P-C-13

Influence of abiotic and biotic factors on abundance of stream-resident westslope cutthroat trout *Oncorhynchus clarki lewisi* in Montana streams

Final Report to:
USDA, Forest Service, Rocky Mountain Research Station
316 East Myrtle Street
Boise, Idaho 83702

Contract: INT-92682-RJVA
(Part 3)

1998

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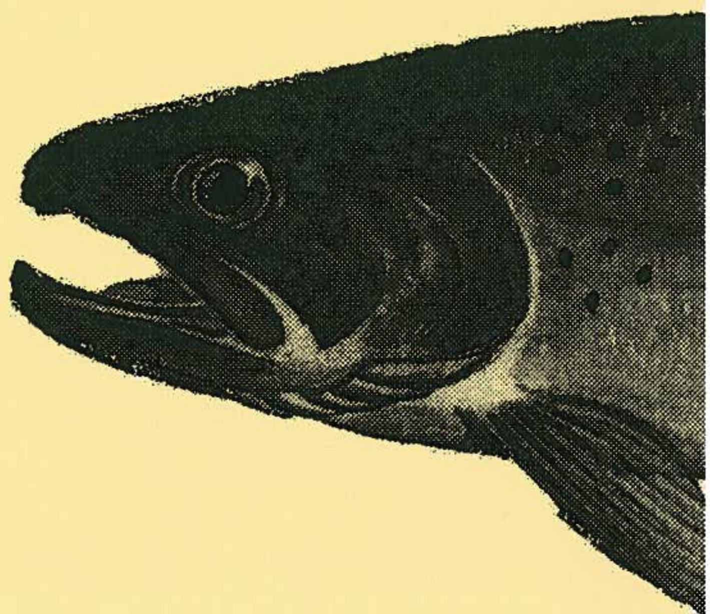

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Executive Summary

Westslope cutthroat trout have declined dramatically and are now restricted to isolated headwater habitats over much of their historical range. This decline has been attributed to several factors; however, the two factors presently exerting the most pressure on westslope cutthroat trout are believed to be nonnative salmonids and habitat degradation. Fish managers must know the relative impacts of these two factors on westslope cutthroat trout populations to effectively prioritize conservation efforts. In addition, suitable habitats for re-founding populations of westslope cutthroat trout need to be identified, regardless of whether these habitats presently support nonnative salmonids.

The influence of the population estimator, annual climatic conditions, physical characteristics of habitat, and nonnative salmonids on estimated densities of westslope cutthroat trout were assessed by making 223 fish population estimates in 94 sample sections within 17 tributaries using depletion and mark-recapture estimators. Estimates were made for fish 75 mm (fork length) and longer. These estimators may produce negatively biased population estimates. However, we believe that these estimates provided reasonable indices of abundance. Ninety percent of estimates had coefficients of variation within 15% of the estimate and over 65% had estimated probabilities of capture over 0.80. When the relative proportion of pool habitats were compared between sample sites and longer reaches of stream surrounding sample sites, sample sites generally contained a similar proportion of pool habitats. We recommend using length, rather than number, to assess proportion of each macro-habitat type. Eight habitat factors were derived from 19 habitat variables using principal component analyses to reduce colinearity problems. These eight factors were relatively easy to interpret and were used in multiple regression analyses.

Spearman rank correlations indicated that densities of westslope cutthroat trout were negatively correlated to densities of brook trout ($P<0.001$), ranked drainage aspect ($P<0.05$; indicating less solar radiation), ranked impacts from roads and mining ($P<0.10$), stream order ($P<0.10$), and streambank cover ranking ($P<0.10$). Cutthroat densities were positively correlated to the proportion of boulder in the streambed ($P<0.05$). Densities of brook trout were positively correlated to ranked drainage aspect ($P<0.05$; indicating more solar radiation), ranked road and logging impacts ($P<0.001$), latitude ($P<0.10$), and frequency of large woody debris ($P<0.10$). Brook trout densities were negatively correlated to predicted air temperature ($P<0.10$), proportion of the streambed in small gravel ($P<0.10$) and sand ($P<0.05$) and ranked level of isolation ($P<0.001$). Drainage, site and year were entered as class variables in a mixed regression model with the estimated density of westslope cutthroat trout as the dependent variable. Drainage and site explained a very significant ($P < 0.001$) amount of the variation in estimated densities of westslope cutthroat trout, but year did not appear to explain much of the observed variation in density.

Multiple regression of the eight habitat factors against densities of westslope cutthroat trout for 53 allopatric sites (Habitat Model) indicated that pool habitat, mining impacts, temperature, and channel size all influenced cutthroat trout densities ($R^2 = 0.79$). Pool habitat entered the model with a positive coefficient and as a simple term. The other factors entered as second order terms indicating that intermediate levels of these factors resulted in higher fish densities. The model also included six interaction terms. When 22 sites where brook trout were sympatric with westslope

cutthroat trout were added to the Habitat Model to develop a Full Model the R^2 increased slightly to 0.80. Additional terms in this Full Model included an indicator that brook trout were present (y-intercept adjustment downward of –2.23), density of brook trout, and three interaction terms between brook trout densities and mining development, non-mining development, and gradient factors. When the data from the 22 sympatric sites were run through both the Habitat and Full models the Habitat Model did an extremely poor job of predicting densities ($R^2 = 0.04$), while the Full Model did fairly well ($R^2 = 0.67$).

We illustrated that both habitat condition and brook trout influenced the abundance of westslope cutthroat trout. We suggest that, while it was difficult to precisely allocate the level of influence each of these major factors had, these two factors probably operate in synergy. When brook trout invade habitats supporting westslope cutthroat trout they can reduce and ultimately eliminate populations of westslope cutthroat trout, especially if habitats have been degraded by land management activities. We hypothesize that under ideal habitat conditions, westslope cutthroat trout may be able to compete with brook trout and persist, but that in degraded or naturally lower quality habitats, brook trout are more likely to displace westslope cutthroat trout. In degraded habitats where westslope cutthroat trout exist in allopatry, they can maintain a viable, though lower than potential, population. However, in habitats that have been degraded and invaded by nonnative brook trout, westslope cutthroat trout will not likely persist due to the negative influences of these two factors. The interactions between brook trout and temperature, and brook trout and management impact components in the sympatric model also suggest brook trout may gain a competitive advantage in degraded habitats.

Associations between physical variables, nonnative salmonids, and three relative abundance classes of westslope cutthroat trout (absent, uncommon, abundant) were assessed in 1,826 upper Missouri River stream reaches using a fish resource database linked to geographic information system (GIS) layers. More westslope cutthroat trout populations classified as abundant occupied higher elevation reaches that had higher valley slopes and more variation in valley slopes (Kruskal-Wallis test; $P<0.001$). Higher relative abundance was also positively correlated with elevation (Spearman rank correlation; $P<0.05$) and mean and S.D. of valley slope ($P<0.10$).

Stepwise discriminant analyses showed associations between westslope cutthroat trout and latitude, longitude, variation (S.D.) of valley slope, predicted air temperature, and the relative abundance of rainbow and brook trout with an overall correct classification rate of about 60%. Filtering these data to remove reaches where data was rated to be of lower quality, or where the genetic status of westslope cutthroat trout was less certain, resulted in slightly higher rates of correct classification. Stepwise logistic regression was also used to test for associations between these covariates and presence/absence of westslope cutthroat trout. Elevation, latitude, longitude, elevation, S.D. and mean valley slope, and the presence/absence of nonnative salmonids were retained as covariates in the final model of main effects. When interaction terms were added the only main effects retained were elevation and S.D. of valley slope along with eight interaction terms. However, the fits of these logistic regression models were not very good. Classification tree analysis produced a similar result. We concluded that since the results from a relatively broad variety of statistical analyses generally concurred, those concurrent results should be robust.

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Introduction

The abundance and distribution of westslope cutthroat trout (Oncorhynchus clarki lewisi) have declined from historical levels throughout their range (Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995; Van Eimeren 1996; Shepard et al. 1997). Factors associated with this decline include introductions of nonnative fishes, habitat changes, and over-exploitation (Hanzel 1959; Liknes and Graham 1988; Behnke 1992; McIntyre and Rieman 1995). Genetic introgression with introduced rainbow (O. mykiss) and Yellowstone cutthroat (O. c. bouveri) trout represents a serious threat to westslope cutthroat trout throughout their range (Allendorf and Leary 1988). Leary et al. (1987) suggested that the subspecies westslope cutthroat trout should be accorded the same attention given to taxonomically recognized species due to their high amount of biochemical divergence. Allendorf and Leary (1988) recommended that conservation of many populations throughout its historic range is necessary to conserve the genetic diversity presently contained within this subspecies.

The state of Montana has recognized the need to conserve and restore westslope cutthroat trout (Shepard et al. 1997). Montana has focused its initial restoration efforts within the upper Missouri River basin because that basin has experienced more dramatic declines of westslope cutthroat trout populations than have occurred in other major basins of the state. Shepard et al. (1997) estimated that genetically pure populations of westslope cutthroat trout within the upper Missouri basin currently occupy less than 5% of their historical range. Many historical habitats once occupied by westslope cutthroat trout now contain populations of nonnative trout, particularly brook trout Salvelinus fontinalis (Behnke 1992; McIntyre and Rieman 1995).

Westslope cutthroat trout have been found to utilize microhabitats with water velocities ranging from 0.1 to 0.3 m/sec (Griffith 1972; Pratt 1984) and water deeper than the average available (Brown and Mackay 1995). The distribution and abundance of cutthroat trout have been strongly associated with the presence of pool habitats (Shepard 1983; Pratt 1984; Peters 1988; Hoelscher and Bjornn 1989; Heggenes et al. 1991; Ireland 1993; Young 1998). Bozek and Rahel (1991) found that young Colorado River cutthroat trout (O. c. pleutiticus) also preferred pool habitats and used microhabitats where velocities were less than 0.03 m/sec and water was deeper than 3 cm. In winter adult westslope cutthroat trout have been reported using deep water, often over a streambed composed predominantly of finer substrate material (Lewynsky 1986; Peters 1988; Brown and Mackay 1995). However, young cutthroat trout have often been observed using instream cover, particularly interstitial spaces within larger substrate material, and woody debris during the winter (Bustard and Narver 1975; Peters 1988; Griffith and Smith 1993; Vore 1993). While Griffith (1970), Pratt (1984), and Lider (1985) suggested that cutthroat trout prefer habitats which provide cover, Nakano et al. (1992) found that westslope cutthroat trout were found further from overhead cover than bull trout (Salvelinus confluentus) in a comparative study.

Young-of-the-year coastal cutthroat trout (O. c. clarki) were found at stream margins and in backwaters and side channels in coastal mountain streams of Oregon (Moore and Gregory 1988).

Populations of nonnative salmonids, particularly brook, have often replaced westslope cutthroat trout populations (MacPhee 1966; Griffith 1972; Behnke 1979; Liknes and Graham 1988). This type of replacement has also been suggested for other cutthroat trout subspecies (Behnke 1979 and several papers in Gresswell 1988). Fausch (1989) suggested that distributions of brook and westslope cutthroat trout might be influenced by stream gradient. He suggested that brook trout occupied lower gradient stream reaches (with maximum abundance observed at gradients less than 3%), while westslope cutthroat trout occupied primarily higher gradient reaches (with maximum abundance in gradients ranging from 6 to 14%). He suggested three potential mechanisms that may limit brook trout distribution and abundance in higher gradient stream reaches. First, brook trout may be poorer swimmers than westslope cutthroat trout, so cannot ascend into higher gradient reaches. Second, brook trout have not had enough time since their introduction to invade all the available higher gradient headwater portions of streams. Finally, reproduction and recruitment of brook trout in high gradient stream reaches may be limited due to lack of groundwater up-welling areas and lack of slow water rearing habitats for young of the year brook trout.

Griffith (1988) reviewed the literature on competition between cutthroat trout and other salmonids. He concluded that interactions with native rainbow trout probably resulted in westslope cutthroat trout either occupying upper headwater portions of tributaries, or that selective segregation had resulted in cutthroat trout occupying different niches than rainbow trout. He attributed this segregation to the co-evolution of these two species. Griffith's (1988) review did not determine whether declines and elimination of westslope cutthroat trout from many of their historical habitats by nonnative salmonids was due to competitive exclusion or replacement following changes in habitat quality. Griffith (1972) documented dietary overlap between brook and westslope cutthroat trout. Thomas (1996) observed young brook trout inhibited the foraging efficiency of juvenile Colorado River cutthroat trout. She suggested this inhibition might be the mechanism responsible for decreased growth rates in cutthroat trout she documented. Underwater microhabitat observations on positions occupied by brook trout and greenback cutthroat trout O. c. stomias by Cummings (1987) indicated that juvenile brook trout excluded juvenile cutthroat trout from "more profitable" stream positions.

Relationships between salmonid abundance and habitat variables have been studied and modeled in many studies (see Fausch et al. 1988 for a review). Platts (1974) identified relationships between habitat variables estimated at a large-scale and abundance of several species of salmonids. Nelson et al. (1992) related the distribution of Lahontan cutthroat trout (O. c. henshawi) and their habitats to the geology and geomorphology of the North Fork Humboldt River basin in Nevada.

For restoration efforts to have a reasonable chance of success, sites selected for restoration will need to contain high quality habitats (Griffith et al. 1989). Restoration sites should contain a mosaic of habitats that will change over time (Young 1995), and ideally these sites should include refugia (Sedell et al. 1990; Pearsons et al. 1992) where some individuals could withstand extreme events and subsequently disperse to re-colonize vacant habitats.

The USDA Forest Service's Rocky Mountain Research Station (formerly the Intermountain Research Station) funded this study under contract INT-93845-RJVA to:

1. Quantify availability and condition of aquatic habitats occupied by westslope cutthroat trout in selected headwater tributaries of the Missouri and Clark Fork river basins; and

2. Relate habitat availability and condition to density of westslope cutthroat trout and attempt to account for variability in abundance of westslope cutthroat trout attributed to habitat differences.

Our study was a two-part study to investigate how habitat condition, measured at several different scales, influenced the abundance of westslope cutthroat trout in streams. We evaluated how physical habitat condition and presence and abundance of brook trout influenced densities of westslope cutthroat trout. We also investigated the feasibility of identifying stream reaches that might be best suited as sites for expansion or restoration of westslope cutthroat trout, and explored if existing geographic information (GIS) data might contain enough information to help identify suitable reaches for restoration. We have split this report into two chapters. Chapter 1 explores relationships between site-level population estimates of westslope cutthroat trout and estimates of physical habitat variables, land management impacts, and nonnative brook trout. Chapter 2 documents exploratory data analyses to determine if broad-scale data can be used to identify associations between presence/absence or relative abundance of westslope cutthroat trout and physical characteristics of stream reaches and presence/absence or relative abundance of nonnative salmonids. Analyses in Chapter 2 used a statewide fish resource database linked to various GIS layers.

Chapter 1

Influence of physical habitat characteristics, land management, and non-native brook trout Salvelinus fontinalis on the density of stream-resident westslope cutthroat trout Oncorhynchus clarki lewisi in Montana streams

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Study Area

We sampled 94 sample sections in 23 streams within 17 different tributaries to the upper Clark's Fork (2 tributaries) and upper Missouri (15 tributaries) river drainages from 1992 to 1995 (Figure 1 and Table 1). Streams that supported populations of westslope cutthroat trout were chosen based on genetic purity of the westslope cutthroat trout. Streams that supported genetically pure populations of westslope cutthroat trout usually had some type of barrier to upstream fish movement that prevented potentially hybridizing species from invading habitats occupied by westslope cutthroat trout. Flow conditions during this study (1991-1995) were obtained from U.S. Geologic Survey stream flow gauge sites located near sampled streams. We compared both average monthly and annual flows for the period of record. Average annual flows were lower in 1992 than long-term averages in all five gauged basins (Figure 2). Peak flows were generally near or below the long-term average, while summer flows were generally higher than average during the summer of 1993, near average during 1992 and 1995, and lower than average during 1994 in the four gauged drainages (Figure 3).

Methods

Fish Populations

A total of 223 fish population estimates were made in 94 sample sections using depletion and mark-recapture estimators (Van Deventer and Platts 1983 and 1986; Vincent 1968). Sample sections were selected to represent all available types of habitat within each stream occupied by westslope cutthroat trout. Sample sections were randomly selected within different stream segments, but care was taken to ensure that the upper boundary of each sample section was located where a velocity or habitat break would limit possible movement of fish out of the section during sampling. In most streams channel gradients were relatively high, providing vertical breaks at the upper and lower bounds of sample sections. In the few stream reaches where channel gradients were relatively low (< 3%) we placed 6.25 mm mesh block nets at the bottom and top bounds of the sample sections. Stream segments were stratified in the field based on channel gradient, valley shape, channel sinuosity, and channel size.

