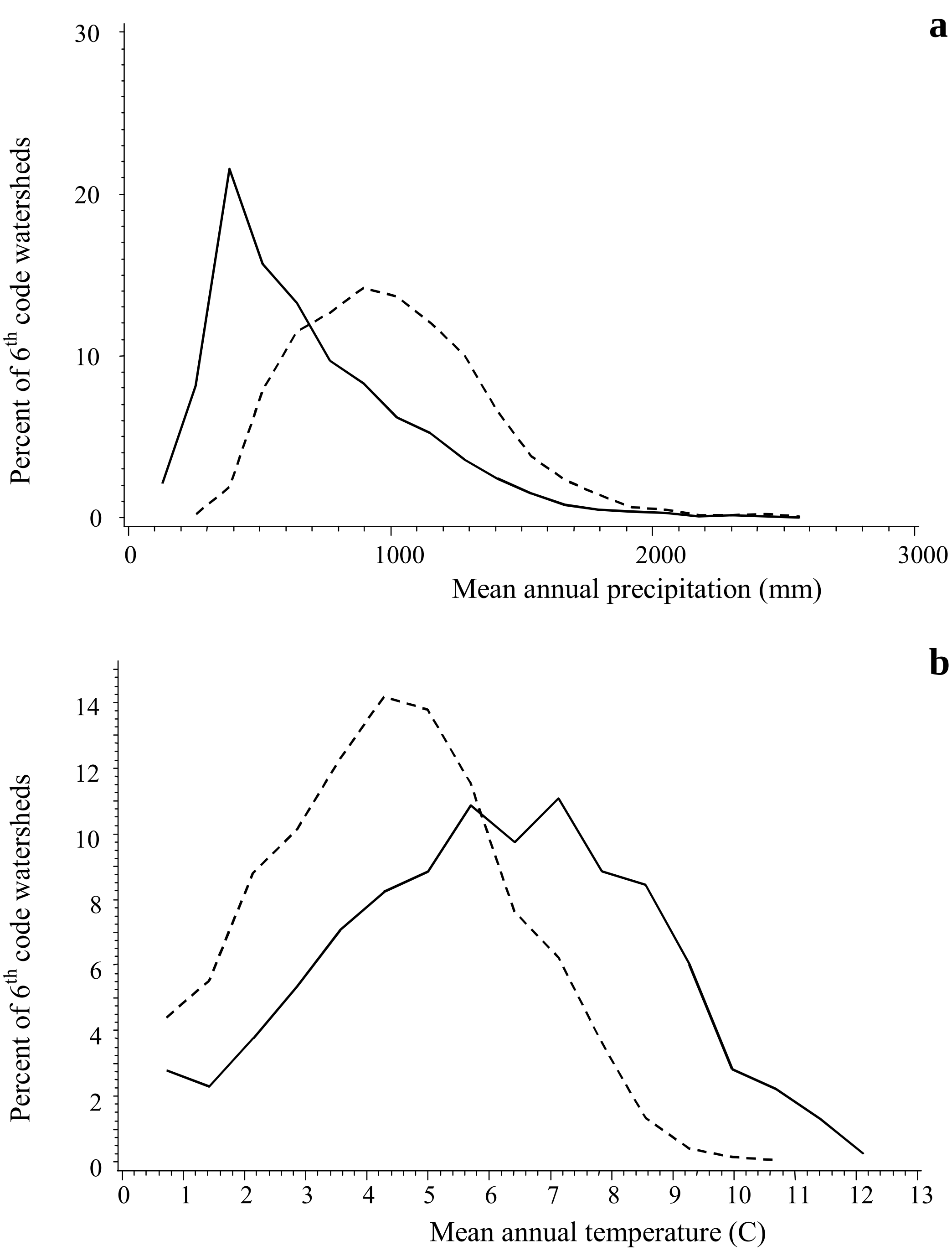

Figure 10. The frequency distributions of mean annual (a) precipitation and (b) temperature for 6^{th} code watersheds in the Interior Columbia River Basin with ≥ 50% probability of westslope cutthroat trout presence (broken) and 6^{th} code watersheds containing sampled streams (solid).

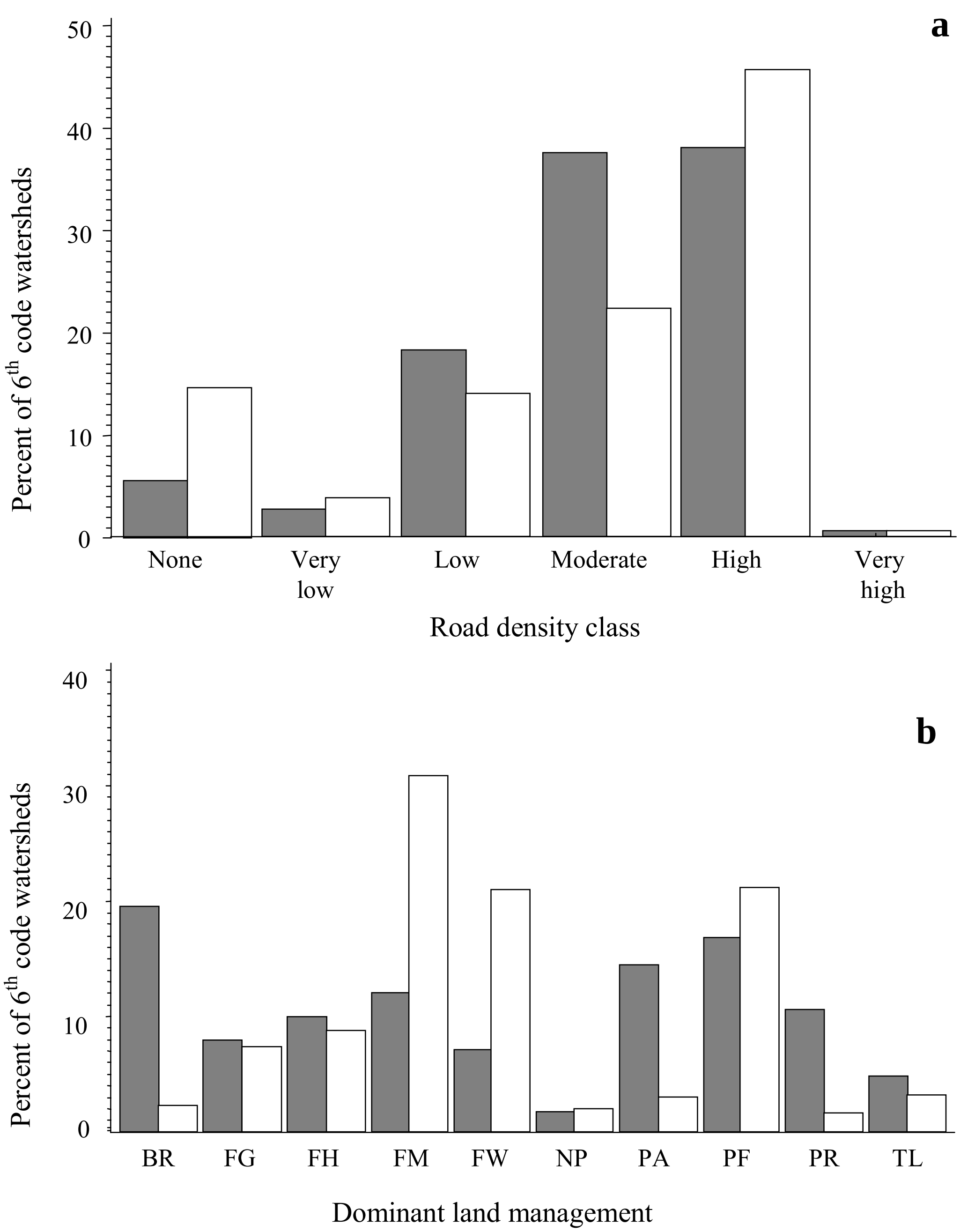

Figure 11. The frequency distributions of (a) road density class and (b) dominant land management type for 6th code watersheds in the Interior Columbia River Basin with ≥ 50% probability of westslope cutthroat trout presence (open) and 6th code watersheds containing sampled streams (solid). Land management types include: *Br*- Bureau of Land Management (BLM) rangeland, *Fg*- Forest Service (FS) forest and rangeland, moderate impact grazed, Fh- FS forest, high implact, grazed, *Fm*- FS forest, high-moderate impact, no grazing, *Fw*- FS managed wilderness, *Np*- National Park Service forest land, *Pa*- private agriculture, *Pf*- Private land and FS forest land, *Pr*- private land and BLM rangeland, and *Tl*- tribal lands.