Fish were captured using a Smith-Root BP-15 backpack electrofisher. We operated the unit at voltages in the range of 100 to 600 volts, frequencies under 50 Hz, and pulse widths less than 2 msec to maximize the number of fish captured, while minimizing injury to fish caused by the shock (W. Fredenberg, U.S. Fish and Wildlife Service, personal communication). An electrofishing crew consisted of one person who wore the backpack shocker that had a net on the anode, one person who netted fish by the anode, and one person who held a large dip net ("back-stop" net) in the stream's thalweg immediately below the electrofisher. The backstop net was large enough that it spanned at least 25% of the channel in most sample sections and usually captured fish missed by the primary netter. This backstop netter reduced the chance of fish moving down and out of the sample section. The backstop netter also carried a live bucket to hold captured fish.

Almost all depletion passes in a sample section were conducted within four hours after sampling had begun. The combination of velocity breaks at the upper and lower ends of all sample sections (or block nets), the use of a back-stop netter during sampling, and the short time it took to complete depletion electrofishing passes all helped ensure we met the assumption of sampling a "closed" population. Population estimates were calculated for fish 75 mm and longer (fork length; FL) and converted to density of westslope cutthroat trout 75 mm and longer per 1000 m^2 for all sampling events (Appendix A). While we acknowledge that sampled populations were not truly closed and the estimators used probably led to negative bias, we believe that estimates of densities provided a reasonable population abundance index for comparison purposes.

In sections 5 and 15 of McVey Creek habitat data were collected from a sub-sampled portion of each estimate section that comprised about 35% of the length of the estimate section. We reduced brook trout populations using electrofishing removal in McVey Creek in 1993 and in White's Creek in 1993, 1994, and 1995 as part of a study to test what effect brook trout removal had on densities of westslope cutthroat trout. Our data indicated that we were unsuccessful in reducing brook trout populations very much in McVey Creek due to rapid re-invasion by brook trout and low capture efficiencies. We did not observe much, if any, of a response in densities of westslope cutthroat trout to reduction of brook trout populations in McVey Creek. In White's Creek we were more successful in removing brook trout (Appendix A), but did not record much of a response in densities of westslope cutthroat trout to the reduction of the brook trout population until 1995.

Habitat

We estimated various habitat parameters at two scales (site and watershed) by: 1) measuring habitat variables at each sample site in the field; 2) interpreting 7.5 minute (scale of 1:24,000) U.S. Geological Survey contour maps; and 3) using a geographic information database. Field habitat surveys estimated the following parameters from 1992 to 1995 within 76 of the 94 sample sections (termed "sites") where fish population estimates were made, except where noted (Appendix B):

1. length (m), wetted width (m), total number and proportion of each macro-habitat type (classified as pool, riffle, or run);
2. average pool depth and average pool thalweg depth (cm), and residual pool volume (computed by measuring residual depth as defined by Lisle [1987] and multiplying residual depth times surface area);
3. surface area of suitable spawning habitat (defined as patches of substrate dominated by material 1 to 3 cm diameter comprising at least 0.3 m^2 of the streambed's surface);

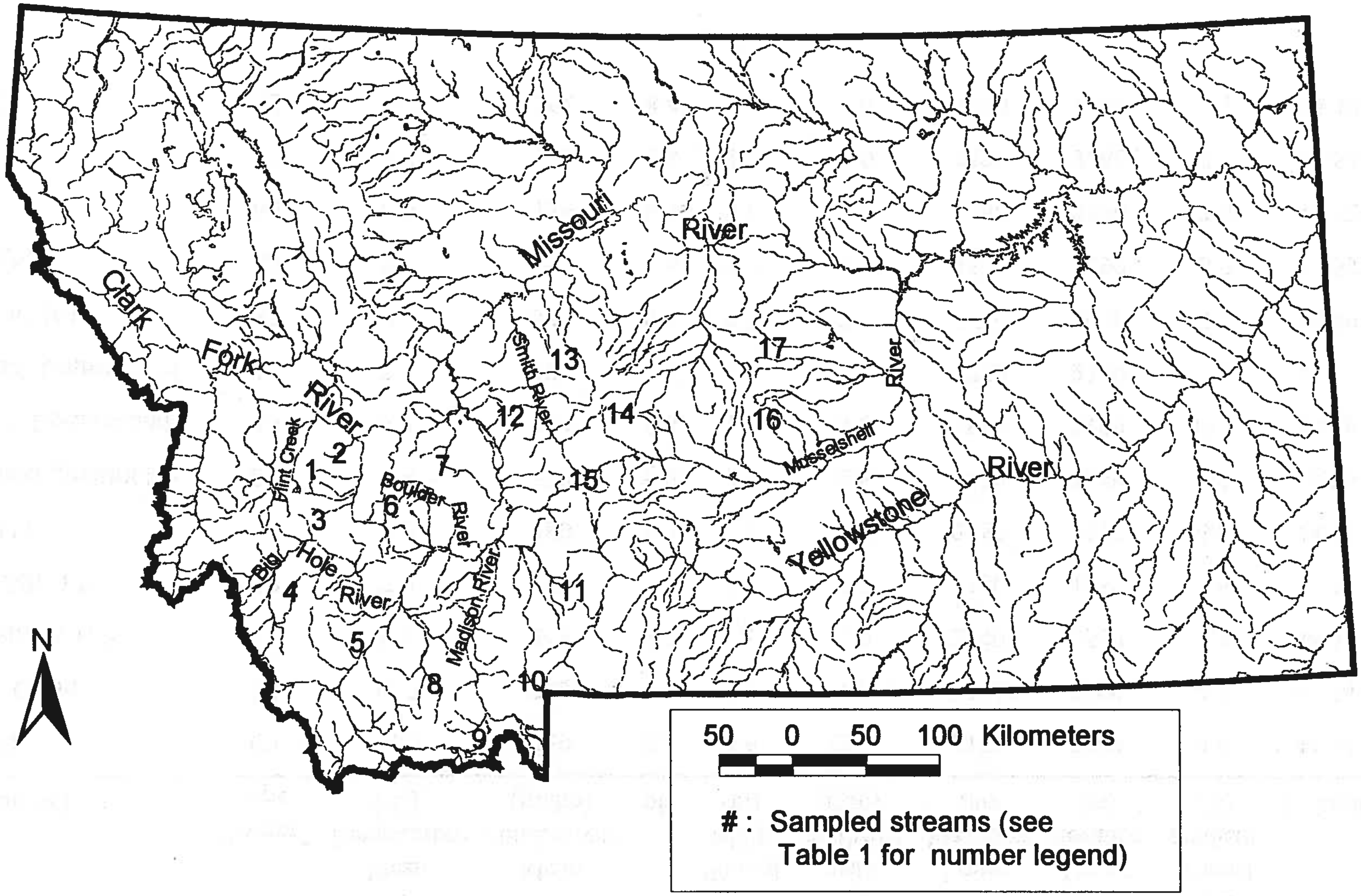

Figure 1. Map of Montana showing the locations of 17 tributary drainages sampled from 1992 to 1995 for assessing the effects of habitat and brook trout on abundance of westslope cutthroat trout. Numbers adjacent to each location are referenced in Table 1. Rivers where U.S. Geological Survey flow gauges were located are named.

Table 1. Physical features of streams (numbers in parentheses are map locations shown in Figure 1) where densities of westslope cutthroat trout were estimated from 1992 to 1995. Mean temperatures, conductivities, and pH's are averages for several point estimates taken during field sampling.

Stream (map number)	Rosgen[a] type	Mean Temperature (°C)	Mean Conductivity (µmho)	pH	Mean Wetted width (m)	Length with cutthroat (km)	Lower Elevation (m)	Upper elevation (m)	Mean channel gradient (%)	Latitude	Longitude
Cabin (10)	C3	14.0	329	8.8	6.6	2.9	2170	2304	4.6	44.54	111.18
M Fork Cabin	B3	11.7	203	8.7	3.3	7.0	2300	2600	4.2	44.54	111.16
Unnamed Trib	B3	8.1	268	8.7	1.6	1.0	2540	2560	2.4	44.53	111.15
Collar Gulch (17)	B2	7.9	174	8.3	2.0	2.7	1450	1550	3.6	47.12	109.10
Geyser (11)	A3	9.0	380	8.6	1.6	1.6	2460	2570	6.6	44.55	112.53
Cottonwood (Smith)(15)	B1	7.8	130	8.9	2.5	0.6	1830	1850	4.0	46.26	110.49
East Fork Cottonwood	A3	9.3	144	8.8	1.5	3.0	1850	2190	11.4	46.26	110.49
West Fork Cottonwood	A3	8.8	126	8.1	2.5	2.8	1850	2110	9.1	46.26	110.49
Half Moon (16)	A2	9.9	344	8.7	3.0	7.3	1710	2010	4.2	46.49	109.16
Halfway (6)	B3	9.5	72	8.8	1.7	7.8	1830	2290	5.9	45.59	112.18
Jerry (3)	A3	6.5	156	8.7	5.8	2.8	2050	2220	3.0	45.52	112.52
Delano	A3	6.5	166	8.3	1.2	1.9	2120	2260	7.1	45.54	112.51
Lick (11)	A3	10.6	262	8.4	2.3	2.0	1950	2020	6.1	45.30	110.59

Table 1. (Continued).

Stream (map number)	Rosgen[a] type	Mean Temperature (°C)	Mean Conductivity (µmho)	pH	Mean wetted width (m)	Length with cutthroat (km)	Lower elevation (m)	Upper elevation (m)	Mean channel gradient (%)	Latitude	Longitude
McVey (4)	B3	6.1	64	9.3	1.5	2.3	1860	1940	3.4	45.40	113.23
Muskrat (7)	A2	7.8	NA[b]	NA[b]	3.6	2.2	1570	1700	5.6	46.18	112.02
N. Fork Deadman (14)	A3	6.3	235	8.6	1.7	2.5	1960	2130	6.8	46.79	110.40
N. Fork Gold (2)	B3	6.8	166	8.5	1.9	4.2	1880	2010	3.2	46.29	113.01
N. Fork Douglas (1)	B2	8.4	252	8.5	1.5	3.1	1650	1790	4.7	46.29	113.09
Soap Creek(10)	A3	8.2	72	8.5	2.5	3.9	1910	2170	6.6	44.51	111.36
Stone Creek (5)											
Left Fork	A3	10.0	296	8.0	2.1	3.5	1920	2150	6.6	45.12	112.20
Middle Fork	B4	10.6	336	8.0	1.4	1.2	1920	1970	4.6	45.12	112.20
Tenderfoot (13)	A3	6.7	116	8.6		8.1	1730	3000	4.5	46.55	110.58
White's Gulch (12)	B3	8.6	661	8.2	1.5	4.6	1320	1470	3.3	46.37	111.29

[a] Rosgen channel types based on Rosgen (1994).
[b] Data were not collected ("Not Available").

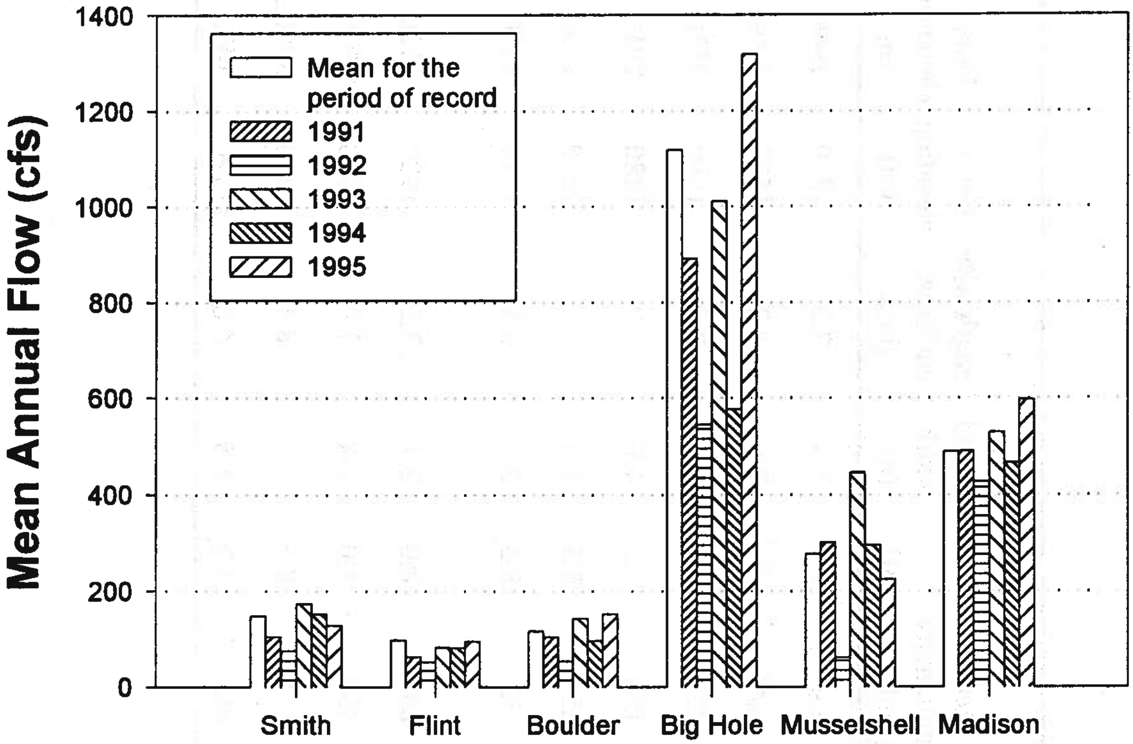

Figure 2. Average annual stream flows from 1991 to 1995 and for the period of record at six gauged streams and rivers located near sampled streams to show relative flow conditions during the study.

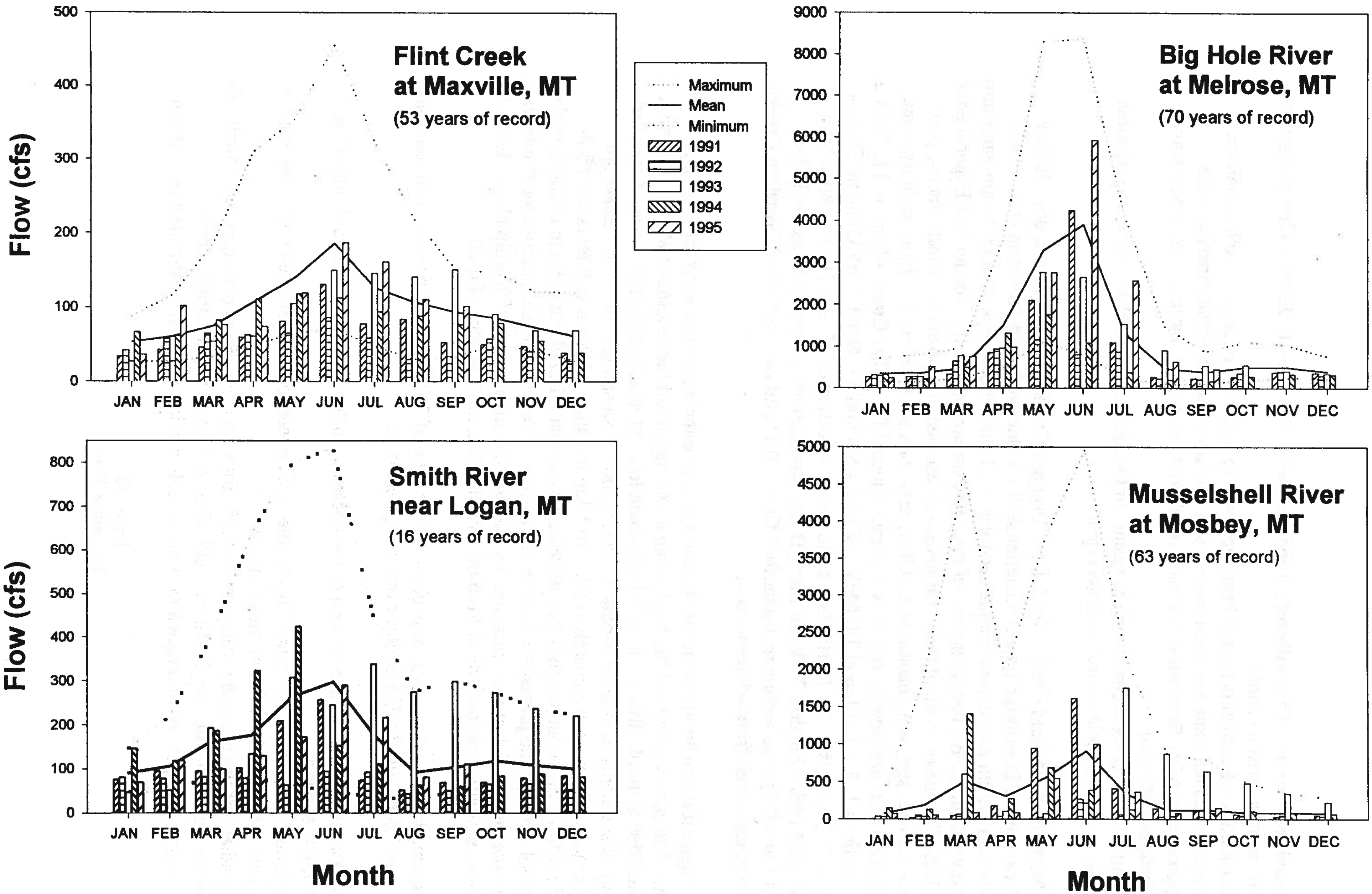

Figure 3. Average monthly stream flows from 1991 to 1995 and for the period of record at six gauged streams and rivers located near sampled streams to show relative flow conditions during the study.

4. number of large ($\geq$15 cm diameter) and small (<15 cm) woody debris within and across the wetted stream channel;
5. qualitative assessments (ranked from low = 1 to high = 3) of stream bank condition, instream cover, bank overhead cover, and land use impacts within riparian areas;
6. percentage of surficial substrate material in boulder, cobble, large gravel, small gravel, sand, and silt; and
7. temperature, conductivity, and pH (using an Omega™ model PH-H-10) were measured over several sample periods and averaged.

For the North Fork of Gold Creek, North Fork Douglas Creek, Douglas Creek, and Halfway Creek, Beaverhead-Deerlodge Forest Fisheries staff conducted R1/R4 (Overton et al. 1997) habitat surveys within population sample sections. In Tenderfoot Creek, Rocky Mountain Station staff conducted an R1/R4 habitat survey of the entire stream within the Tenderfoot Experimental Forest. Data for one or more of these variables - streambed composition, woody debris, pool depth and volume, spawning habitat availability, rank data for pool quality, bank stability, bank cover, riparian use, or instream cover - were not collected for Collar Creek - Section 11; Halfway Creek - Sections 1, 3, 11, 13, and 14; McVey Creek - Section 15; North Fork Douglas Creek - Sections 3, 7, 10, 17, and 20; North Fork Gold Creek - Sections 3, 7, and 10; and West Fork Cottonwood Creek - Section 7. Values for pH and conductivity in two sections of Halfway Creek (0.1 and 0.3), one section in Tenderfoot Creek (0.1) and two sections of Muskrat Creek (7 and 8) were estimated from adjacent sections.

To investigate if the make-up of macro-habitat types in sample sections represented longer segments of stream we counted the total number and measured the lengths of all macro-habitat units (classified as pool, riffle, or run) in a sub-sample of 11 stream segments within 8 tributaries. All surveyed segments contained allopatric populations of westslope cutthroat. Surveyed segments ranged from approximately 0.5 km to 5 km in length. Stream segments were sub-sampled portions of stream reaches that were designated based on differences in channel gradient, geomorphology, and the presence of tributary junctions. Length of each macro-habitat unit in meters to the nearest 0.1 m was measured by walking the streambank with a hip chain. Estimates of habitat composition were derived from both counts and total lengths of each type.

The following habitat information was obtained for each of 76 fish population estimate sections (sites) using 7.5 minute USGS contour maps (Appendix B):

1. elevation of each sample section to the nearest 5 m (measured at the mid-point of the sample section);
2. channel gradient to the nearest 0.1% over a kilometer portion of stream with the sample section as the mid-point of the kilometer;
3. gradient of the channel to the nearest 0.1% from its headwaters (the uppermost limit of a stream as delineated on 7.5 minute USGS maps) down to the sample section;
4. integrated aspect of drainage above the sample section where the estimated proportion of

the drainage above the sample section was rated using criteria to indicate the amount of solar radiation the drainage received (Figure 4);

5. stream order, link magnitude (Scheidegger 1965), and downstream link (Osborne and Wiley 1992) at the sample site;
6. latitude and longitude of each site converted to decimal degrees;
7. ranked isolation of the sample site from downstream habitats (0 = no known isolation; 1 = isolated from downstream habitats due to recent causes [anthropogenic – culverts, dams, etc.]; 2 = isolated from downstream habitats during all times except during extreme high stream flow events due to an intermittent segment of channel; and 3 = isolated from all downstream habitats due to a geologic barrier such as a waterfall); and
8. relative impact on the stream channel at the site from livestock grazing, timber harvest, roads, and mining activity rated from 0 (no impact) to 2 (high impact).

The approximate distribution limits of westslope cutthroat trout within each stream were determined by electrofishing, underwater, and above water surveys. Lower bounds were usually associated with a barrier to upstream fish movement. Where no fish barrier was present, it was more difficult to assign a lower bound. We usually found that abundance of westslope cutthroat trout declined dramatically as abundance of nonnative fishes began to increase in a downstream direction. Lower bounds of distribution were assigned as the uppermost point where no westslope cutthroat trout were captured. We usually continued sampling downstream by sampling several more sample sections to ensure that we had properly located the boundary of occupied habitat. We occasionally captured a single westslope cutthroat trout in a sample site located below several sites where none had been captured. In that case, we assumed the westslope cutthroat trout we encountered represented incidental migrants. Upper bounds were assigned when no fish were captured or observed by electrofishing and/or snorkel or ground observation. We usually made several sampling efforts to locate the upper bounds of distribution. The following information was collected over the documented distribution of westslope cutthroat trout in each of the 23 streams (watershed-scale) using 7.5-minute USGS contour maps (Appendix B):

1. lower, upper, and mid-reach stream elevations to the nearest 5 m;
2. channel gradient to the nearest 0.1%;
3. relative impact on the stream channel from livestock grazing, timber harvest, roads, and mining activity rated from 0 (no impact) to 2 (high impact);
4. total length (km to nearest 0.1 km) of stream occupied by westslope cutthroat trout;
5. integrated aspect of stream rated using criteria to indicate the amount of solar radiation the drainage received (Figure 4);
6. stream order, link magnitude, and downstream link of the lower extant of known distribution of westslope cutthroat trout in the stream; and
7. ranked relative isolation (see #7 above) of the stream from downstream habitats.

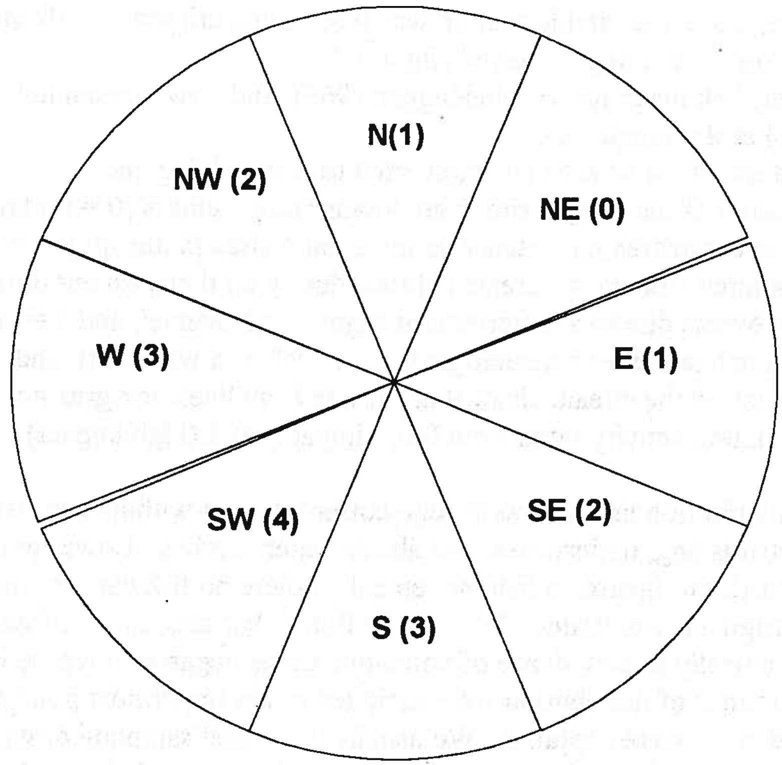

Figure 4. Criteria used to rank stream channel aspect for deriving integrated channel aspect above each sample site. Aspect compass directions and numeric ranks assigned to each compass direction are shown. Numeric ranks indicate relative solar radiation the drainage likely receives.

Sites sampled during this study were located within 27 EPA-identified reaches from a 1:100,000-scale stream hydrography geographic information system (GIS) layer. Mean valley slope, standard deviation of valley slope, valley aspect, upper elevation of reach, lower elevation of reach, and mean elevation for each reach were estimated using GIS layers. Environmental Systems Research Institute (ESRI) Arc/INFO vector layers of stream hydrography (derived from 1:100,000 scale U.S. Environmental Protection Agency data; File 3 data set) were used. The GIS stream hydrography layer was converted to 60 m rasterized data cells (pixels) by combining the Defense Mapping Agency's rasterized (60 m pixels) 1:250,000 scale Digital Elevation Models (DEM's) with the stream hydrography layer using the Arc/INFO GRID module. Combining these data resulted in a data set containing elevation values for each unique arc that identified each cell representing a stream segment. Each unique stream segment contained the original stream reach code that corresponded to the original stream vector data. Elevations were summarized by stream reach across all stream arc segments (60 m pixels) that made up each stream reach using Arc/INFO's STATISTICS command to calculate the variables mean, minimum, and maximum elevation for each reach.

Valley slope (expressed as a percentage) and valley aspect (expressed as degrees) were derived using the elevation data for each stream arc segment and summarized over each reach to estimate mean valley slope, standard deviation of valley slope, and mean aspect using the STATISTICS command in Arc/INFO. Valley slope was defined as the maximum rate of change in elevation (rise over run) from each cell to its neighbors, expressed as percent slope (ie. 45° slope = 100% slope). Median valley slope was calculated for each reach with a dBase macro. Aspect was defined as the down-slope direction (the maximum rate of change in elevation along the stream channel) from each cell to its neighbors, expressed in positive degrees from 0 to 360, measured clockwise from the north. Latitude and longitude in decimal degrees of the lower boundary of each reach were also included. These data were imported into dBase files for analyses. Sine and arcsine transformations were made on aspect data to convert degrees to a north to south axis (sine transformation) and an east to west axis (arcsine transformation) standardized with ranges from -1 to 1.

Data Analyses

The primary goal of this study was to determine which habitat variables were associated with the density of westslope cutthroat trout, assess whether associations were positive or negative, and assess how brook trout densities affected any identified associations. Our ultimate goal is to identify potential habitats where westslope cutthroat trout would persist when re-established in the absence of brook trout. To accomplish these goals we first correlated densities of westslope cutthroat trout to habitat variables and brook trout densities using Spearman rank correlation. We then evaluated how site-level, wateshed-level, and year affected variation in densities of westslope cutthroat trout using a mixed regression model. Next, we developed habitat factors from estimates of habitat variables to reduce problems caused by colinearity. We also considered the precision of population estimators and discussed how the use of these estimators may have biased density estimates. Finally, we conducted multiple regression analyses to develop models for assessing how habitat factors were associated to densities of westslope cutthroat trout and, after accounting for habitat conditions, how brook trout presence and abundance were related to residuals from the habitat factor model.

Habitat

Principal component analysis (PCA) was used to investigate relationships among habitat variables estimated at the site, 7.5 minute map, and GIS levels (SYSTAT version 7.0; 1997). Prior to running PCA we removed the variables "percentage of total habitat in run macro-habitat types" and "percentage of the streambed in small gravel". These two variables were removed because the information they provided was contained within other retained macro-habitat (percentage of habitat in pools and riffles) and streambed composition (percentage of streambed composed of all size classes except small gravel) variables. Since some habitat variables were not estimated at all sites, we ran two separate PCA's on site level data: 1) one using all 76 sites that included only those variables measured at all 76 sites; and 2) another using 53 sites where all variables were estimated. We found that varimax rotation helped to logically interpret the factors. We selected the number of factors from PCA's using scree plots and eigenvalues greater than 1.0 as criteria to include or exclude factors (Jolliffe 1986). We considered variables with the highest coefficients within each factor to be important for that factor, thus all variables that had a coefficient of at least 50% of the variable having the highest coefficient for each factor were considered to be "heavily weighted" variables making up that factor.

Early exploration of the data indicated that a factor with relatively large coefficients for latitude and elevation was always included within one of the top four factors within each analysis. Keleher and Rahel (1996) found that mean July air temperature (°C) was strongly related (R^2 = 0.90; $P<0.0001$) to latitude (in decimal degrees) and elevation (m) for the Rocky Mountain Region and developed the following model to predict mean July air temperature:

$$\text{KRTemp} = -11.468 + 2.812*(\text{Lat}) - 0.0007*(\text{Elev}) - 0.043*(\text{Lat})^2;$$

where, "KRTemp" is mean July air temperature (°C), "Lat" is the latitude at the site expressed in decimal degrees, and "Elev" is elevation in meters.

We tested whether predicted mean July air temperatures correlated well with measured mean July air temperatures at 65 climate stations in Montana. We also tested whether model predicted mean July air temperatures correlated with measured mean July water temperatures for several study streams. We correlated mean July water temperatures for 33 streams where water temperatures were recorded every 0.5 hour with Onset Optic Stowaway™ thermographs from 1995 through 1998. Some thermographs were put out in mid-July, consequently water temperatures were not always recorded throughout July in a few streams.

We were interested if GIS-level data showed similar associations with densities of westslope cutthroat trout as data collected on a finer scale. GIS-derived estimates for habitat variables upper, lower, and mean elevation of the reach, mean channel gradient, standard deviation of channel gradient, and latitude and longitude were used in place of site-level estimates of these variables. These GIS-derived estimates were combined with map-derived estimates of land-use, stream order, link magnitude, and downstream link and site-derived estimates of wetted width, conductivity, pH, and percentage of pool and riffle habitats. We used map-derived estimates of variables as surrogates for variables we believe might be obtained from GIS layers, but which were not readily available or interpretable for this analysis. PCA was completed for this data set to see if factors created from these data were similar to factors created from site-level data.

The proportions, estimated using total number and length, of each macro-habitat type (pool, riffle, and run) within each surveyed reach were compared between estimation methods. Proportions of pool habitats estimated by length for reaches and sample sections were compared to determine if sample sections accurately represented reaches. Differences between macro-habitat type compositions obtained from numeric and length estimates, and by reach and site surveys were compared using Wilcoxon match-pairs sign-ranked test (Daniel 1978).

Factors Influencing Abundance of Westslope Cutthroat Trout

We identified four potential sources of variation in our estimated densities of westslope cutthroat trout:

1. the population estimator (White et al. 1982; Riley and Fausch 1992);
2. annual variation in population abundance (Platts and Nelson 1988; House 1995);
3. physical characteristics of occupied habitats (for a review see Fausch et al. 1988); and
4. the presence and abundance of brook trout, the only other salmonid which occurred in sympatry with westslope cutthroat trout populations we sampled (Griffith 1988).

To assess how much variation and bias likely existed in population estimates due to the estimation procedure, coefficients of variation, expressed as percentages of estimates, and estimated capture probabilities were plotted for each estimate of westslope cutthroat trout 75 mm and longer (Riley and Fausch 1992). Riley and Fausch reported that negative bias decreased as initial capture probability increased and recommended three passes be made for all estimates, especially when capture probabilities fall below 0.9. We usually made only two passes and discuss the implications of that practice in the discussion.

Densities of both westslope cutthroat and brook trout 75 mm and longer were transformed to normalize these values. Transformations were done by: $\ln[(\text{Number}/1000\ m^2) + 1]$. This transformation ensured that estimates of 0 transformed to 0.

Spearman rank correlations were computed between lognormal transformations of the average estimated densities of westslope cutthroat and brook trout 75 mm and longer, and between estimates of habitat variables and transformed average densities of westslope cutthroat and brook trout 75 mm and longer (SYSTAT version 7.0; 1997). Correlations were done for 53 sites where all habitat information was collected. Approximations of significance were calculated for $P<0.001$, $P<0.05$, and $P<0.10$ using z-score estimations recommended by Daniel (1978; page 304).

We tested for the effects of drainage, sample site within drainage, and sampled year on lognormal transformations of densities of westslope cutthroat trout using PROC MIXED in SAS (SAS for Windows version 6.12; 1997). Drainage, site, and year were all entered as class variables. Drainage and site within drainage were entered as fixed variables, while year was entered as a random variable. We used the Wald statistic to test for significance of random effects. These statistical analyses were used to determine whether averaging estimates across years within sites was justified.

Regression analyses were conducted to determine which variables affected population densities of westslope cutthroat trout, termed variable screening by Myers (1990) and applied by Dunham and Vinyard (1997). We used site-level factors generated from the 19 variables estimated at all sites by PCA to build multiple regression models to reduce problems associated with colinearity of covariates. Transformed densities of westslope cutthroat trout were entered as the dependent variable. We first developed a model to account for the influence of habitat on cutthroat trout densities (Habitat Model) by using the 51 sites containing allopatric populations of westslope cutthroat trout (brook trout absent). We included simple and squared terms for all eight factors, as well as all possible interactions when developing this model. We used second order terms because initial bivariate plots of the factors, and estimates of variables used to create those factors, versus densities of westslope cutthroat trout indicated that intermediate values of some factors, and variables, related to higher estimated fish densities. The effect of brook trout was then investigated by regressing the residuals of cutthroat trout densities from the Habitat Model against brook trout densities and interactions of brook trout density and any retained habitat factors by adding the 22 sites where westslope cutthroat and brook trout occurred in sympatry. We did this by adding an "indicator" term of brook trout presence (0 if absent; 1 if present) and the transformed density of brook trout as simple and second order terms. The Full Model was constructed by combining the habitat and brook trout models. This hierarchical strategy was deemed more effective than building a joint habitat/brook trout model because exploratory analyses indicated that effects of brook trout were so strong that brook trout effects dominated these models. Thus, they were not effective for discovering associations between habitat and cutthroat trout in the absence of brook trout. Our model selection was guided by Schwarz's Information Criterion (SIC; Schwarz 1978). Like Akaike's Information Criterion (AIC; Akaike 1973; Chatfield 1995), the SIC can be thought of as a goodness of fit measure penalized for the number of parameters to prevent over-fitting the model. The AIC, while it does penalize for parameters, can still over-fit. The parameter penalty for the SIC is greater than that for the AIC, thus the SIC should have a reduced likelihood of over-fitting (Stone 1979; Bozdogan 1987; Hooten 1995).