Patterns in Distribution and Abundance

Preliminary data analyses and inspection of scatter diagrams indicated little meaningful correspondence between occurrence and elevation for WCT. The distribution of occurrences in the sample (Figure 12) indicated that small cutthroat trout were frequently detected at all sampled elevations across the region. Minimum site elevations decreased as a function of latitude (indexed by ITM northings), but that pattern parallels geographic variation in topography within the region. Occurrence of small cutthroat trout was positively related to latitude (ITM northing) and elevation, and inversely related to longitude (ITM easting). Occurrence of any WCT was positively related to latitude, longitude and stream width, and inversely related to maximum summer air temperature. A comparison of the geographic distribution of occurrences for small and larger WCT revealed obvious regional discrepancies, particularly in the northern extent of the range (Figure 13). Small cutthroat trout were not reported in the northernmost sites, most obviously in the northeast. In contrast, larger cutthroat trout were common throughout this range.

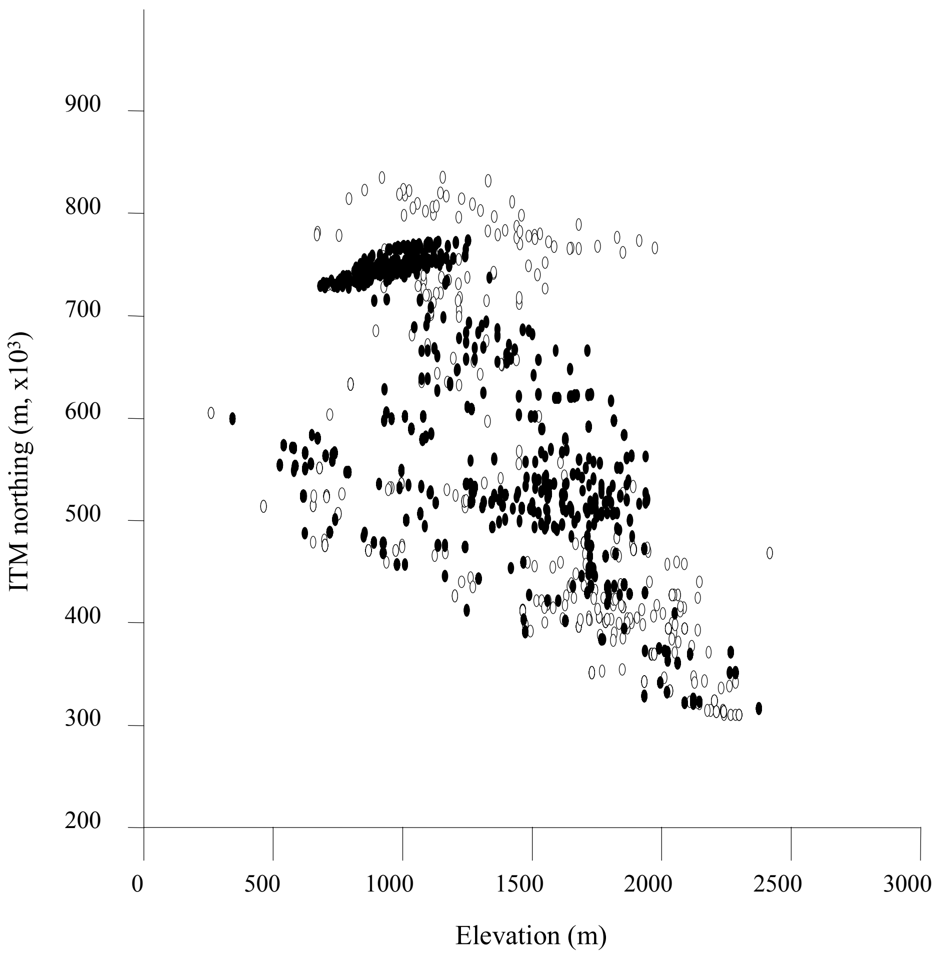

Figure 12. Plot of occurrence os small westslope cutthroat trout in relation to geographic location (ITM northing) and elevation. Filled and unfilled circles represent sites where cutthroat trout were present and not observed ("absent"), respectively.