Our model selection procedure used a combination of stepwise and all possible subsets regression. In our procedure, regressions with all possible subsets of order seven or less were evaluated. The variable most prominent in the five models with the lowest SIC values was then forced into future models. All possible models of order less than eight and containing the forced variable were evaluated to select a new set of five test models. This process was continued until a Habitat Model with ten variables was selected. As with stepwise regression this protocol is not guaranteed to select the "best model". It should select a good model. Further, one should be wary of over-interpreting the selected model because many alternative models may be nearly equivalent to the one found. All regression analyses were done using regression programs written in MATHCAD 6.0 Plus and by SAS (MATHCAD 1995; SAS for Windows version 6.12; 1997). One sample site, Section 11 of Halfway Creek, was excluded from the allopatric analysis because it supported extremely high densities of westslope cutthroat trout 150 mm and longer and was an obvious outlier. This sample section is located immediately below an old sediment settling pond that contained relatively high densities of large (>200 mm) westslope cutthroat trout. Many large westslope cutthroat trout sampled in Section 11 had probably moved downstream into this sample section from the above sediment pond over a dam spillway. This spillway was impassable to upstream movement. We tagged all fish over 120 mm during each sampling event, but seldom recaptured previously tagged fish over 200 mm in Section 11 during subsequent sampling events. These larger fish apparently left this sample section within a year. Thus, we concluded that densities of westslope cutthroat trout estimated in this section were not related to local conditions at this sample site.

Results

Fish Population Estimates

Coefficients of variation for population estimates, expressed as percentages, illustrated that about 90% of the estimates had coefficients of variation within 15% of the estimates, while over 95% of the estimates had coefficients of variation within 25% of the estimates (Figure 5; see Appendix A for the full data set). Most (>80%) estimated capture probabilities were higher than 0.70 (Figure 5). Nearly 65% of the population estimates had estimated capture probabilities higher than 0.80. Neither coefficients of variation nor capture probabilities could be estimated for sample events when no fish were captured, or when no fish were captured in the second pass of a two-pass effort.

Fish Habitat

Most (88%) of the sample sites were second or third order stream channels (Table 2; Appendix B). Relatively few sites had high ranked impacts from land management activities, however, many sites had impacts from livestock grazing ranked as moderate. Bank stability was ranked as "high" for many sites, however, riparian use was also ranked as "high" for over half of the surveyed sites. Most riparian use impacts we observed were by domestic livestock.
Sites occupied by westslope cutthroat trout had channel gradients averaging about 5% (based on map-derived estimates), while gradients above occupied habitats averaged over 8% (Table 3). Sites averaged about 2000 m in elevation. Conductivities ranged from 55 to 670 μmhos (mean: 222) and pH's averaged 8.5. Riffle habitats predominated and wetted widths averaged 2.5 m. Average composition of the streambed's surface indicated that cobble and large gravel predominated. Woody debris, where it was present, was usually abundant. Spawning habitats generally appeared to be adequate, averaging about 40 m^2 of spawning habitat per kilometer of stream length.

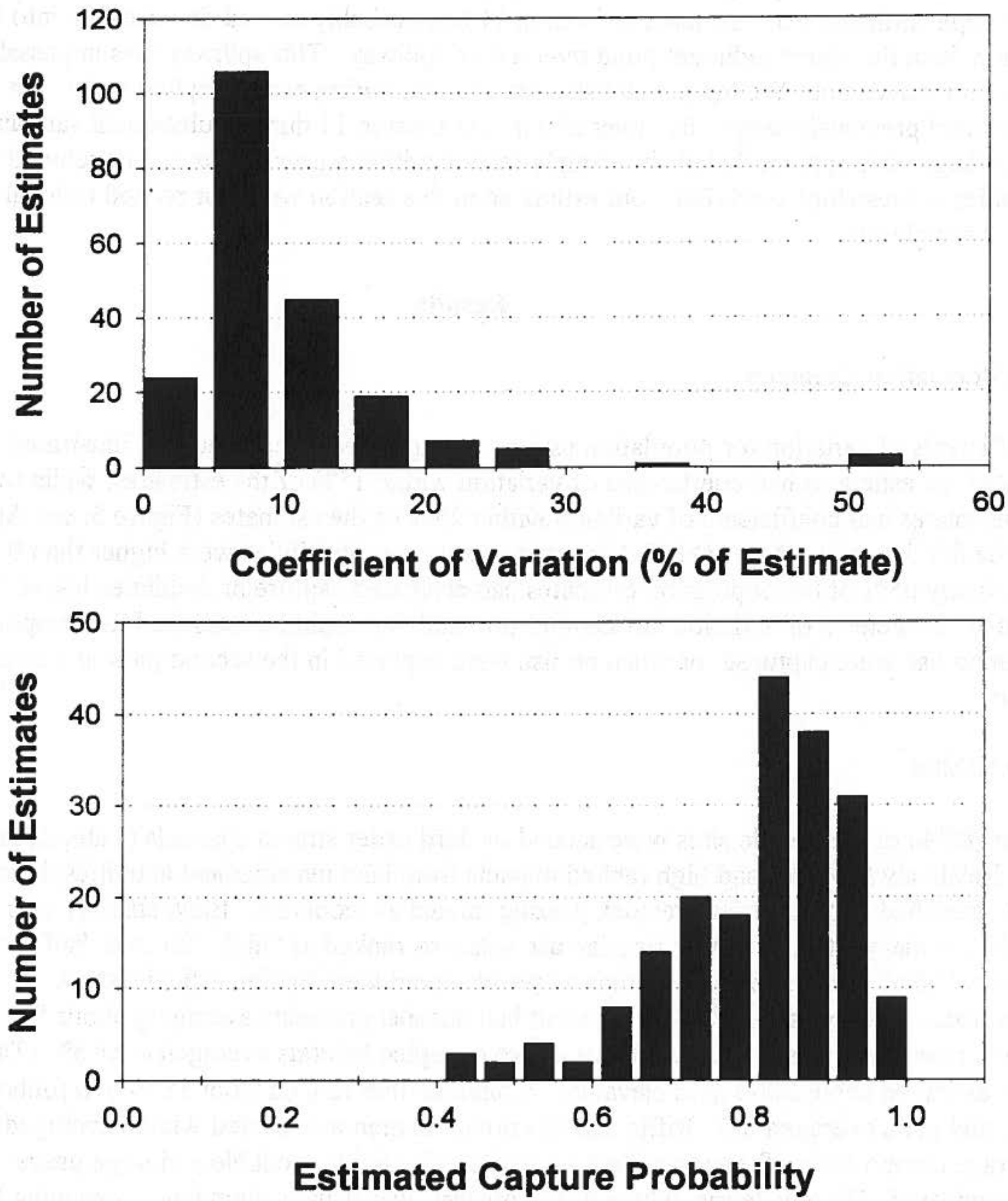

Figure 5. Histograms for coefficients of variation, expressed as a percentage of each estimate, for estimates of the number of westslope cutthroat trout 75 mm and longer (top) and histograms for estimated capture probabilities (bottom) estimated using a maximum likelihood depletion estimator.

Table 2. Summary of the number of sites (%) by rank of each habitat variable used to relate habitat condition to abundance of westslope cutthroat trout.

Variable	Rank			
	0	1	2	3
DRAINAGE VARIABLES RANKED FROM MAP BY STREAM				
Isolation	4 (17)	5 (22)	8 (35)	6 (26)
Road impacts	5 (22)	13 (56)	5 (22)	-
Logging impacts	8 (35)	11 (48)	4 (17)	-
Mining impacts	14 (61)	6 (26)	3 (13)	-
Grazing impacts	4 (17)	13 (56)	6 (26)	-
Stream order[a]	-	1 (4)	10 (43)	11 (48)
SITE VARIABLES RANKED FROM MAP				
Isolation	13 (17)	14 (18)	23 (30)	26 (34)
Road impacts	31 (41)	27 (36)	18 (23)	-
Logging impacts	41 (54)	22 (29)	13 (17)	-
Mining impacts	54 (71)	16 (21)	6 (8)	-
Grazing impacts	23 (30)	31 (41)	22 (29)	-
Stream order[a]	-	8 (11)	34 (45)	33 (43)
SITE VARIABLES RANKED IN FIELD AT SITE				
Instream cover rating	-	6 (10)	38 (61)	18 (29)
Pool rating	-	4 (6)	42 (68)	16 (26)
Bank stability rating	-	5 (8)	28 (45)	29 (47)
Bank cover rating	-	6 (10)	39 (63)	17 (27)
Riparian use rating	-	7 (11)	19 (31)	36 (58)

[a] One site and one stream had a stream order of 4.

Table 3. Summary of simple statistics by habitat variable used to relate habitat condition to abundance of westslope cutthroat trout.

Variable	n	Mean	Range	Median
DRAINAGE VARIABLES OBTAINED FROM GIS				
Gradient (%)	26	16.8	8.0 – 30.6	15.2
S.D. of Gradient (%)	26	11.1	4.9 – 20	11.4
Latitude (decimal degrees)	23	46.04	44.86 – 47.13	46.22
Longitude (decimal degrees)	23	111.61	108.73 – 113.43	111.57
Upper elevation (m)	26	2235	1506 – 2700	2310
Mid-elevation (m)	26	2050	1455 – 2560	2080
Lower elevation (m)	26	1895	1280 – 2476	1890
KRTemp (°C)	23	25.4	24.4 – 26.6	25.4
Aspect (degrees)	26	225	83 - 307	240
DRAINAGE VARIABLES OBTAINED FROM MAPS BY STREAM				
Gradient (%)	23	5.3	2.4 – 11.4	4.6
Latitude (decimal degrees)	23	45.70	44.51 – 47.12	45.59
Longitude (decimal degrees)	23	111.43	109.1 – 113.23	111.29
Upper elevation (m)	23	2090	1469 – 2597	2110
Mid-elevation (m)	23	2000	1393 – 2548	2010
Lower elevation (m)	23	1905	1317 – 2536	1880
KRTemp (°C)	23	25.8	24.5 – 27.1	25.9
Aspect (ranked)	23	2.7	0.5 – 3.7	3.0
Link magnitude	23	8.5	2.0 – 28.0	5.0
Downstream link	23	17.6	3.0 – 100.0	12.0
Length occupied (km)	23	3.6	0.6 – 8.1	2.9

Table 3. (Continued).

Variable	n	Mean	Range	Median
<u>SITE VARIABLES MEASURED FROM MAP</u>				
Gradient (%)	76	5.1	1.2 – 11.0	4.9
Gradient Above (%)	76	8.5	3.4 – 16.7	8.6
Latitude (decimal degrees)	76	46.14	44.85 – 47.20	46.44
Longitude (decimal degrees)	76	111.37	109.18 – 113.37	111.26
Elevation (m)	76	1980	1433 – 2585	1955
KRTemp (°C)	76	25.3	24.3 – 26.8	25.2
Link Magnitude	76	6	1.0 – 28.0	5
Downstream Link	76	13	2.0 – 100.0	8
<u>SITE VARIABLES MEASURED IN FIELD AT SITE</u>				
pH	76	8.5	7.0 – 9.3	8.6
Conductivity (μmho)	76	222.0	54.7 – 670.0	182.1
Pool habitats (%)	76	21	1 – 64	20
Riffle habitats (%)	76	60	21 – 94	61
Run habitats (%)	76	19	0 – 62	19
Average width (m)	76	2.5	1.0 – 6.6	2.4
Average pool depth (cm)	60	19	7 - 35	18
Maximum pool depth (cm)	60	39	10 – 73	38
Residual pool volume (m^3)	60	4.14	0.19 – 27.60	2.65

Table 3. (Continued).

Variable	n	Mean	Range	Median
Substrate Composition (%)	69			
Boulder/Bedrock		15	0 –38	15
Cobble		28	0 – 55	30
Large Gravel		25	5 – 80	20
Small Gravel		16	5 – 50	15
Sand		9	0 –30	8
Silt		8	2 – 30	5
Frequency of Woody Debris (# per km of stream length)				
Small (≤ 150 mm) Total	61	150	0 – 420	133
Small Cross Channel	56	5	0 – 100	0
Large (>150 mm) Total	61	108	0 – 489	73
Large Cross Channel	56	20	0 – 284	20
Density (m^2 per km of stream length) of Spawning Habitats	56	41.8	6.6 – 298.9	26.0

Keleher-Rahel Temperature Model Testing

There was a relatively strong correlation between mean July air temperatures predicted by the Keleher-Rahel model and measured mean July air temperatures for 65 climate sites in Montana ($r = 0.706$; $P<0.001$). However, air temperatures predicted by the model were consistently lower than those actually measured (Figure 6; top graph). There was also a relatively strong correlation between mean July air temperatures predicted by the Keleher-Rahel model and measured mean July water temperatures in 33 streams ($r = 0.613$; $P<0.001$). However, mean July air temperatures predicted by the model were consistently higher than measured July water temperatures (Figure 6; bottom graph). These two correlations suggest the Keleher-Rahel model may be slightly biased in predicting higher than actual air temperatures, but the temperatures predicted by the model correlate fairly well with air and water temperatures.

Comparison of Reach to Site Habitat Composition

Significant differences were observed between estimates of habitat composition using counts versus length of each type (Wilcoxon match-pairs sign-ranked test; $P<0.01$; Table 4). A higher proportion of pool habitats was almost always estimated using count, rather than length, data. Most of the surveyed streams were in relatively high gradient channels where lengths of individual pools were relatively short. Conversely, counts estimated lower proportions of riffle and run habitats than length estimates. We concluded that length estimates were probably a better indicator of habitat composition and used length-derived estimates of pools to test for differences between reach and section surveys. A comparison of pool frequency (expressed as proportion by length) estimates between habitat surveys conducted within sample sections versus those done over relatively long reaches of stream indicated that sample section estimates were almost significantly different ($P = 0.054$; Wilcoxon matched-pairs sign-ranked test) than reach estimates (Figure 7).

Major deviations between reach and sample section estimates of pools were seen in main Cottonwood, East Fork Cottonwood, Delano, and Middle Fork Stone creeks, where higher pool frequencies were estimated from surveys of the entire reach compared to those estimated from surveys of sample sections. We expected this result for the Middle Fork of Stone Creek, which contained a large number of beaver ponds throughout the reach, in contrast to the estimate section within this reach that did not include any large beaver ponds due to sampling difficulties. However, deviations between the other three reach and site surveys represent a sampling problem. Comparisons between estimated proportions of pools from reach and sample site surveys in the other nine reaches indicated that sample sections reasonably estimated pool frequencies for those reaches.

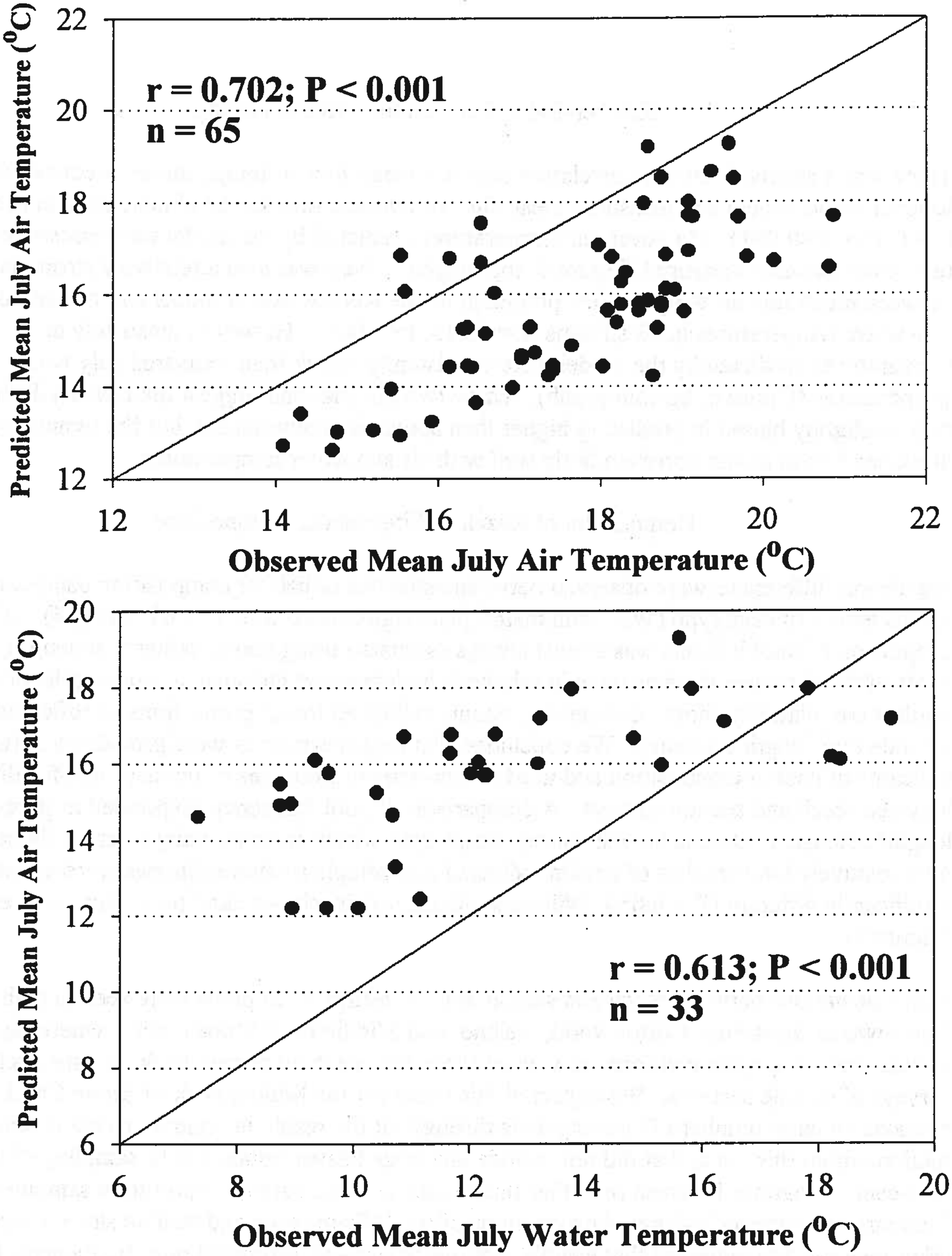

Figure 6. Relationships between predicted mean July air temperatures and measured mean July air temperatures (top graph) at 65 climate sites and measured mean July water temperatures at 33 streams (bottom graph). Correlation coefficients and P-values are shown for each comparison.

Table 4. Number and mean length (m) of pool, riffle, and run habitat types and proportion of each type (in parentheses) estimated from counts and lengths of habitat types over reaches. Wilcoxon signed rank test shown for each habitat type.

Stream	Pools		Riffles		Runs	
	n	Mean length	n	Mean length	n	Mean length
Collar Creek	70 (28)	3.2 (14)	146 (57)	8.0 (74)	38 (15)	4.7 (11)
Cottonwood Creek	32 (40)	5.3 (29)	39 (48)	9.0 (59)	10 (12)	7.0 (12)
Delano Creek	61 (35)	2.6 (24)	93 (54)	4.7 (66)	19 (11)	3.4 (10)
E Fk Cottonwood Ck	57 (43)	4.0 (31)	44 (33)	6.8 (41)	32 (24)	6.2 (27)
Geyser Creek	67 (32)	3.6 (24)	118 (57)	5.9 (68)	22 (11)	3.9 (8)
Half Moon Creek	240 (28)	4.8 (23)	461 (53)	6.6 (60)	162 (19)	5.5 (17)
Halfway Creek	56 (37)	3.5 (32)	77 (51)	4.1 (52)	19 (12)	5.1 (16)
Left Fork Stone Ck	106 (23)	1.6 (6)	329 (71)	7.4 (89)	26 (6)	4.9 (5)
Middle Fk Stone Ck	27 (71)	10.8 (67)	4 (11)	8.5 (8)	7 (18)	15.1 (25)
N Fk Douglas Ck	62 (35)	1.8 (21)	83 (47)	3.8 (60)	31 (18)	3.1 (19)
W Fk Cottonwood Ck	95 (35)	4.0 (22)	107 (39)	7.4 (46)	73 (26)	7.6 (32)

<u>Wilcoxon sign ranked test results between proportion by count versus length</u>

	Pools	Riffles	Runs
z-value	-2.938	2.759	0.665
P-value	0.003	0.006	0.506

Associations among Habitat Variables

Eight factors were derived from 19 habitat variables collected at all 76 sites using varimax rotated PCA (Figure 8; Appendix C). Most of these factors were relatively easy to interpret. The relatively heavy weighting of the downstream link (D_Link) variable in the temperature factor (#2) makes sense, higher KRTemp estimates were associated with streams located lower in a basin, nearer larger streams. However, the positive relation between KRTemp and elevation (Elev) in this factor is hard to explain. The heavy weighting of pH, being negatively related to mining impact, within the mining impact factor (#4), seems intuitively reasonable. However, the negative relation between mining impacts and channel gradient above the site (Ab Grad) within this factor is less clear, but may be related to the presence of mining activity in headwater areas of lower channel gradients. The pool habitat factor (#6) was easy to interpret and was heavily weighted with proportion of habitat in pools (% Pool) and the negative of proportion of habitat in riffles (% Riffle). The longitude and width factor (#7) indicated that the further west (higher in longitude) a sampled site was located, the narrower the stream became (negative Width coefficient to positive Long coefficient). Regression analyses were run using these eight factors.

Eleven factors were derived from estimates of all 38 habitat variables collected at 53 of the sites using varimax rotated PCA (Appendix C). Four of the factors created using this full suite of habitat variables were nearly identical to four of the eight factors derived from 19 habitat variables collected at all 76 sites based on habitat variables that were heavily weighted in both sets of factors. Mining development was included within two factors in this second PCA. The inclusion of woody debris, substrate composition, and streambank variables led to factors that were heavily weighted for these variables in the remaining five factors.

When we replaced estimates made from 7.5 minute maps with GIS derived estimates for those variables that could be derived from map-level data (elevation, KRTemp, latitude, longitude, channel gradient, and aspect), we again obtained eight factors (Appendix C). Several factors weighted the habitat variables somewhat differently than they were weighted in the initial PCA. Latitude, longitude, elevation, and KRTemp variables were split into two separate factors (#1 and #2), rather than a single factor as in the first PCA. This difference may be partially explained by the inclusion of mean, minimum, and maximum elevation variables in this PCA. The elevation factor (#1) contained these three elevation variables plus gradient variables. The temperature factor (#2) contained the KRTemp variable and latitude and longitude. Impacts of land management activities were also treated differently in this PCA. Logging and road impacts grouped together with downstream link in factor #5. Mining and road impacts grouped together in factor # 6 and contained positive associations with two gradient variables (average gradient of the reach and standard deviation of reach gradient), and inversely with east to west aspect and downstream link. A non-logging impact factor (#7) contained all management impact variables, except logging, and the variables isolation, average wetted width, and conductivity. The stream

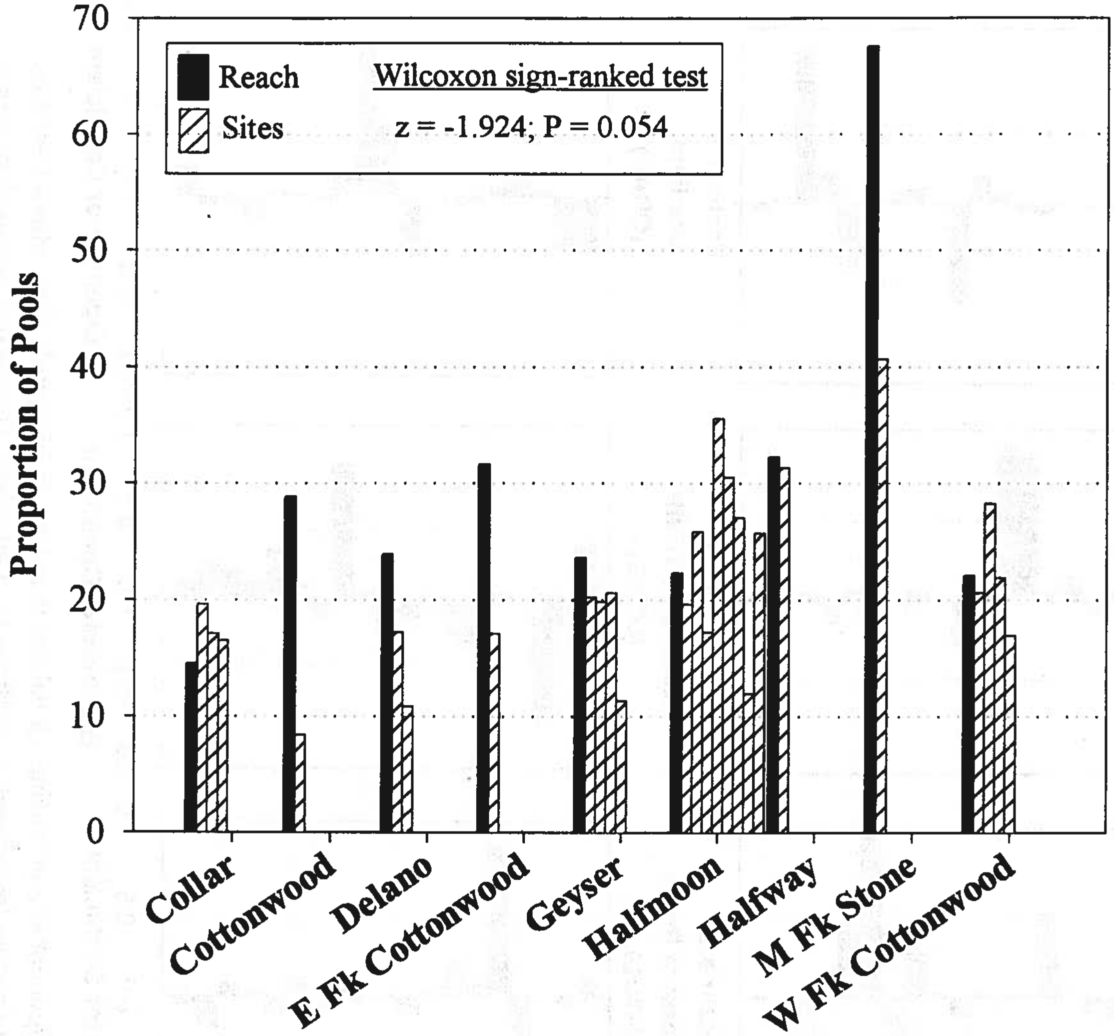

Figure 7. Comparisons between estimates of pool frequencies obtained by measuring lengths of pool habitats over an entire reach versus those made at sample sites within the reach. The result of a Wilcoxon matched-pairs sign-ranked test is shown.

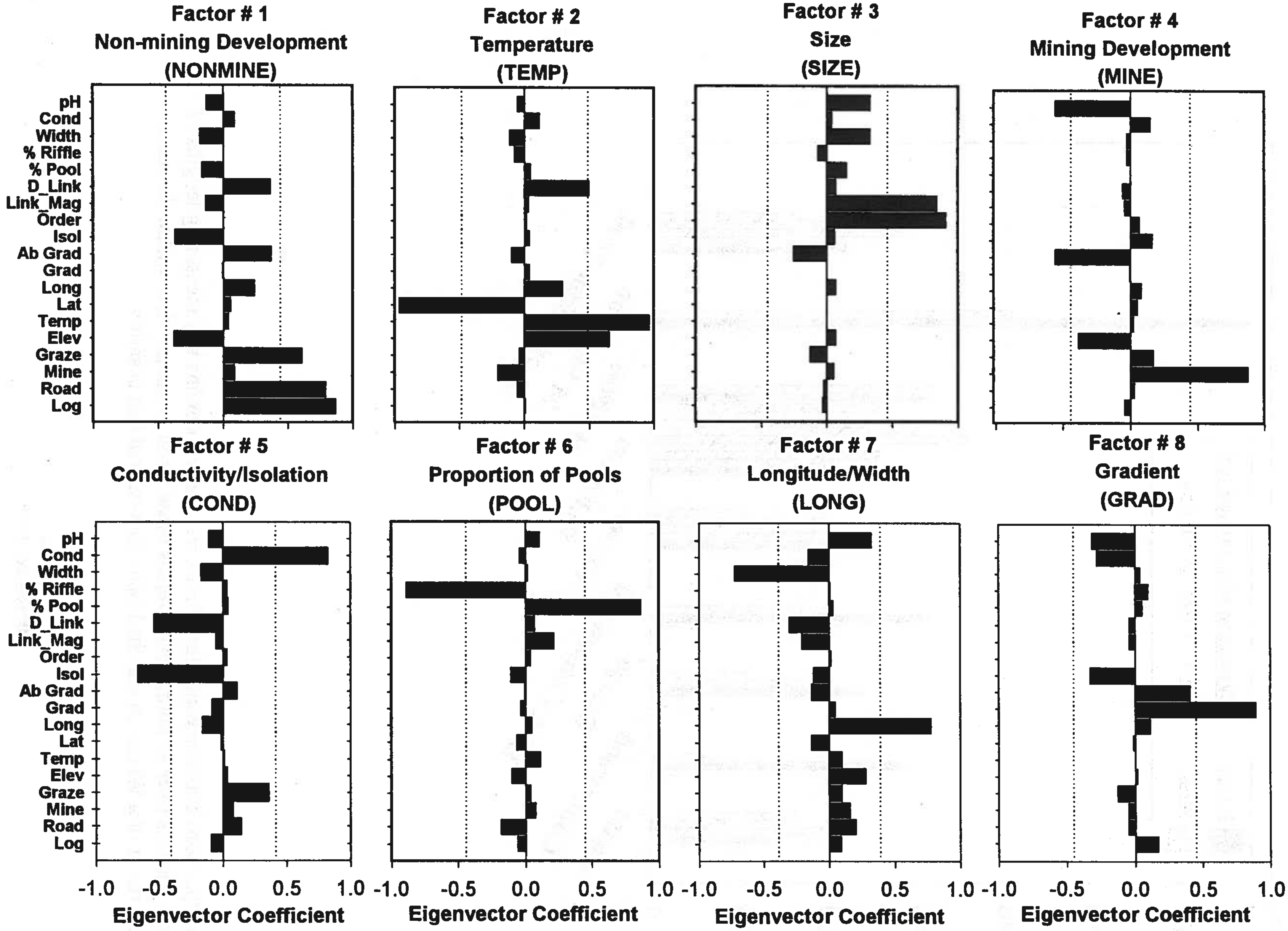

Figure 8. Eight factors identified by principal component analysis using 19 habitat variables in 76 sample sites where westslope cutthroat trout densities were estimated showing eigenvector coefficients. Only these factors had eigenvalues larger than 1.0. The name and abbreviations used to identify each factor are shown below each factor number. Vertical dotted lines represent values that are half the maximum eigenvector coefficient for each factor. Variables whose eigenvector coefficients cross the vertical dotted lines were considered heavily weighted for that factor.

size (#3) and pool (#4) factors were easily interpreted and were similar to two factors derived from the initial PCA. The final factor (#8) was heavily weighted for both north to south aspect and pH. We are unsure what relationship might exist between these two variables.

Relationships among Habitat Variables and Fish Densities

Densities of westslope cutthroat trout were highly and negatively correlated to densities of brook trout (Table 5). Drainage aspect, impacts of roads, impacts of mining, stream order, and bank cover ratings were also negatively correlated to densities of westslope cutthroat trout. Densities of westslope cutthroat trout were positively correlated to the proportion of boulder-sized substrate making up the streambed. The level of isolation a site had from downstream habitats was negatively and highly correlated to densities of brook trout. Impacts of roads and logging were highly and positively correlated to densities of brook trout. Latitude, drainage aspect, proportion of the streambed in sand and silt, and frequency of large woody debris were also positively correlated to densities of brook trout.

When the effects of drainage, site within drainage, and year were compared to the transformed (ln[density +1]) estimates of westslope cutthroat trout in a mixed model both drainage and site within drainage were significantly ($P<0.001$) associated with density of westslope cutthroat trout (Table 6). There was a somewhat, but much less significant, effect of the drainage by year interaction ($P = 0.035$) on estimated densities of westslope cutthroat trout. The estimated year component of variance was negative (Table 6). We were concerned about how year might effect densities of westslope cutthroat trout for sites in White's and McVey creeks because we removed brook trout from these streams. To assess how year effected predicted densities we compared predicted and estimated densities for all streams and years and found there was a significant difference between predicted and estimated densities for White's Creek in 1995. Based on this analysis we removed the 1995 samples from White's Creek and re-ran the mixed model. The drainage by year interaction did not show a significant effect on densities of westslope cutthroat trout ($P = 0.234$) when White's Creek 1995 estimates were excluded. Based on results from these mixed model population estimates within sites were pooled across years for all sites, except for those in McVey and White's creeks, to test the influence of habitat and brook trout on densities of westslope cutthroat trout. For McVey and White's creeks only the estimates for 1993, prior to brook trout removals, were used to ensure that any confounding affect of brook trout removal did not influence our results. Estimated densities of westslope cutthroat trout were pooled across years by averaging density estimates within each site across all years a site was sampled. These pooled densities were then transformed (ln[density +1]) and used as dependent variables in subsequent regression models.

We used the eight factors generated by PCA on the 19 habitat variables collected at all 76 sites (Figure 8) for all multiple regression analyses. First, PCA components were regressed against lognormal transformations of westslope cutthroat trout densities for 51 sites containing allopatric

Table 5. Spearman rank correlations along with estimated significance (*** = P<0.001; ** = P<0.05; and * = P<0.10) for transformed densities of westslope cutthroat and brook trout 75 mm and longer and habitat variables estimated at 53 sites where estimates were made from 1993 to 1995.