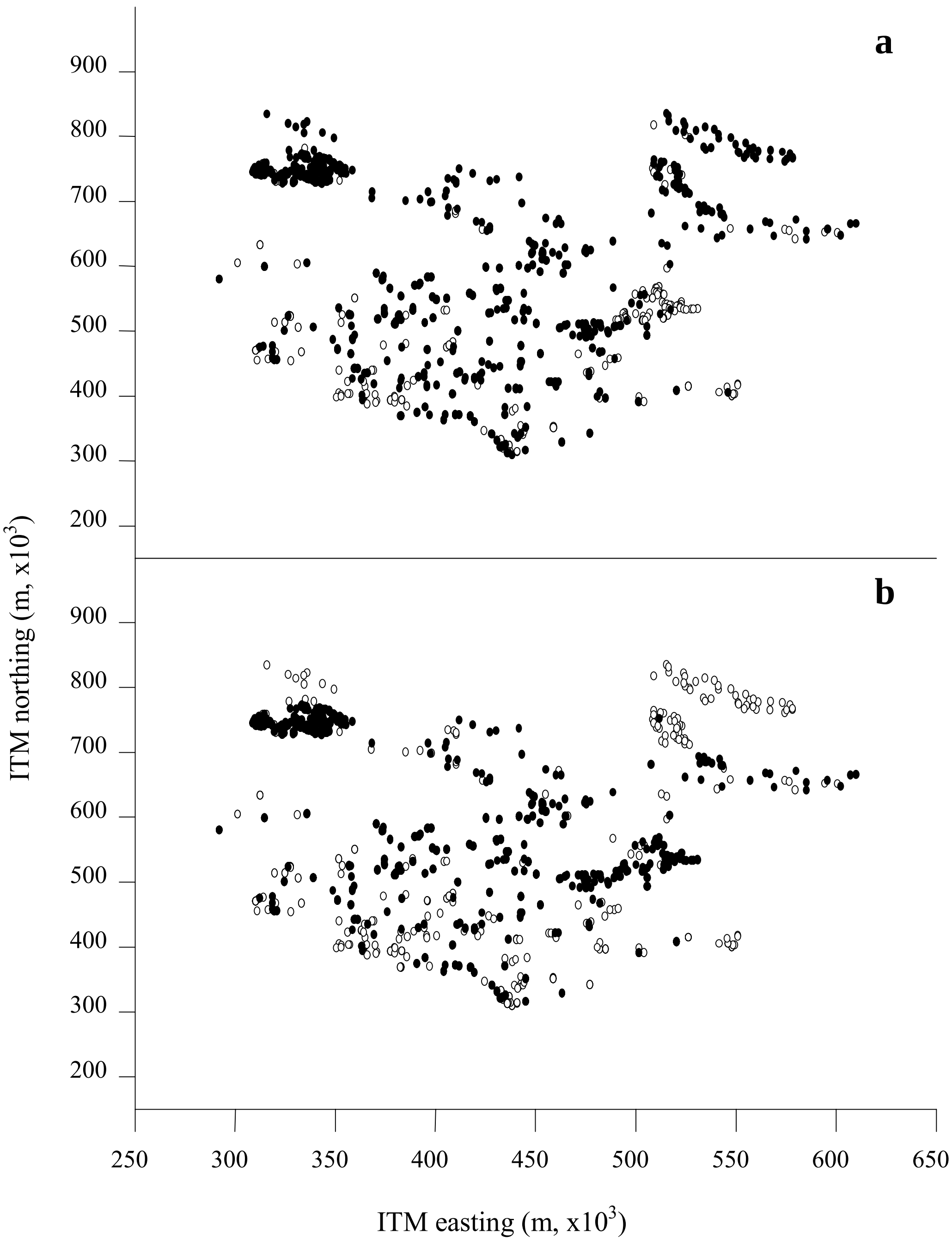

Figure 13. Geographic distribution of occurrences for (a) any westslope cutthroat trout and (b) small westslope cutthroat. Symbols as in Figure 12.

Fish densities used in the analysis of local variation were summarized as fish per meter and fish per square meter and examined independently for three geographically distinct data sources (Table 4). Mean densities of fish in the BIT sample were the highest of any data source, in terms of small or total cutthroat trout. Densities of cutthroat trout in the GPM data source were the lowest of any data source.

Table 4. Densities of small westslope cutthroat trout (SMWCT), any westslope cutthroat trout (TOTWCT), small brook trout (SMBRK), and any brook trout (TOTBRK), for all data sources with density information. Data sources are as follows: BIT = Bitterroot; CDA = Coeur d'Alene; GPM = General Parr Monitoring.

Source	Species	Variable	*n*	Mean	S.D.	Min	Max
BIT	SMWCT	Fish/m^2	.	.	.	.	.
BIT	SMWCT	Fish/m	.	.	.	.	.
BIT	TOTWCT	Fish/m^2	111	0.1199	0.1069	0	0.6250
BIT	TOTWCT	Fish/m	111	0.2469	0.1598	0	0.6957
BIT	SMBRK	Fish/m^2	.	.	.	.	.
BIT	SMBRK	Fish/m	.	.	.	.	.
BIT	TOTBRK	Fish/m^2	111	0.0113	0.0308	0	0.1510
BIT	TOTBRK	Fish/m	111	0.0271	0.0771	0	0.4679
CDA	SMWCT	Fish/m^2	430	0.0656	0.0858	0	0.6667
CDA	SMWCT	Fish/m	430	0.0656	0.0858	0	0.6667
CDA	TOTWCT	Fish/m^2	430	0.0731	0.0893	0	0.6733
CDA	TOTWCT	Fish/m	430	0.1877	0.2065	0	1.5778
CDA	SMBRK	Fish/m^2	.	.	.	.	.
CDA	SMBRK	Fish/m	.	.	.	.	.
CDA	TOTBRK	Fish/m^2	430	0.0026	0.0201	0	0.3457
CDA	TOTBRK	Fish/m	430	0.0077	0.0552	0	0.9333
GPM	SMWCT	Fish/m^2	3372	0.0031	0.0129	0	0.2217
GPM	SMWCT	Fish/m	3372	0.0031	0.0129	0	0.2217
GPM	TOTWCT	Fish/m^2	3372	0.0061	0.0186	0	0.2949
GPM	TOTWCT	Fish/m	3419	0.0488	0.1132	0	1.5082
GPM	SMBRK	Fish/m^2	3372	0.0087	0.0545	0	1.4174
GPM	SMBRK	Fish/m	3419	0.0446	0.2441	0	4.7818
GPM	TOTBRK	Fish/m^2	3372	0.0107	0.0599	0	1.4174
GPM	TOTBRK	Fish/m	3419	0.0557	0.2736	0	5.5455

Brook trout were observed in all data sources. We focused on the GPM data source, however, because smaller size classes of cutthroat trout were distinguished. Within the GPM data source, small brook trout and small cutthroat trout rarely occurred together in sites (about 2% of sites). In sympatry, mean densities of small brook trout were more than twice as great as densities of small cutthroat trout (0.12 fish/m versus 0.05 fish/m, or 0.018 fish/m^2 versus 0.007 fish/m^2, respectively). Similarly, overall densities of small brook trout in the GPM data source were at least twice as great as densities of small cutthroat trout, except when total numbers of fish were summarized in terms of fish per square meter (Table 4). While small brook trout and small cutthroat trout rarely co-occurred, the characteristics of habitat used by either species overlapped. This pattern held even for sites when only one of either species (i.e., allopatric sites) was considered (Table 5).

Table 5. Distribution of habitat characteristics in which brook trout and cutthroat trout were detected. Data are for allopatric sites only.

Variable	*n*	Mean	S. D.	Minimum	Maximum
			Brook trout		
Width	797	8.69	6.12	1.40	51.04
Gradient	404	0.68	0.66	0.02	6.35
			Cutthroat trout		
Width	800	10.64	6.67	1.70	60.60
Gradient	514	1.34	1.26	0.05	8.91

Plots of local fish density in relation to stream width suggested maximum densities of small cutthroat trout and brook trout may decline strongly in relation to increasing stream width (Figure 14). Small cutthroat trout densities were more variable in relation to stream gradient, but small brook trout densities also appeared to decline strongly in relation to gradient (Figure 15). Small cutthroat trout were found in a greater range of gradients, ranging up to 16.5%, whereas small brook trout were never found in sites with gradients exceeding 4.6%.