Variable	ln(WCT≥75 mm)	ln(EBT≥75 mm)
ln(WCT≥75 mm)	1.0000	
ln(EBT≥75 mm)	-0.4312 ***	1.0000
Aspect	-0.4013 **	0.3654 **
Road Impact	-0.2292 *	0.4500 ***
Log Impact	-0.1819	0.4685 ***
Mine Impact	-0.2470 *	0.1641
Grazing Impact	-0.1747	0.2230
Elevation	0.1614	-0.1530
KRTemp	-0.0154	-0.2705 *
Latitude	-0.0469	0.2586 *
Longitude	0.0852	0.2048
Channel Gradient	0.1581	0.0482
Gradient Above Site	0.0993	0.0652
Isolation	0.1853	-0.5676 ***
Stream Order	-0.2468 *	0.2117
Link Magnitude	-0.1679	0.0845
Downstream Link	-0.0824	0.0020
% Boulder	0.2936 **	-0.1539
% Cobble	-0.0184	-0.0783
% Large Gravel	-0.1365	-0.0644
% Small Gravel	-0.0383	0.2406 *
% Sand	-0.1561	0.3126 **
% Silt	-0.1523	-0.1440
Instream Cover	0.0108	0.1437
Small Woody Debris	0.0518	0.1552
Large Woody Debris	-0.0091	0.2509 *
Small Debris Cross	-0.0457	-0.1734
Large Debris Cross	0.0025	-0.1446
Spawning Habitat	0.0168	0.1540
Pool Rating	0.1535	-0.1302
Bank Stability Rating	-0.1301	-0.1035
Bank Cover Rating	-0.2484 *	0.0559
Riparian Use Rating	-0.2004	-0.0354
% Pool	0.1355	0.0423

Table 5. (Continued).

Variable	ln(WCT≥75 mm)	ln(EBT≥75 mm)
% Riffle	-0.093	-0.028
% Run	0.084	-0.000
Average Width	0.076	-0.107
Average Depth Pools	0.081	-0.049
Maximum Depth Pools	0.142	-0.008
Residual Pool Volume	0.033	-0.024
Conductivity	-0.093	-0.072
pH	0.142	0.051

Table 6. Results of mixed regression model to predict transformed estimated density of westslope cutthroat trout > 75 mm per 1000 m^2 (ln[density +1]) using year (Y) of estimate, drainage (D), site within drainage (S[D]), and year by drainage interaction (Y*D). Year, drainage, and site within drainage were all entered as class variables. Drainage and site within drainage were always entered as "fixed" variables and year was always entered as a "random" variable. The Type III F value and associated probability value are shown for fixed effects and the component of variance, and Wald test for the Z-value and associated probability are shown for random effects. There were a total of 223 observations at 94 sites within 17 drainages over four years for "all observations" and 216 observations for "White's 1995 removed".

	Fixed effects		Random effects		
Model	Type III F	P	Component of variance	Z-value	P
Y + D + S(D) + Y*D; Y and Y*D random, D and S(D) fixed; all observations					
D	40.46	< 0.001			
S(D)	9.87	< 0.001			
Y			< 0.000	-	-
Y*D			0.053	2.11	0.035
Residual			0.161	7.19	< 0.001
Y + D + S(D) + Y*D; Y and Y*D random, D and S(D) fixed; White's 1995 removed					
D	58.43	< 0.001			
S(D)	9.63	< 0.001			
Y			0.009	0.64	0.520
Y*D			0.024	1.19	0.234
Residual			0.166	6.90	< 0.001

westslope cutthroat trout populations. The "best" Habitat models, based on SIC criteria, selected by our regression procedure used 10 independent terms. The five "best" Habitat models, based on SIC criteria, were statistically indistinguishable from each other. All five Habitat models included the simple term pool habitat and second order terms for mining development, temperature, and channel size. Interactions included in all five Habitat models were between channel size and longitude-wetted width, mining development and pool habitat, non-mining development and gradient, temperature and gradient, mining development and conductivity-isolation, and longitude-wetted width and gradient (Table 7). We arbitrarily selected the model with the best SIC value. The R^2 for this model was 0.79. This model seems to make biological, as well as, statistical sense. First, the pool habitat factor (Factor #6) entered the model with a positive coefficient. In this factor the proportion of pools was positively weighted and the proportion of riffles was negatively weighted. This result indicates that westslope cutthroat trout were found at higher densities in sites containing a higher proportion of pools. Second, factors heavily weighted for temperature/location (Factor #2) and stream size (Factor #3) entered the model with negative coefficients as second order components indicating that intermediate values of these components resulted in higher densities of fish than low or high values.

For stream size this suggests that in extremely small (i.e. first order) streams located near the headwaters (i.e. lower link magnitude), or large (i.e. third and fourth order) streams located lower in a drainage (i.e. higher link magnitude) densities of westslope cutthroat were lower than in intermediate sized streams. The relationship with the temperature/location factor is not quite as clear, but suggests that densities of westslope cutthroat trout are lower at extremely high and low elevations associated with lower and higher KRTemp predictions, than at intermediate elevations and temperatures.

When brook trout variables were added to the model by adding the 22 sympatric sites the resulting Full Model had an R^2 of 0.80 (Table 7). This model contained a y-intercept term (indicator of brook trout) that adjusted the y-intercept from the original Habitat Model downwards (-2.23) based on the presence of brook trout. This downward adjustment to the Habitat Model regression line illustrates the negative effect brook trout had on densities of westslope cutthroat trout. The Full Model also included first and second order terms for brook trout abundance, and interactions between brook trout abundance and the temperature factor, brook trout abundance and the mining and non-mining development factors, and brook trout abundance and the channel gradient factor (Table 7). Densities of westslope cutthroat trout were generally higher in allopatry than in sympatry with brook trout (Figure 9), however, there were several sympatric sites that contained relatively high densities of westslope cutthroat trout and a few allopatric sites that contained relatively low densities. The observed low densities of westslope cutthroat trout in allopatry fit the Full Model pretty well, but at least one site containing relatively high densities of westslope cutthroat trout in sympatry did not fit as well (arrow on Figure 9). We address the likely reason for this deviation in the discussion.

Table 7. Multiple regression analysis results showing how habitat and land management factors influenced densities of westslope cutthroat trout for 51 allopatric westslope cutthroat trout sites (HABITAT MODEL) and for the model that fit brook trout variables to residuals of westslope cutthroat trout densities from the habitat model (FULL MODEL). Habitat and land management factors were derived from varimax rotated PCA (names of factors and variables that were "most important" in each factor are shown on Figure 8). The brook trout model included 22 additional sympatric westslope cutthroat and brook trout sites. Regression results are also shown for runs made with the 22 sympatric sites in both the HABITAT and FULL models.

MODEL TYPE Model	R^2
HABITAT MODEL	
ln(WCT density+1) = 3.148 - 0.306(MINE) + 0.179(POOL) - 0.166(TEMP^2) - 0.130(SIZE^2) - 0.235(MINE*POOL) + 0.213(SIZE*LONG) - 0.250(NONMINE*GRAD) - 0.181(TEMP*GRAD) - 0.261(MINE*COND) - 0.206(LONG*GRAD)	0.79
FULL MODEL	
ln(WCT density+1) = HABITAT MODEL - 2.230(EBT indicator) + 3.209(EBT) - 0.983(EBT)^2 + 0.500(EBT*NONMINE) + 0.628(EBT*KRTEMP) + 0.207(EBT*MINE) + 0.276(EBT*GRAD)	0.80
ONLY 22 sympatric sites using the:	
HABITAT MODEL	0.05
FULLMODEL	0.69

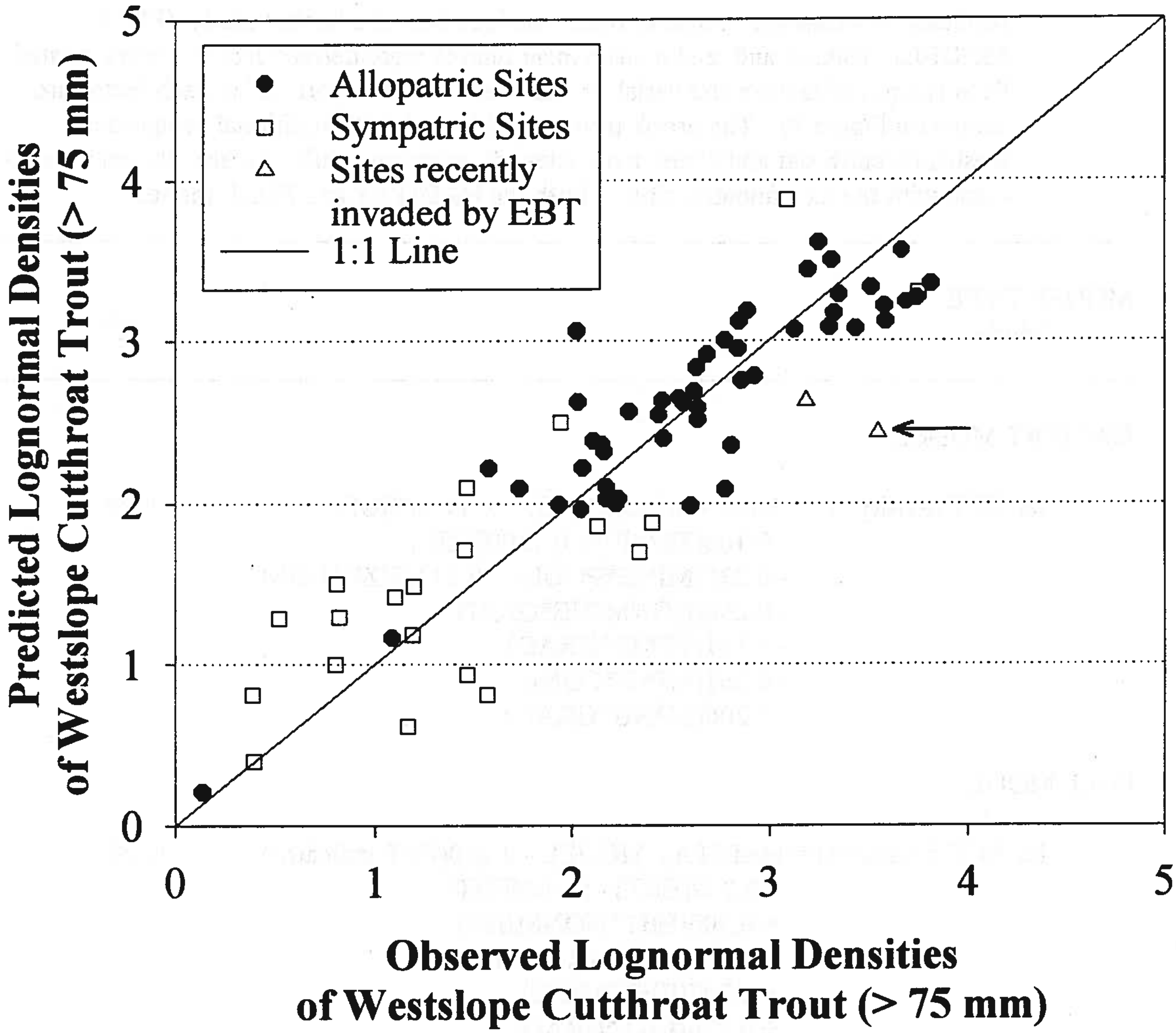

Figure 9. Comparison between observed versus predicted densities of westslope cutthroat trout 75 mm and longer (lognormal transformation) derived from a multiple regression model (Full Model) using habitat condition factor and brook trout abundance covariates. Solid circles indicate sites where westslope cutthroat trout occurred in allopatry. Open squares indicate sites where westslope cutthroat trout occurred in sympatry with brook trout. Two sites where brook trout recently invaded (within 5 years) habitats occupied by westslope cutthroat trout are shown by open triangles. An arrow points to a site that does not fit the model very well.

When the 22 sympatric sites were run through the Habitat Model the R^2 dropped to 0.05. When these 22 sympatric sites were run through the Full Model (habitat and brook trout effects) the R^2 increased to 0.68. The effects of brook trout densities on densities of westslope cutthroat trout were not linear. We explore those relationships further in the discussion.

Discussion

Fish Abundance Estimates

Since we used depletion estimators to estimate fish densities and often conducted only two passes, our estimates probably have an under-estimate bias (Riley and Fausch 1992). Riley and Fausch (1992) suggested two-pass estimates consistently under-estimated actual fish populations and this bias is more pronounced as probability of captures drop below 0.90. Our "rule of thumb" was to make two passes in the field and conduct a third pass only if a field calculated capture probability (based on the formula provided by Seber and LeCren [1967]) for the first two passes was under 0.8. Of the 30 estimates that had estimated capture probabilities less than 0.7, 14 estimates were made using at least three passes. Riley and Fausch (1992) suggested that three removals reduced estimate bias. In some cases low two-pass probability of capture estimates occurred only during a single year. Since we averaged estimates across years, the bias potentially associated with low probability of captures during any one year should have been somewhat mitigated by those estimates with relatively high probabilities of capture conducted in other years. However, in a few cases, particularly in some of the larger streams with complex habitats, estimated probabilities of capture were relatively low across all years due to sampling difficulties. In these cases, the under-estimate bias might have compromised the validity of our results. While density estimates may not be accurate, they should reflect relative abundance fairly well, since almost all estimates were conducted using a depletion estimator. We discuss the implications of this problem in the following section dealing with habitat factors influencing the abundance of westslope cutthroat trout.

The consistent movement of large westslope cutthroat trout out of Section 11 of Halfway Creek, that forced us to eliminate this sample site from our analysis, was an interesting behavior. We speculate that these larger fish could not meet their energetic and/or space requirements in this small stream (e.g. Chapman and Bjornn 1969) after they had moved downstream into Section 11 from the settling pond at its upper boundary. Thus, they continued to move downstream out of this small relatively unproductive headwater stream habitat.

Comparison of Habitat Composition between the Reach and Site

Length measurements provided better estimates of the proportion of pool, riffle, and run habitats than counts of each habitat type. The sample sections in this study generally contained a similar proportion of pools to that observed in the longer reaches in which they were located. This similarity suggests that these sample sections reasonably represented the habitats within the streams that were sampled. For those reaches where the relative length of habitat estimated as pools within sample sections was significantly different than the relative length of pool habitats within the reach, our estimates of fish densities may not accurately reflect densities throughout the reach.

Factors Influencing Abundance of Westslope Cutthroat Trout

Drainage and site within drainage significantly influenced the variation in densities of westslope cutthroat trout (Table 6). Dunham and Vinyard (1997) reached a similar conclusion regarding the importance of drainage (stream) on densities of Lahontan cutthroat trout, but did not test annual variation within their analyses. We did not find highly significant effects of year on estimated densities of westslope cutthroat trout. The slightly significant effect of the year by drainage interaction we found for the data set containing all 223 observations became insignificant when we removed the seven 1995 White's Creek observations. These sites were removed based on *apriori* knowledge that removal of brook trout may have influenced densities of westslope cutthroat trout. Platts and Nelson (1988) reported high annual variations in abundance of salmonids, however, their study was done primarily in arid southwest streams where stream flow varied widely between years due to high and low annual precipitation. Spring snowmelt peak and low summer stream flows during our 3 year study ranged widely, though not at the extremes for the periods of record (Figures 2 and 3), yet we were unable to document significant annual effects on population densities. We suggest that in the northern Rocky Mountains, snowmelt and groundwater runoff regimes provide more stable stream flows that may mitigate annual variation in precipitation. Consecutive years of drought could result in less stable stream flows as snowpack and groundwater sources are reduced. Under those conditions, higher annual variations in fish densities than we observed may be anticipated.

We want to make it clear that the regression model we selected as "best" using habitat factors was only one of many potential models that could have been selected based on the data. Other models that included different combinations of factors probably were not statistically different from the model we chose. Our selection was based on SIC values and knowledge about importance of habitat variables from previous studies. Using this final "best" model we wanted to know if habitat variables that had meaningful associations with densities of westslope cutthroat trout could be derived from GIS data. Of seven PCA habitat factors derived from the 19 habitat variables retained in multiple regression analyses, five factors (temperature [#2], channel size [#3], and gradient [#8]) contained habitat variables that could easily be estimated using available geographic information system (GIS) layers. However, two factors (proportion of pool habitats [#6], and longitude/channel width [#7]) would require field data collection at the site.

We explored relationships between habitat and brook trout on westslope cutthroat trout. We found a simple inverse correlation between densities of brook and westslope cutthroat trout. We also found that several habitat and land management variables were positively correlated with densities of brook trout and negatively correlated with densities of westslope cutthroat (Table 5). Habitat condition has often been related to densities of salmonids (see Fausch et al. 1988).

Nonnative salmonids, especially brook trout, replace and may compete with westslope cutthroat trout (Griffith 1970, 1972, and 1988; Fausch 1989), but the exact mechanism and role that physical habitat plays in this replacement has been unclear. Our results provide additional support documenting this replacement and shed some light on the role habitat condition may play. Our multiple regression results suggest that the presence and abundance of brook trout overrode effects of habitat on densities of westslope cutthroat trout (Habitat Model $R^2 = 0.05$ and Full Model $R^2 = 0.68$ for 22 sympatric sites). The Full Model reasonably fit a one-to-one predicted versus observed relationship, illustrating that this model reasonably identified those factors that affected densities of westslope cutthroat trout for our data set (Figure 9).