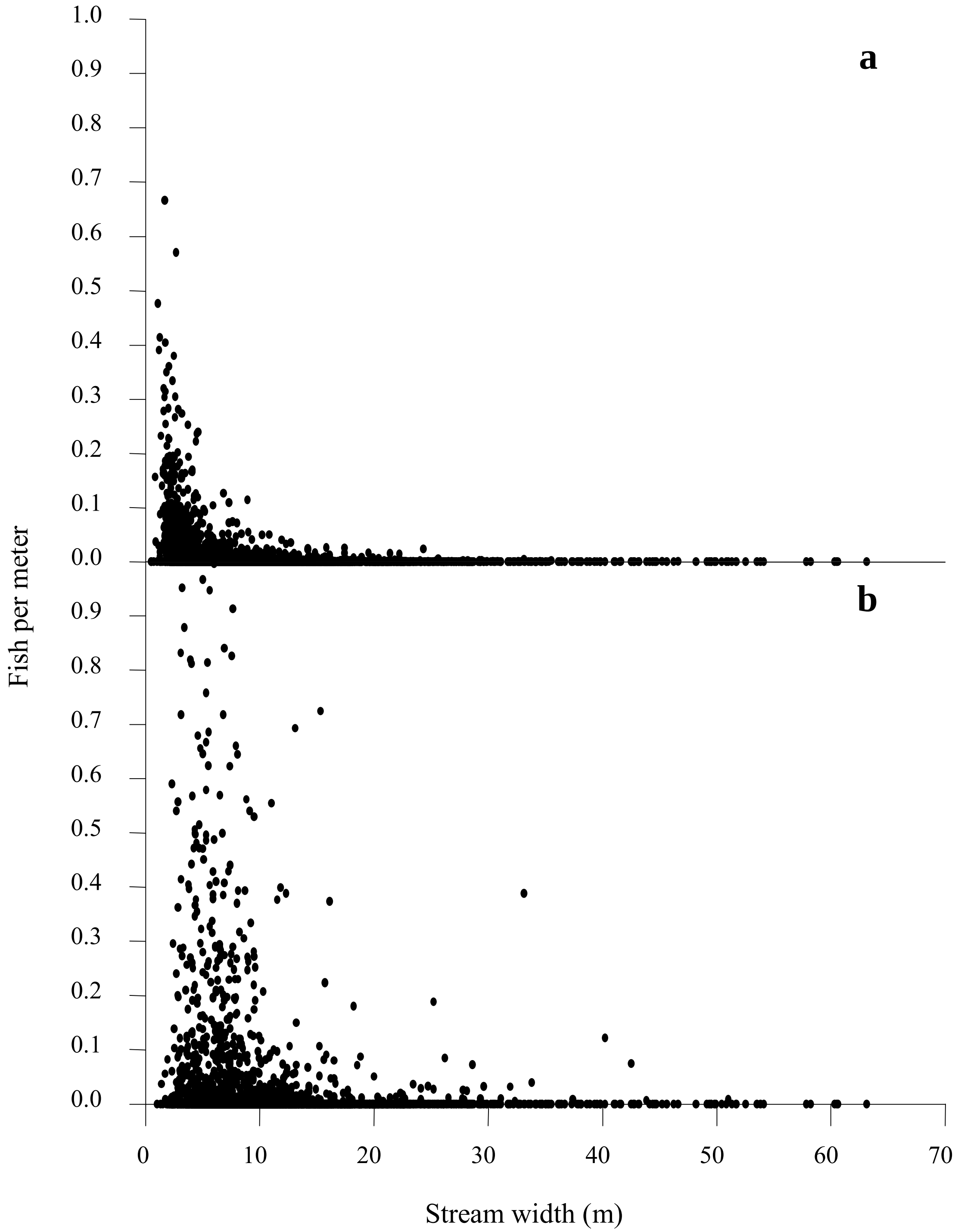

Figure 14. Plot of observed density of (a) small westslope cutthroat trout and (b) small brook trout in relation to stream width. Densities truncated at 1 fish per meter, see table 4 for more detailed density statistics.

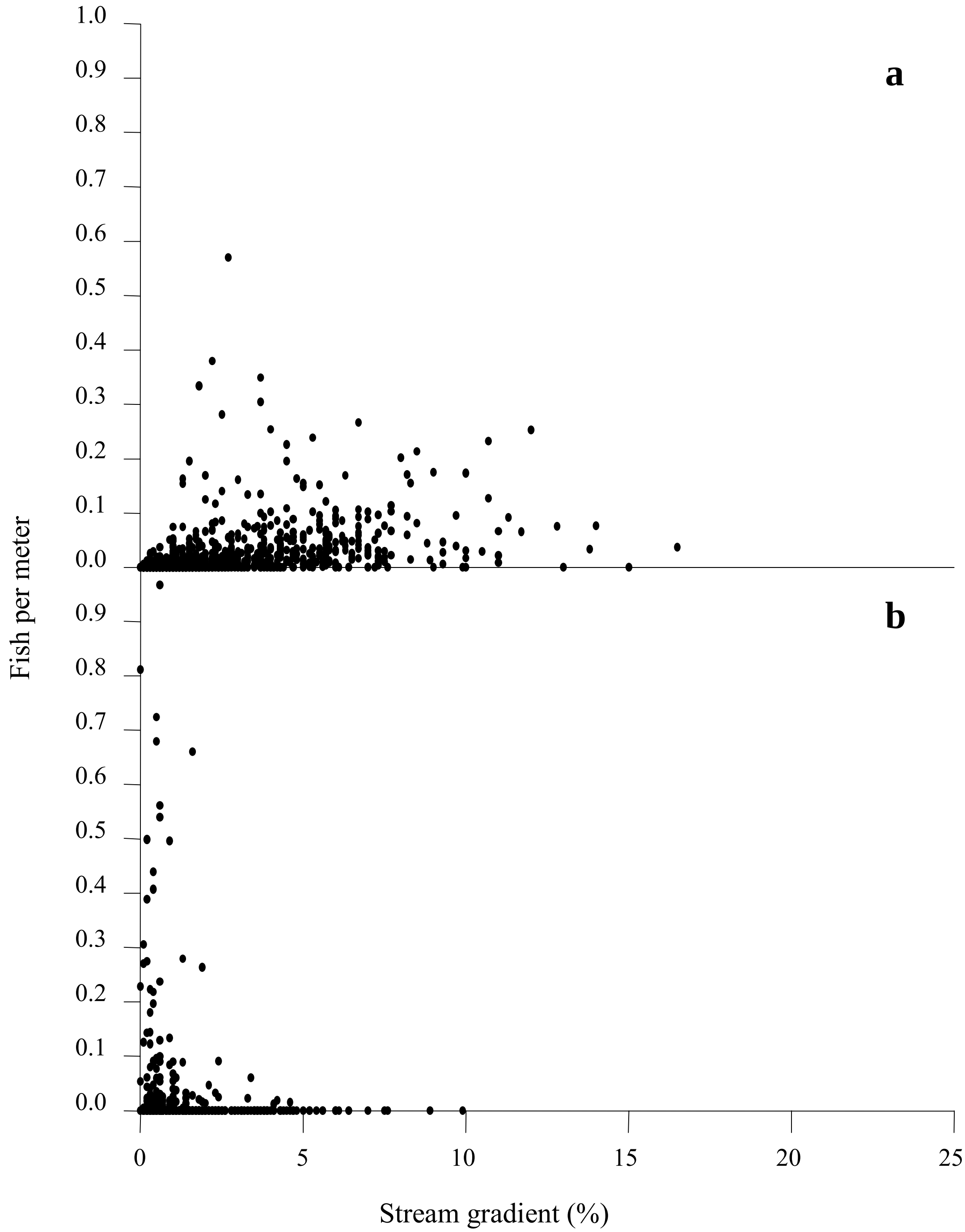

Figure 15. Plot of observed density of (a) small westslope cutthroat trout and (b) small brook trout in relation to stream gradient. Densities truncated at 1 fish per meter, see Table 4 for more detailed density statistics.

Fitting regression quantiles to the data revealed similar insights. Plots of parameter values and confidence intervals in relation to specific quantiles were used to show how relationships vary near the upper bounds of the distribution of densities (Figures 16-17). As quantile values increase, the collection of data points used to estimate regression relationships migrates systematically toward the upper bounds of the distribution of densities in relation to explanatory variables. For heteroscedastic or Awedge-shaped@ distributions, the value of parameter estimates should vary with the quantile considered (Terrell et al. 1996; Cade et al. 1999).

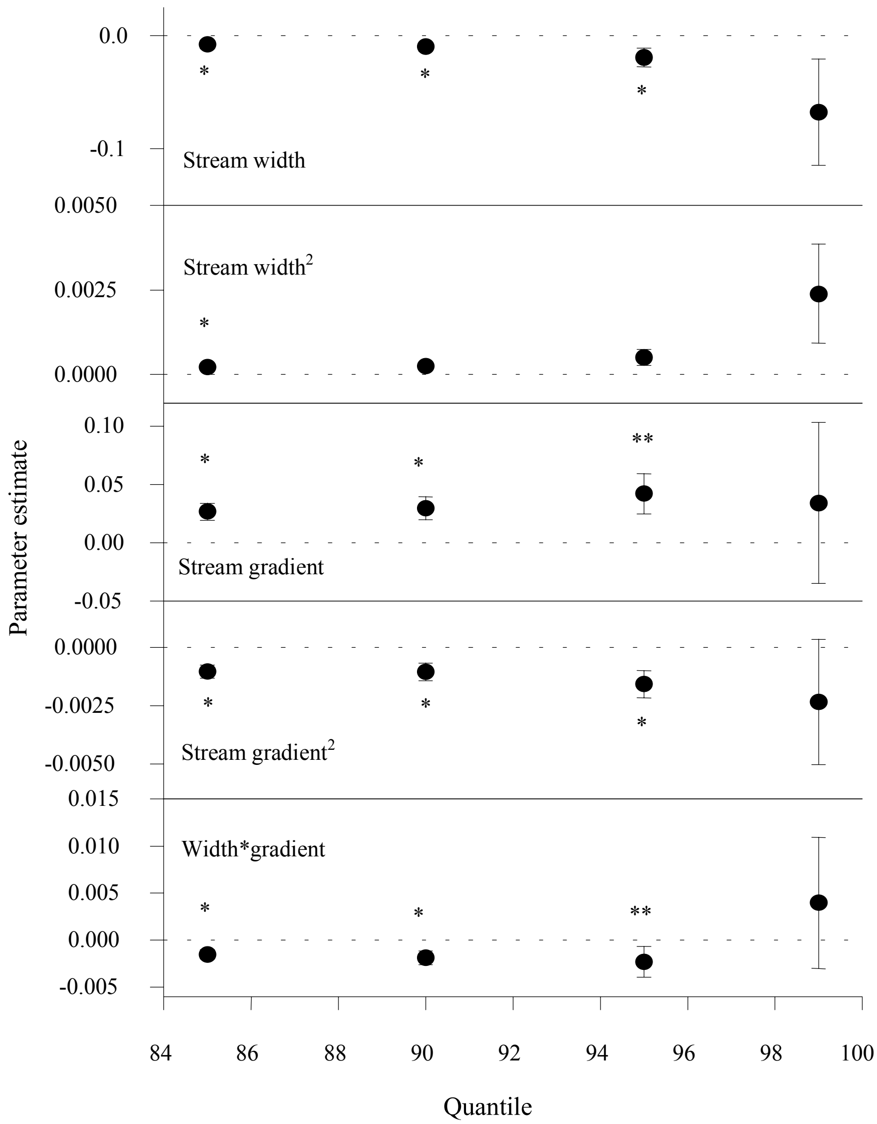

Figure 16. Parameter estimates for models of density of small westslope cutthroat trout corresponding to 80, 90 ,95, and 99th regression quantiles. Bars represent standard errors. Asterisks above or below symbols indicate statistical probabilities (*≤0.05; **≤0.01; ***<0.001).

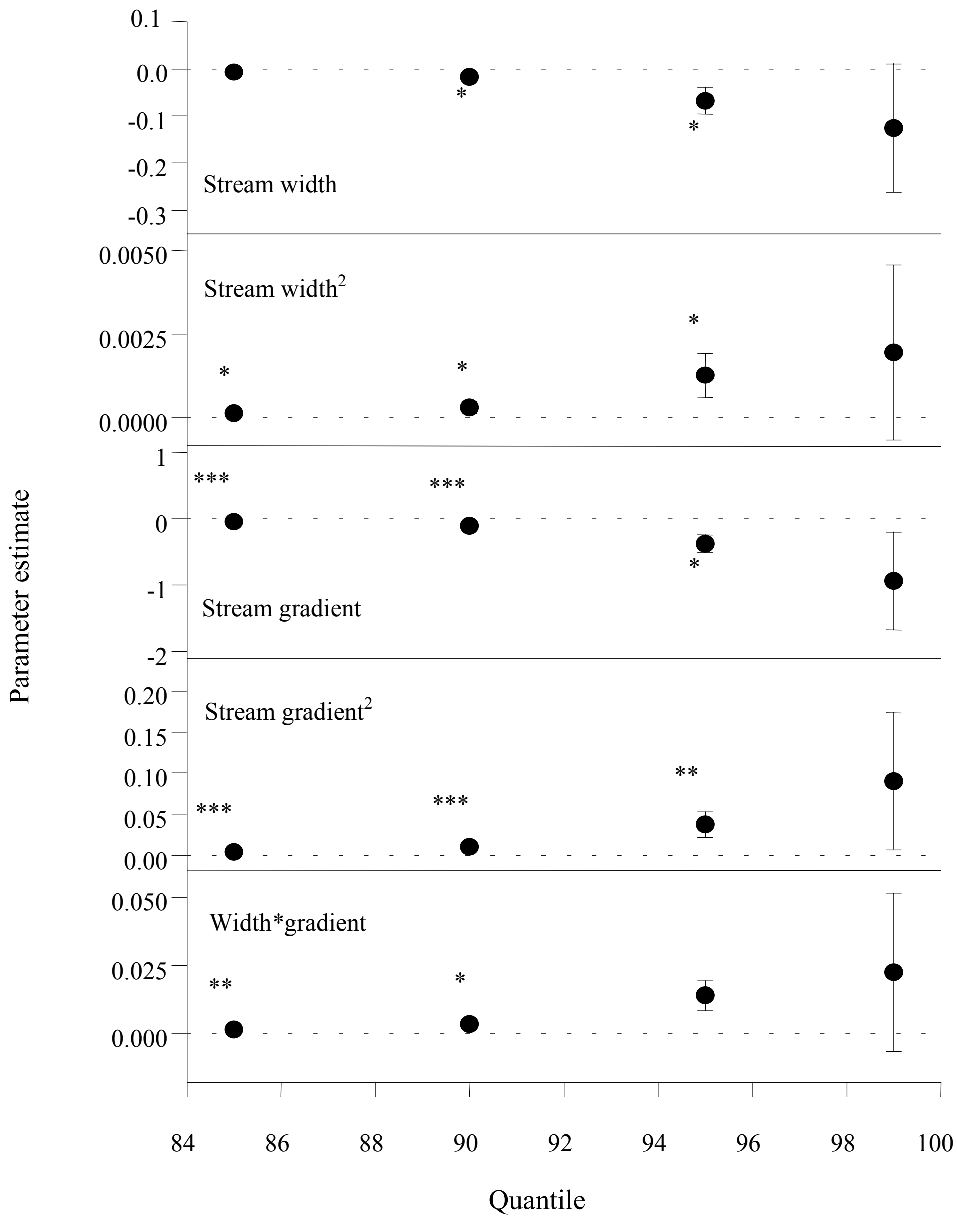

Figure 17. Parameter estimates for models of density of small brook trout corresponding to 80, 90, 95, and 99th regression quantiles. Symbols as in Figure 16.

For most quantiles, cutthroat trout densities increased as a function of stream gradient, and decreased as a function of width (Figure 16). Both linear and quadratic effects of these factors were generally evident. Brook trout densities decreased both in relation to stream gradient and width (Figure 17). Interaction terms (width*gradient interactions) were negative and significant for cutthroat trout, and positive and significant for brook trout. There was some evidence for confounding of the effects of stream width and gradient. Stream width and gradient were correlated (r_s = -0.58, P < 0.0001), and the effects of either may be difficult to determine independently. When fish densities were summarized as fish per square meter (adjusting for width), however, the association between density and gradient for both species remained the same. Cutthroat trout densities increased and brook trout densities decreased in relation to stream gradient.