We plotted the effects of physical habitat (habitat effects) and brook trout densities (brook trout effects) on the residuals of predicted transformed estimated densities of westslope cutthroat trout for the 22 sympatric sites to understand how brook trout densities affected densities of westslope cutthroat trout (Figure 10). This plot suggests brook trout densities may not influence densities of

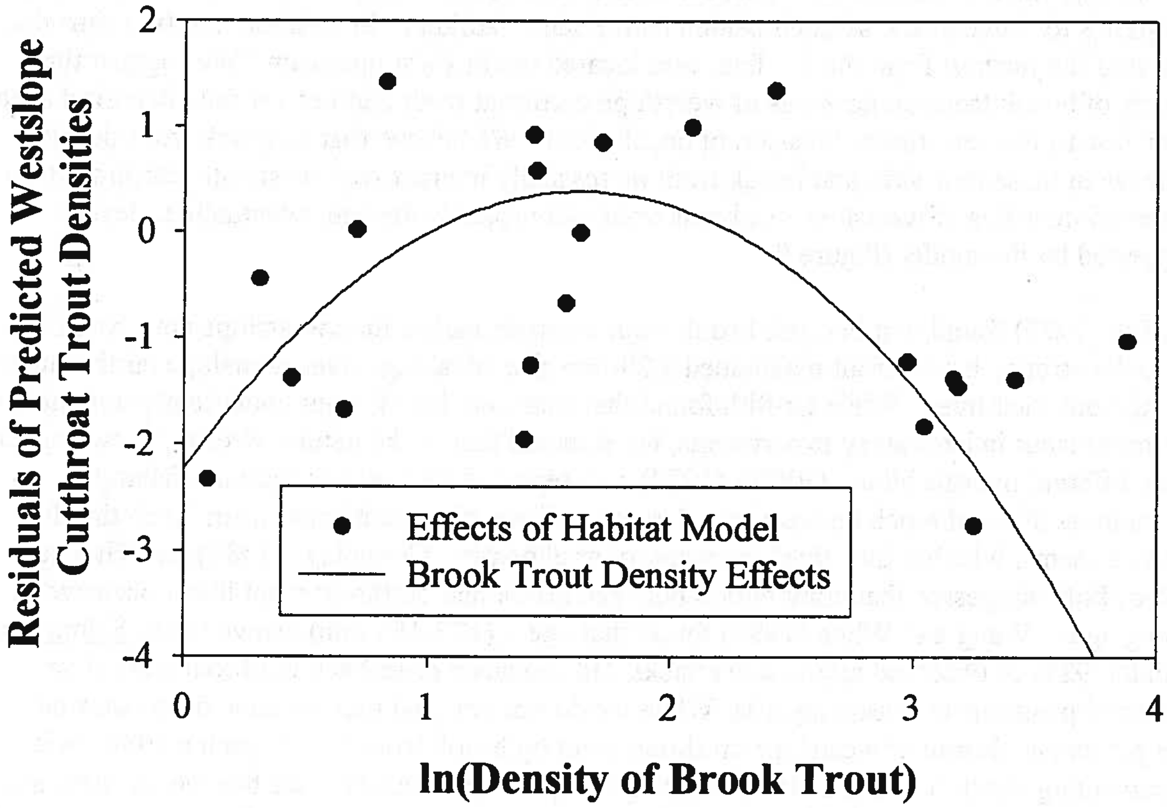

Figure 10. Effects of the Habitat Model (solid circles) and brook trout density (line) on the residuals of predicted densities of westslope cutthroat trout for the 22 sympatric sites.

westslope cutthroat trout at relatively low (< 3/1000 m^2) densities of brook trout, however, once brook trout densities increase above 6/1000 m^2 densities of westslope cutthroat trout are strongly and negatively affected. The interactions between brook trout densities and the temperature factor (Factor #2), brook trout densities and two land-use impact factors (Factors #1 and #4), and brook trout densities and the gradient factor (Factor #8) within the brook trout portion of the model seems reasonable. DeStaso and Rahel (1994) conducted laboratory micro-habitat studies between brook and greenback cutthroat trout, O. c. stomias, at two different water temperatures and observed that brook trout showed a clear competitive dominance over cutthroat trout at water temperatures of 20°C versus 10°C. Nagel (1991) suggested that extinction of local isolated populations of native brook trout in southern Appalachian headwater streams could not be attributed solely to competition with nonnative rainbow trout. He suggested that demographic stochasticity and natural catastrophes probably were also important factors in these extinctions.

We were somewhat concerned that two of the four sympatric sites with the highest densities of westslope cutthroat trout did not appear to fit the model very well (Figure 9; open triangles). We discovered that all four of these sympatric sites that supported high densities of westslope cutthroat trout were located in two adjacent streams making up the headwaters of Jerry Creek, a tributary to the Big Hole River. These four sites had been recently invaded by brook trout (within the past 3 to 5 five years; as documented by the senior author). In addition, the two sites that deviated the furthest from the 1:1 line were located the furthest upstream. We suggest that effects of brook trout on densities of westslope cutthroat trout had not yet fully occurred at these sites, due to the very recent invasion of brook trout. We believe that as brook trout densities increase in these four sites and brook trout increasingly interact with westslope cutthroat trout, observed densities of westslope cutthroat trout will probably decline, eventually to levels suggested by the model (Figure 9).

Griffith (1972) found that because brook trout emerged earlier than westslope cutthroat trout in an Idaho stream, brook trout maintained a 20-mm size advantage over westslope cutthroat trout throughout their lives. While Griffith found that same age brook trout consistently dominated cutthroat trout in laboratory experiments, he observed that in the natural stream the two species used different microhabitats. Griffith (1974) also reported that neither food nor habitat preferences differed much between age 0 brook and westslope cutthroat trout inhabiting four Idaho streams, whether they lived in sympatry or allopatry. Cummings (1987) and Thomas (1996) both suggested that competition between brook and cutthroat trout likely occurred at young ages. Wang and White (1994) found that age 1 (127-154 mm) brown trout, Salmo trutta, initiated 92% of observed aggressive attacks and displaced greenback cutthroat trout from preferred positions in stream aquaria. While we do not contend that we have demonstrated competitive exclusion of westslope cutthroat trout by brook trout (see Fausch's 1988 review documenting the difficulties in demonstrating competitive exclusion), we believe our data and the literature suggest competitive interactions occur and may be most intense between young-of-the-year. This speculation is inferred from the consistent and extremely low juvenile (< 150 mm) densities we observed in sympatric populations. Scoppettone (1993) investigated mechanisms for the decline of Moapa dace (Moapa coriacea) following the introduction of nonnative shortfin mollies (Poecilia mexicana) in the upper Muddy River system of Nevada. He suggested that spatial overlap between the two species was low at all life stages, but that predation by shortfin mollies was the primary mechanism responsible for the decline of the dace. We contend that predation upon westslope cutthroat trout by brook trout cannot be ruled out as a potential factor that allows brook trout to replace westslope cutthroat trout.

We sampled only in streams supporting known populations of westslope cutthroat trout because a major objective of our research was to estimate demographic parameters for westslope cutthroat trout (Downs et al. 1997). Because of this sampling criteria we probably sampled a narrower range of stream sizes and locations than if we had randomly sampled over all available lotic habitats. Westslope cutthroat trout populations have been displaced from most of their historical habitats, especially in larger streams and rivers, and now persist only in isolated headwater refugia, especially in the Missouri River basin (Shepard et al. 1997). We suggest that sampling over this relatively narrow range of habitats probably limited our ability to detect effects of habitat condition and, perhaps, brook trout on densities of westslope cutthroat trout.

The regression model that "best" explained estimated densities of westslope cutthroat trout in allopatry contained factors heavily weighted for mining impacts, temperature and location, proportion of pool habitat, and stream order (Table 7). Important interactions included stream order and longitude/width, mining impacts and pools, management impacts other than mining and channel gradient, temperature/location and channel gradient, mining impacts and conductivity/isolation, and longitude/width and channel gradient. The pool habitat component entered the model with a positive coefficient and as a simple term meaning that a higher proportion of pools indicated higher densities of westslope cutthroat trout. Several studies have suggested that the proportion of habitat in pools is related to densities and distribution of westslope cutthroat trout (Shepard 1983; Pratt 1984; Peters 1988; Hoelscher and Bjornn 1989; Heggenes et al. 1991; Ireland 1993; Young 1998). Our analyses indicated that low densities of westslope cutthroat trout were associated with very small and relatively large streams. While sampling design problems could have influenced this result, westslope cutthroat trout are not now found in many larger mainstem tributaries and rivers. Our results suggest that for the populations we sampled, even in allopatry, densities declined as stream size increased. We are unsure if the fluvial component of these stocks has been lost, either because nonnative salmonids have displaced them, physical habitat conditions and management impacts have made larger lotic habitats unsuitable, or a combination of these two factors.

The potential bias associated with under-estimating fish populations using two-pass estimates could affect the validity of our results, especially if these under-estimates were correlated with some of the habitat variables we assessed. Our experience indicated that low probability of captures were usually associated with larger streams and more complex habitats. This association might compromise the relationship we found between $[\text{stream size}]^2$ and densities of westslope cutthroat trout. If unbiased estimates resulted in higher westslope cutthroat trout densities in larger streams than in intermediate-sized streams the relationship might be linear and not curvilinear (quadratic). Potential bias associated with under-estimates should not dramatically affect the relationship we found between the proportion of pool habitat factor (Factor #6) and densities of westslope cutthroat trout. This pool habitat component entered the model as a simple term with a positive association to densities of westslope cutthroat trout and even if densities were higher than estimated in sites with more complex habitats (i.e. more pools), this linear relationship should still hold. Estimator bias should not have influenced the sympatric model because we suspect that estimator bias is similar for the two species at any particular site.

Despite some of the shortcoming of this analysis, we showed that both habitat condition and nonnative brook trout influence population densities of westslope cutthroat trout in streams. We suggest that, while it is difficult to precisely allocate the level of influence each of these major factors has, these two factors probably operate in synergy. When brook trout invade habitats supporting westslope cutthroat trout they can reduce and ultimately eliminate populations of westslope cutthroat trout, especially if habitats have been degraded by land management activities. We hypothesize that under ideal habitat conditions, westslope cutthroat trout may be able to compete with brook trout and persist, but that in degraded or naturally lower quality habitats, brook trout are more likely to displace westslope cutthroat trout. In degraded habitats where westslope cutthroat trout exist in allopatry, they can maintain a viable, though lower than potential, population. However, in habitats that have been degraded and invaded by nonnative brook trout, westslope cutthroat trout will not likely persist due to the negative influences of these two factors. The interactions between brook trout and temperature, and brook trout and management impact components in the sympatric model also suggest brook trout may gain a competitive advantage in degraded habitats.

Conclusions

1. Densities of westslope cutthroat trout were most affected by stream-level effects, followed by site-level effects. Effect of time (year or year*drainage interaction) did not seem to significantly influence densities of westslope cutthroat trout over the 4 years of this study, even though stream flow regimes varied widely between years.

2. A pair of regression models, developed from sites containing allopatric westslope cutthroat trout populations and sites where westslope cutthroat trout populations were sympatric with brook trout, using PCA factors generated from habitat and management impact variables accounted for about 80% of the variation in observed densities of westslope cutthroat trout.

3. The allopatric (Habitat) model indicated that temperature, stream size, amount of pool habitat, and land management impact factors influenced densities of westslope cutthroat trout.

4. The addition of brook trout to the allopatric (Habitat) model indicated that the presence and abundance of brook trout strongly influenced densities of westslope cutthroat trout, and that brook trout interacted with land management impacts, stream gradient, and temperature factors to influence westslope cutthroat trout densities.

5. The best possible subsets regression model strategy developed for this analysis allowed us to efficiently evaluate a large set of variables using Schwarz's Information Criteria (SIC) in an attempt to avoid over-fitting the model.

6. The model to predict mean July air temperature based on elevation and latitude developed by Keleher and Rahel (1996) for the Rocky Mountains correlated fairly well with both air temperatures at 65 climate sites and water temperatures in 33 streams of Montana. However, this temperature model may have a negative bias for predicting air temperatures and a positive bias for predicting water temperatures.

7. Length rather than counts of habitat units was deemed a better measure for estimating proportion of the stream in pool, riffle, and run habitat types.

Recommendations

1. To conserve westslope cutthroat trout in the Missouri River basin, high quality habitats containing a high proportion of pools, maintain cool water temperatures, and are located in intermediate-sized headwater streams that cannot be invaded by nonnative salmonids must be maintained.

2. Conservation of westslope cutthroat trout will probably require removal of nonnative salmonids from some streams where these two species occur in sympatry, especially in degraded habitats and in locations where water temperatures are warmer and channel gradients are lower.

3. Future investigations should focus on better quantifying and predicting water temperature regimes, using GIS layers to estimate land use impacts, sampling a wider range of potential stream habitats in a more random design, and conducting three- and four-pass depletion estimates to reduce estimator bias.

Chapter 2

Assessing the influence of elevation, aspect, gradient, latitude, longitude, and abundance of non-native salmonids on the abundance of stream-resident westslope cutthroat trout Oncorhynchus clarki lewisi in streams of the Upper Missouri River basin of Montana using a GIS

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Study Area

Meriwether Lewis first described westslope cutthroat trout (Oncorhynchus clarki lewisi) from six fish ranging in length from 16 to 23 inches caught by Private Silas Goodrich at the Great Falls of the Missouri River (Moring 1996). Hanzel (1959) reported that westslope cutthroat trout were distributed in the Missouri River basin down to the mouth of the Musselshell River in the late 1950's. Behnke (1992) reported that the known distribution of westslope cutthroat trout included the upper Missouri River and its tributaries downstream to Fort Benton, as well as the headwaters of the Judith, Milk, and Marias rivers. For this assessment we included all stream reaches from the headwaters of the Missouri River drainage down to about Fort Benton, Montana (Figure 11). We only assessed the portion of the Missouri River basin we were relatively certain had been historically occupied by westslope cutthroat trout. We excluded the Sun River drainage because we were unsure if the upper Sun River drainage had been occupied above the present location of Diversion (B. Hill, Montana FWP, personal communication). Westslope cutthroat trout may have historically occupied the Missouri River basin below Fort Benton, however, their exact historical distribution is unclear (Behnke 1992).

Methods

Relative Fish Abundance and Genetic Status

The Montana Rivers Information System (MRIS) is a fish information summary database that is linked to geographic information system (GIS) hydrography layers. These hydrography layers were derived from 1:100,000 scale U.S. Environmental Protection Agency data (File 3 data set). The MRIS breaks streams and rivers into reaches based on locations of tributary confluences, and in rare cases, channel gradient, valley shape, and administrative boundaries. Reaches ranged in length from 0.2 to 48 km (Figure 12). The MRIS contains information provided by local state and federal fisheries biologists on the relative abundance of each species within each reach. Biologists rated the quality of fish abundance information using a scale of 0 to 9 (Table 8). Genetic purity of westslope cutthroat trout populations were evaluated based on starch gel electrophoresis and, for those genetically untested populations, on the presence of potentially hybridizing species (rainbow trout O. mykiss and Yellowstone cutthroat trout O. c. bourveri) within the same reach. We updated and verified these data by visiting all local field biologists within the upper Missouri drainage during 1994 and 1995 to ensure their data was updated and accurately entered into the MRIS. The MRIS was again updated in 1996 to reflect new information on genetic status, fish distributions, and abundance. Exact distributions of fish species within any particular reach were not usually known, therefore if a fish species was encountered anywhere within a designated reach the MRIS database indicated that species was present throughout the reach.

Fish abundance was rated as abundant, common, uncommon, rare, incidental and present based on the estimated number of fish per 300 m of stream length related to stream width (Figure 13).