Discussion

Exploratory analyses reported here should be interpreted cautiously because several issues regarding data quality and scale were unresolved. We focus on these issues before providing discussion of the potential meaning of habitat relationships suggested by the exploratory data analyses.

Data Quality and Utility

Sampling consistency as inferred from replicated measurements of width and gradient appears to be a problem for some of the data. Not all data sources had replicate samples, but the variability in those that did was substantial. Some variation in physical characteristics is expected across time particularly with variation in flow (Herger et al. 1996), so some of the variation in the observations is undoubtedly real. It seems unlikely, however, that gradients can change as much as two or three fold between years. Sampling error either in measurement or location of the sites must be important. In any case, these results suggest high variation in the data representing physical characteristics that, in most analyses, we assume to be unchanging. Regardless of the source, that variation may well obscure any relationships with fish distribution that are not quite strong.

Fish sampling efficiency can also have a profound effect on data quality. Fish sampling efficiency is influenced by the type of method employed (Hayes et al. 1996), the size and species of fish (Buttiker 1992; Riley et al. 1993; Anderson 1995) as well as physical habitat features (Rodgers et al. 1992; Bayley and Dowling 1993). Failure to account for differences in sampling efficiency introduces a systematic error or bias into the data, which can significantly affect fish density estimates (Bayley and Dowling 1993) and systematic error either in the imposition of treatments or in sampling or measurement procedures renders an experiment (or observational study) invalid or inconclusive (Hurlbert 1984). We compared associations between densities of westlope cutthroat trout and brook trout using density data with and without adjustment or Acorrection@ for unequal sampling efficiencies. Adjusting catch data for unequal sampling efficiency is necessary to avoid spurious inferences, but the precision and/or bias of a model used to adjust the data or the variability of the sampling technique may also be important (Thompson et al. 1998).

Adjusting catch data for sampling efficiency is necessary to provide improved estimates of abundance, but also important to identify potential confounding of sampling efficiency and fish-habitat associations. For example, stream temperature and visibility appeared to influence snorkeling efficiency (Table 2) and both varied with stream discharge during sampling (Figure 18). Thus, sampling efficiency and hence, fish abundance estimates were likely negatively biased during high discharge years. An analysis of the influence of environmental factors on fish abundance might erroneously conclude that fish production was related to discharge when in fact the observed pattern was due to the differences in sampling efficiency. Our analysis also revealed that sampling efficiency may be a function of stream width and gradient. Thus, part of the association we found between fish density and habitat may be an artifact of sampling method.

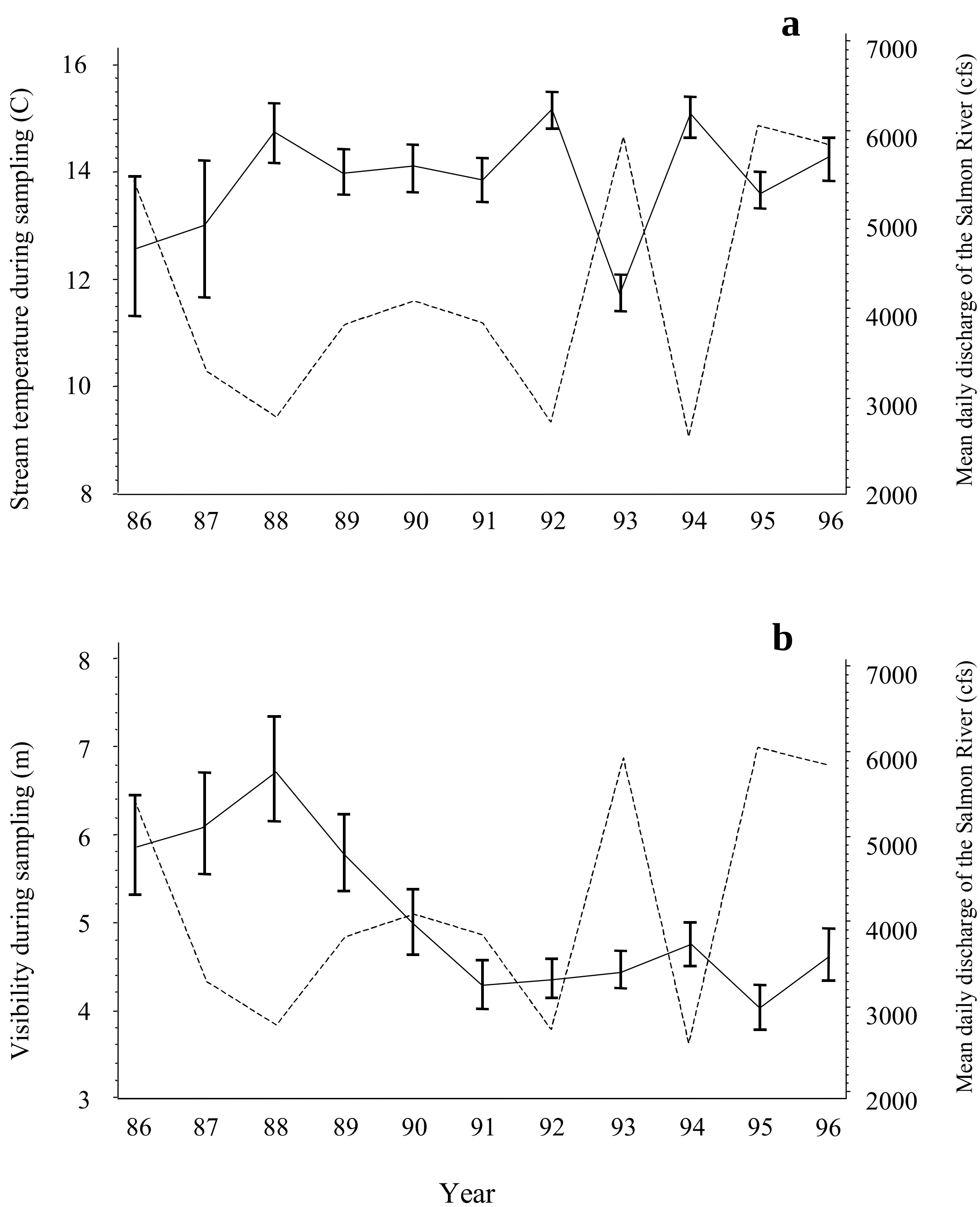

Figure 18. (a) Mean water temperature and (b) visibility (solid lines) and mean discharge (broken lines) for the Salmon River during snorkel sampling from 1986 to 1996. Discharge records for USGS station 133155000 near French Creek, Idaho.

Clearly more work is needed to address sampling efficiency. Improved and standardized sampling protocols would make data sets such as those analyzed here more useful outside of their specific applications. To avoid this type of confounding in the interim, we recommend extreme care in the evaluation of sampling methods with adjustments for sampling efficiency as part of the original data summary. Interpretation of single pass electrofishing or snorkel estimates as a reliable measure of “relative” abundance is likely to be misleading particularly if used for comparison among sites or times that may vary in characteristics likely to influence sampling efficiency (e.g., width, depth, flow, cover, temperature, turbidity). The use of minimally biased population estimators is the only appropriate approach whenever information on abundance rather than occurrence is important (Gould et al. 1997).

Presence and absence data are also affected by sampling bias because the probability of detecting a species is a function of its probability of capture (sampling efficiency) and its density, both of which are influenced by habitat features and vary systematically (Peterson and Bayley 1998). For most sites where cutthroat trout were not detected, we would not have expected to find them even if they were present (Figure 7). One means of reducing the influence of sampling bias on presence and absence data would be to increase sampling effort (e.g., number of samples or size of sampling unit) to maintain a consistent level in probability of detection. For example, consider the situations where average sampling efficiency is 30, 20, and 10% at three different study sites. Assuming a constant density threshold of 0.015 fish/m^2 and an average stream width of 3 m, if sampling efficiencies were 30, 20, and 10%, to achieve a constant 95% probability of detection would require sampling approximately 187, 299, and more than 500 m, respectively (Figure 19). An alternative approach could be to estimate the probability of occurrence, given that the species was not collected (Figure 8, for example). This, however, requires relatively accurate predictive models of abundance. We believe that future research efforts should focus on collecting high quality data for the synthesis of such models. Traditional inventories intended to describe the distribution of a species or support analyses, such as we proposed here, should incorporate a flexible, adaptive, sampling effort that accounts for limited and variable detection probabilities.

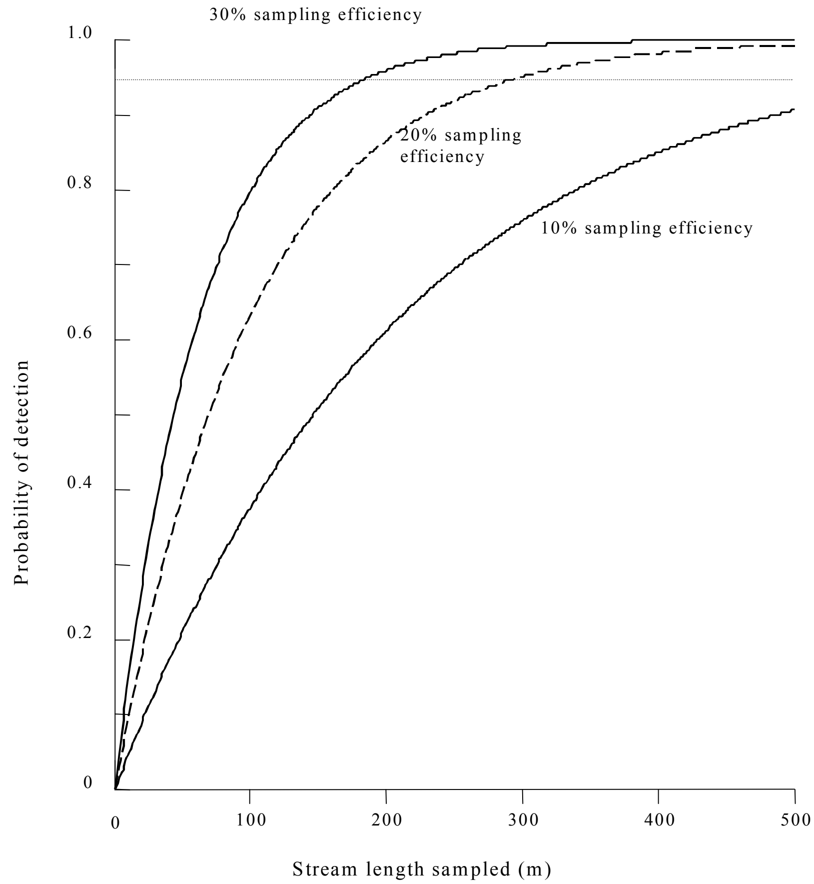

Figure 19. The probability of detection and stream length sampled for 3 levels of sampling efficiency. Probability of detection based on simple binomial estimate for 3 m wide streams and threshold densities of 0.015 fish/m^2.

The representativeness of samples and their utility in useful inference depends on the quality of site scale observations, but also on the distribution of those sites. The distribution of sampled sites across the region appeared to be biased towards warmer, drier, lower gradient, and higher impact areas (Figures 9-11). Sites were chosen for a wide variety of purposes that depended on the needs of individual natural resource agencies. In many instances, sampling data were collected to provide an annual index of chinook salmon and steelhead production (e.g., IDFG parr monitoring). Consequently, the site selection bias was probably an artifact of practical considerations such as accessibility. Nonetheless, this bias could limit regional assessments and reduce the ability to make informed, defensible management decisions.

Nonrandom selection of sites may affect inferences about fish-habitat relationships in a number of unpredictable ways, even if the number of observations is very large. For example, an analysis of management related effects on WCT occurrence and abundance, as we originally proposed, would be problematic using the current data because any inferences would have to be restricted to areas where management impacts are probably higher. In preliminary analyses we found that the sign and significance of coefficients describing relationships between occurrence of WCT and elevation and sampling efficiency varied widely among the different data sets we used. Is this due to regional influences on fish-habitat associations, or to differences in sampling methods and/or nonrandom selection of sites? Nonrandom selection of sites may unintentionally confound fish-habitat relationships if site selection corresponds to important environmental gradients not considered in the analysis. In further work, to ensure that data are adequate for addressing the needs of decision makers, we suggest that sampling design and monitoring efforts should be coordinated at the appropriate scale (e.g., regional goals = regional coordination).

We fully recognized the non-random nature of the observations we obtained. AFound@ data can lead to useful inferences about patterns related to environmental gradients but caution is important in the interpretation of parameter estimates and effects. We hoped that a broad geographic sample would provide some evidence of broad geographic patterns that could guide more focused studies. The observations we obtained, however, may not have been adequate to represent a gradient in climate we expected to be important for WCT. We consider this issue further below.

Patterns in Distribution

Geographic scale.- Broad discrepancies in occurrence of small versus larger cutthroat trout (Figure 13) may be a function of the regional environmental gradients, the distribution and characteristics of sampling sites, or alternatively, bias in sampling of smaller fish (see above). We suspect the latter may be important, but have no convincing evidence available to evaluate these alternatives. The widespread absence of small cutthroat trout in more northerly sites is problematic, and results of our analyses of occurrence have little meaning if sampling bias cannot be accounted for.

Local scale.- Variation in density of WCT at sites paralleled patterns found in other studies of other salmonids (e.g., Lanka et al. 1987; Fausch 1989; Bozek and Hubert 1992; Dunham et al. 1999). In particular, both species tended to be more abundant in small streams and WCT appeared more likely to be abundant in higher gradient sites than brook trout. The biological meaning of this relationship is unclear, however. Stream size and gradient may be correlated with a wide variety of habitat characteristics in small trout streams (Hubert and Kozel 1993; Schroeter 1998) and the estimates of occurrence and abundance can be confounded by patterns in sampling efficiency that are also related to gradient and width. The data suggest that geomorphic characteristics of streams can be an important predictor of potential habitat for these species. This result seems particularly striking given the variation we observed in replicated width and gradient samples. Both effects would be expected to obscure any relationship that was not particularly strong. Further work that clearly addresses the data quality issues we have already discussed, however, will be important to clarify the generality and utility of this pattern.

WCT and brook trout were seldom found together in sites. This may represent a strong interaction between the two species, or possibly selection of different habitat characteristics. The latter seems unlikely because there is considerable overlap in characteristics of habitats both fish were found in, at least with respect to stream size and gradient. Patterns in the data suggest two important classes of evidence for demonstrating the potential for interspecific competition: potential overlap in resource use, and complementary distributions. This is not sufficient evidence of competition (Fausch 1988; Crowder 1990), but the strength of the pattern does warrant further work.

Summary and Conclusions

The database we have assembled on density and occurrence of WCT represents a large effort to synthesize quantitative, site scale information on this species throughout much of its natural range in the United States (see Lee et al. 1997; Thurow et al. 1997 for a watershed-scale analyses). Unfortunately, our attempts to evaluate patterns in distribution of WCT appear to be suffering from the Adata-rich, information-poor@ syndrome described by Ward et al. (1986) for water quality monitoring. Specific and more coordinated attention to this species is needed if we are to gain a better understanding of its landscape-scale patterns of distribution and abundance. The important issues parallel the organization of our report.

Sampling Consistency.- Replicated samples suggest that sampling variation is an important issue. It is not possible to resolve the effects of sampling error and temporal variability, but clearly either may obscure important relationships. Replicated sampling and attention to reliable methods will be important in further work. Recent reviews of measurements of stream slope, for example, point out potentially serious errors associated with use of clinometers (Isaak et al. 1999) a commonly employed tool in the observations we summarized. Validation of methods and a sampling design that allows identification of the sources of variation are important.

Sampling efficiency.- The database provides good information on known occurrences of WCT, but determination of species abundance and absence is limited by uncertainties regarding sampling efficiency. A better understanding of the distribution and abundance of WCT can only come through field surveys specifically designed for this species. The development of standardized field survey methods would benefit from quantitative models of sampling efficiency. It is possible to develop objective corrections for estimates based on snorkeling or single pass electrofishing, but unbiased population estimates may be the only reliable alternative when true abundance information is needed. Because sampling efficiency is likely to vary with habitat characteristics, analyses that rely on single pass or biased methods (i.e., uncorrected snorkeling or prima cord) as measures of Arelative@ abundance are likely to produce spurious and misleading results. The same problem applies to the reliable evaluation of presence and absence. More objective work will require recognition of, and correction for, varying sampling efficiency by adapting sampling effort or by employing new methods for estimating the probability of occurrence given the absence of fish in the sample at hand.

Data representativeness.- Because information collected on WCT comes from many surveys with different objectives, it is unclear if existing samples are representative. Evidence presented here suggests they are not. Better spatial representation in surveys may be accomplished by using information from the database assembled in this effort and the Interior Columbia Basin Ecosystem Management Project (Lee et al. 1997) to design a range-wide survey for WCT. Realistically it will be difficult for any single project to develop a representative, geographic scale sample with consistent methodology in a timely fashion. That was the impetus for our attempt to develop a composite database in the first place. It may be possible with appropriate support, however, to develop a larger collaborative project enlisting a broad distribution of biologists and agencies that share a common goal of understanding WCT distributions and biology. Tying those efforts together with a common experimental design and sampling protocol could greatly accelerate progress toward understanding the large-scale patterns and processes we believe are important.

Geographic distribution.- We were unable to confidently define geographic patterns in distribution limits to delineate occurrence of local populations or Apatch structuring@ of WCT habitat. We are optimistic that geographic patterns can be defined, but they may emerge only with a carefully planned sampling design to provide more reliable data on fish occurrence. Better demographic and genetic data could also help define boundaries associated with local populations and the natural discontinuities of population structure of WCT (Rieman and Dunham In press).

Local Distribution.- We found local habitat factors, gradient and stream size, to be important correlates of local density of WCT and nonnative brook trout as well. There is little information available to provide cause-and-effect linkages between these habitat characteristics and fish distributions (see van Horne 1983). The patterns we observed were consistent with previous work on both species, however, and the strength of these patterns despite the limitations of the data was striking. Our results reinforce the notion that a better understanding of the role of stream size and gradient, or other environmental and ecological characteristics associated with them, could be useful in defining potential habitat for WCT and its mediation of interactions with species like brook trout (Fausch 1989; Adams 1999).

Our primary objective in this project was to develop a database useful for describing multi-scale patterns in WCT distributions. We hoped to identify potential environmental constraints that could prove useful for defining potential habitat and help clarify the influence of finer scale effects. We were largely unable to do that. Sampling consistency, efficiency and detection probabilities, and representation in the sample, were key issues limiting the utility of the composite data set. We hasten to point out that this is not a criticism of the individual projects contributing information to the database. None of these projects was designed for or intended to be used in the analysis we envisioned. We simply hoped to make use of existing data to address an important question that is constrained by the need for a lot of broadly distributed information. Seemingly there is no free lunch. There may be no simple way to reliably describe large-scale patterns without a carefully designed and coordinated large-scale project to address objectives specific to WCT.

Acknowledgments

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Appendix Table 1. List of variables and definitions that are included in the BRD database.

Variable Name	Type	Definition
BRK_PA	Character	Presence/Absence of brook trout (P/A)
BULL_PA	Character	Presence/Absence of bull trout (P/A)
CHIN0	Numeric	Number of chinook age 0
CHIN1	Numeric	Number of chinook age1
CHIN_PA	Character	Presence/Absence of chinook salmon
CUTT_PA	Character	Presence/Absence of cutthroat trout
DATE	Character	Date of sample
ELEV	Numeric	Elevation (m) from a topographic map
ELEV30	Numeric	Elevation (m) from 30m DEMs
GISNO	Numeric	Unique number assigned to point within source
GRADIENT	Numeric	Field measured gradient
HUC6	Numeric	Subwatershed hydrolgic unit code
ITM_EAST	Numeric	Idaho Transverse Mercator easting location
ITM_NORT	Numeric	Idaho Transverse Mercator northing location
LNTH	Numeric	Length (m) of sampled site
MEAN_DEP	Numeric	Mean depth (m) of sampled site
MNWDTH	Numeric	Mean width (m) of sampled site
MTHD	Character	Sampling method (SN=snorkel; EF=electrofishing; EF1=electrofishing 1pass; CORR=primacord)
NO_SITES	Numeric	Number of sites pooled – Couer d' Alene
Q100K	Character	Name of 100K quad
QUAD_NAM	Character	Name of 24K quad
REACH	Numeric	Reach number - Couer d' Alene
SBRK_PA	Character	Presence/Absence of juvenile brook trout (P/A)
SBULL_PA	Character	Presence/Absence of juvenile bull trout (P/A)
SCUTT_PA	Character	Presence/Absence of juvenile cutthroat trout (P/A)
SECTION	Character	Section of stream - GPM data
SMBRK	Numeric	Number of juvenile brook trout sampled
SMBUL	Numeric	Number of juvenile bull trout sampled
SMCUTT	Numeric	Number of juvenile cutthroat trout sampled
SMRBT	Numeric	Number of juvenile rainbow trout sampled
SMSTHD	Numeric	Number of juvenile steelhead sampled
SMWHF	Numeric	Number of juvenile whitefish sampled
SOURCE	Character	Data source (GPM=General Parr Monitoring; DBE=Couer d'Alene; BIT=Bitterroot; RMR=Rocky Mountain Research Station)
STRATA	Character	Strata of stream - GPM
STREAM	Character	Stream name
TEMP	Numeric	Temperature (C)
TEMP8	Numeric	Temperature at 0800 at site - DBE
TEMP12	Numeric	Temperature at 1200 at site - DBE

Appendix Table 1. Continued.

Variable Name	Type	Definition
TEMP16	Numeric	Temperature at 1600 at site - DBE
TOTBRK	Numeric	Total number of brook trout sampled
TOTBUL	Numeric	Total number of bull trout sampled
TOTCOTT	Numeric	Total number of cottids sampled
TOTCUTT	Numeric	Total number of cutthroat sampled
TOTRBT	Numeric	Total number of rainbow trout sampled
TOTSTHD	Numeric	Total number of steelhead sampled
TOTWHF	Numeric	Total number of whitefish sampled
UNIT	Numeric	Sampling unit number - BIT
VIS	Numeric	Visibility (m) when sampled
YEAR	Numeric	Year sampled
YRS_SAMP	Numeric	Number of years sampled