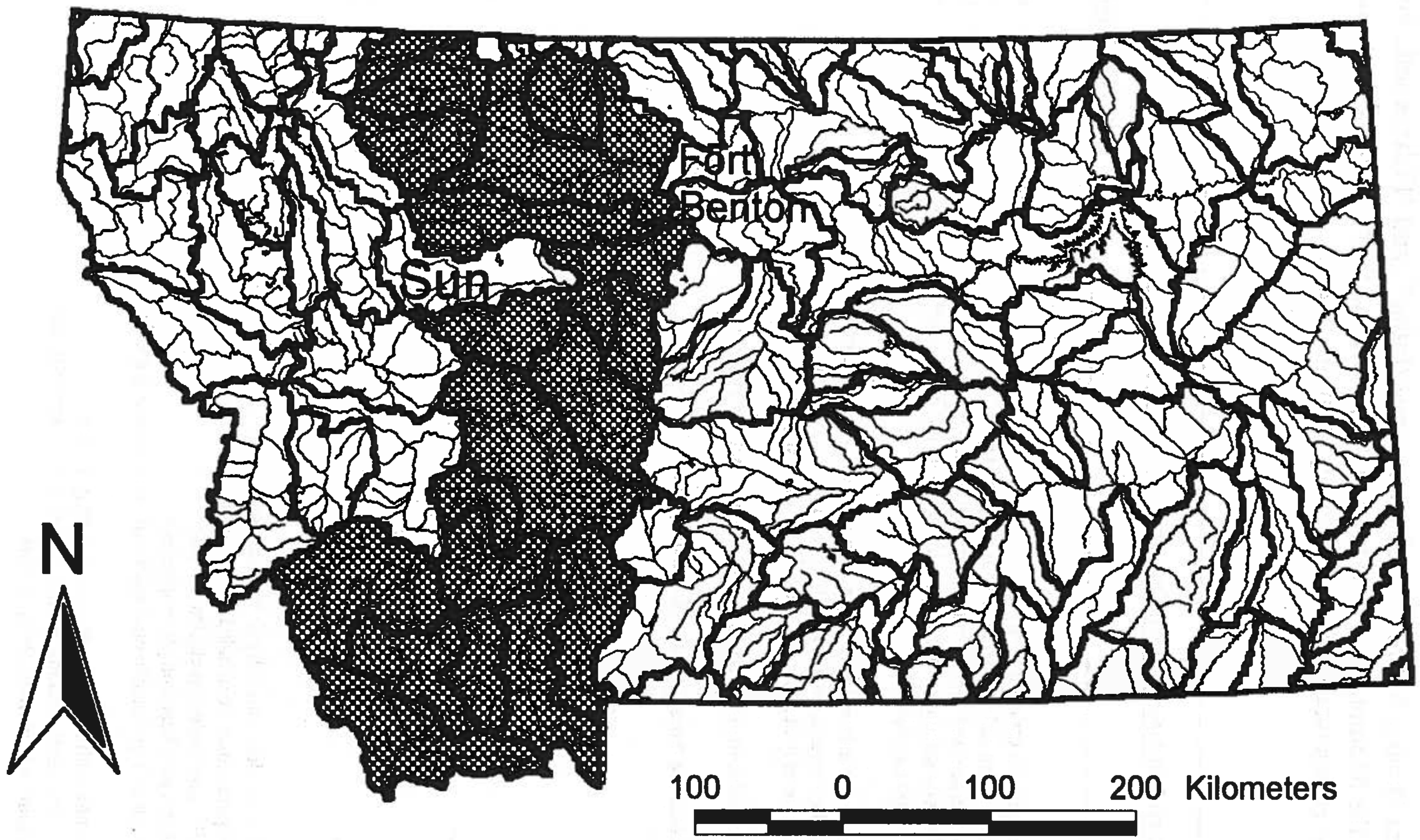

Figure 11. Map of Montana river basins showing the location of the river basins assessed for effects of physical features and presence and abundance of nonnative trout on westslope cutthroat trout within the upper Missouri River basin (shaded area).

Table 8. Codes for "Data Quality Rating", "Fish Abundance Rating", and "Fish Genetic Purity Rating" from the Montana River Information System, the description of those codes and how these codes were reduced for analysis in this study.

Category	Code	Montana River Information System Classifications	Reduced Classification
Data Quality Rating			
	1	Based on judgement estimates (guess)	0
	2	Based on judgement estimates (some knowledge of reach)	0
	3	Based on judgement estimates (visited, but did not sample, reach)	0
	4	Based on limited measurements (single visit to reach, angling or other relative abundance sampling)	0
			0
	5	Based on limited measurements (sampled reach, relative abundance)	1
	6	Based on limited measurements (sampled reach, no estimates made)	1
	7	Based on extensive measurements (population estimate, poor confidence)	1
	8	Based on extensive measurements (population estimates, moderate confidence)	1
	9	Based on extensive measurements (population estimates, high confidence)	1
Fish Abundance Rating			
	A	Abundant	2
	C	Common	2
	R	Rare	1
	U	Uncommon	1
	Y	Present	1
	F	Incidental	0
	N	Not present	0
Fish Genetic Purity Rating			
	A	Genetically pure, determined by electrophoresis	2
	I	Genetically pure; could be invaded by contaminating species	2
	J	99.0%-99.9% pure based on electrophoresis	2
	K	95.0% - 98.9% pure based on electrophoresis	2
	D	Especially valuable genetically pure trout with contaminating species	2
	B	Potentially pure with no record of contaminating species	1
	C	Potentially pure, contaminating species planted in drainage historically	1
	E	Potentially pure with contaminating species	1
	U	Unknown	1
	H	Hybridized species based on electrophoresis	0

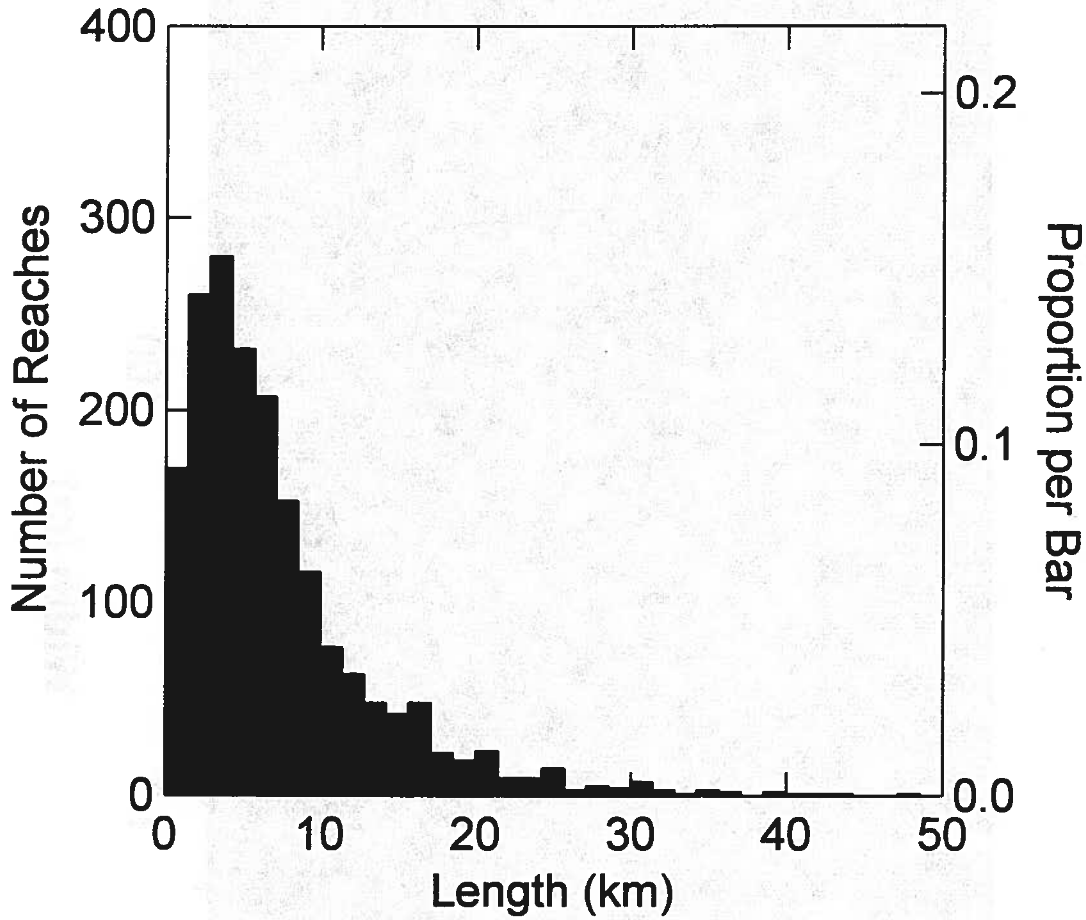

Figure 12. Histogram showing length of stream reaches within the upper Missouri River basin assessed for effects of physical features and presence and abundance of nonnative trout on westslope cutthroat trout.

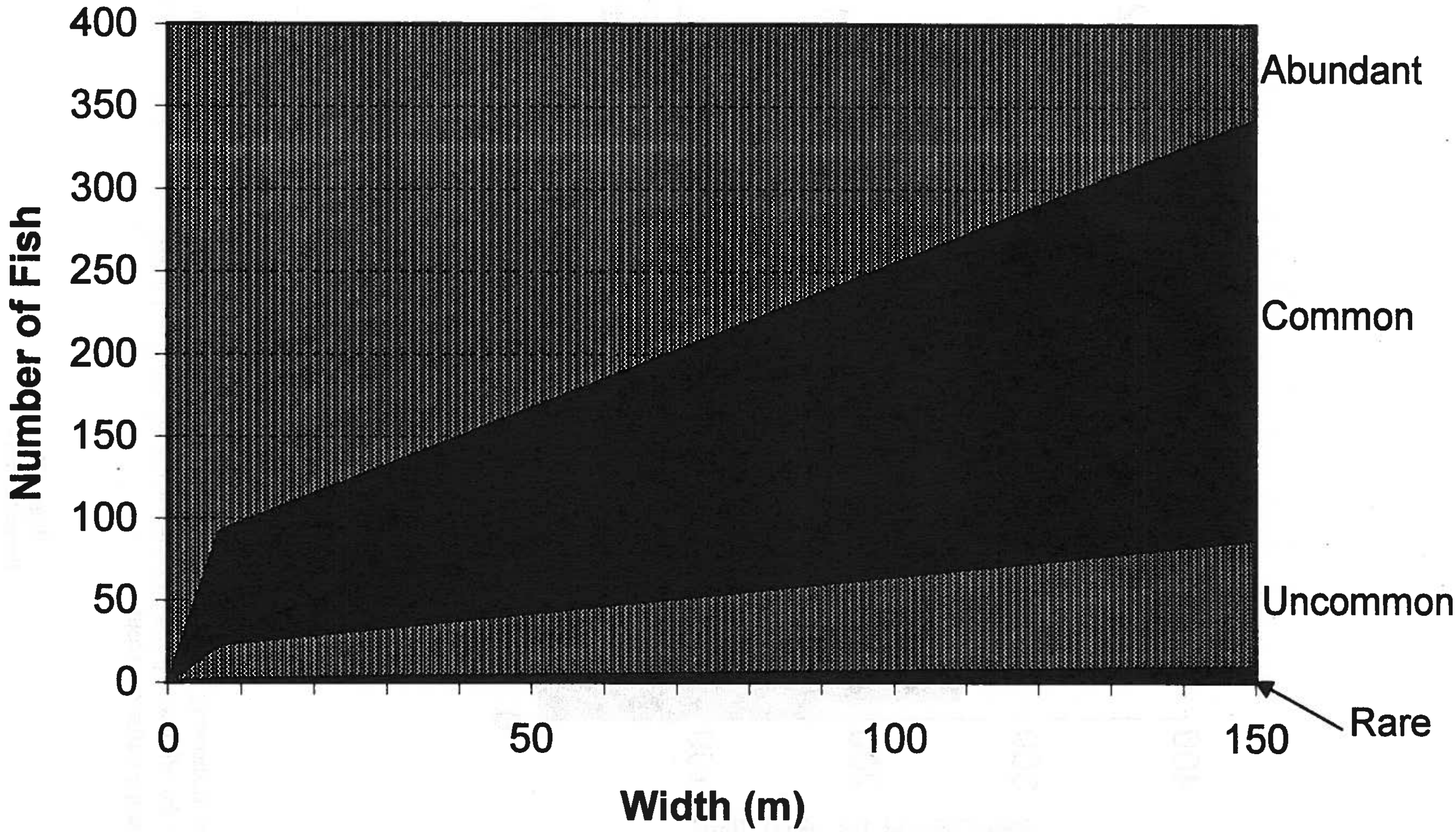

Figure 13. Criteria for assigning relative abundance ratings based on a 300 meter long sample section from the Montana Rivers Information System (Montana Department of Fish, Wildlife and Parks 1992).

We collapsed the MRIS fish abundance ratings in two ways. We first reduced the ratings to absent (0), present, but uncommon or rare (1), and common or abundant (2). We further reduced these ratings to present (1) or absent (0) (Table 8). Fish abundance information was ranked for westslope cutthroat, brook (Salvelinus fontinalis), rainbow (O. mykiss), and brown (Salmo trutta) trout. Brook, rainbow, and brown trout are the nonnative species most likely to presently occur within historical westslope cutthroat trout habitats. We chose to ignore the Yellowstone cutthroat trout subspecies for this analysis. Reaches where fish abundance was classed as "incidental" were placed in the absent rank because "incidental" indicated the reach did not likely support a reproducing population. Abundance in 59 reaches had been classed as "incidental" for westslope cutthroat trout. Abundance of brook trout was classed as "incidental" for one reach and no reaches were classed as "incidental" abundance for rainbow or brown trout.

Prior to 1995 the MRIS database did not explicitly indicate a species was absent. For reaches surveyed prior to 1995 we assumed that a species for which no information was available was absent if any other species within that reach had an abundance code assigned to it. We assumed that if any species had abundance information available, a reach had been surveyed and the lack of information for other species indicated they were not encountered. This assumption may have biased our analysis since any of the four species could have been present, but rare enough so as not to have been captured, thus they were not noted in the MRIS. In addition, there was no protocol for entering data for surveyed reaches where no fish were found into the MRIS prior to 1995. Since we did not know which reaches had been surveyed prior to 1995 where no fish were found, these reaches were not included in this analysis.

The MRIS database has information on the genetic status of many westslope cutthroat trout populations. These data were based on protein allozyme electrophoretic analyses conducted at the Salmon and Trout Genetics Laboratory at the University of Montana, or, for genetically untested populations, on the presence of potentially hybridizing species within the same reach. We completed a separate analysis on all those populations that included both the genetically tested $\geq$ 95% pure and those believed to be pure, based on the absence of potentially hybridizing species, but not genetically tested. The MRIS database contained 116 reaches where genetic testing had shown that some westslope cutthroat trout inhabiting that reach were less than 95% genetically pure. The populations inhabiting these 116 reaches were considered as "hybrids" and excluded from this analysis. The MRIS database has a rating for the quality of the data that ranges from 0 to 9 (Table 8). We arbitrarily selected a data quality rating of "5" or higher for all relative fish abundance assessments as a minimum rating that indicated data were more reliable and conducted a separate analysis for a subset of those reaches which had ratings of "5" and higher.

Mean valley slope, median valley slope, standard deviation of valley slope, valley aspect, upper elevation of reach, lower elevation of reach, and mean elevation for each reach were estimated from GIS layers. Environmental Systems Research Institute (ESRI) Arc/INFO vector layers of stream hydrography were used (derived from 1:100,000 scale U.S. Environmental Protection Agency data; File 3 data set). We combined the rasterized GIS stream hydrography layer with the Defense Mapping Agency's rasterized (60 m pixels) 1:250,000 scale Digital Elevation Models

(DEM) to create 60 m cells using the Arc/INFO GRID module. Combining these data resulted in a data set containing elevation values for each unique arc that identified each cell representing a stream arc segment. Each unique stream arc segment was referenced to the stream reach code corresponding to the original stream reach vector data. Stream reaches often contained numerous stream arc segment cells. Elevations were summarized by stream reach across all stream arc segments (60 m pixels) that made up each stream reach using Arc/INFO's STATISTICS command to calculate the variables mean, minimum, and maximum elevation for each reach.

Valley slope (expressed as a percentage) and valley aspect (expressed as degrees) were derived using the elevation data for each stream arc segment and summarized over each reach to estimate mean valley slope, standard deviation of valley slope, and mean aspect using the STATISTICS command in Arc/INFO. Valley slope was defined as the maximum rate of change in elevation (rise over run) from each cell to its neighbors, expressed as percent slope (ie. 45° slope = 100% slope). Median valley slope was calculated for each reach with a dBase macro. Aspect was defined as the down-slope direction (the maximum rate of change in elevation along the stream channel) from each cell to its neighbors, expressed in positive degrees from 0 to 360, measured clockwise from the north. Latitude and longitude in decimal degrees of the lower boundary of each reach were also included. These data were imported into dBase files for analyses. Aspect data in degrees was converted to north-south (sine transformation) and east-west (arcsine transformation) axes standardized with ranges from -1 to 1. All these data were merged into a single data dBase file that also contained the MRIS fish abundance and genetic status data using unique reach numbers as identifiers. Reaches comprised of a single raster cell were excluded from further analyses.

Keleher and Rahel (1996) found that mean July air temperature (°C) was strongly related (R^2 = 0.90; $P<0.0001$) to latitude (in decimal degrees) and elevation (m) for the Rocky Mountain region. Since mean annual air temperature relates directly to mean water temperature, we used their model to predict mean July air temperatures (which should indicate summer water temperatures) using the formula:

$$\text{KRTemp} = -11.468 + 2.812*(\text{Lat}) - 0.0007*(\text{Elev}) - 0.043*(\text{Lat})^2;$$

where "KRTemp" is mean July air temperature (°C), "Lat" is the latitude at the lower boundary of the reach expressed in decimal degrees, and "Elev" is mean elevation of the reach in meters.

We tested the assumption that mean July air temperatures predicted by this model correlated to mean July air temperatures at 65 climate sites in Montana and mean July water temperatures in 33 streams in Montana and found fairly good correlations (see previous chapter).

Data Analyses

Frequency histograms were plotted for all data to view the distribution and range of data. Means and medians were calculated for estimates of physical variables by the three westslope cutthroat trout abundance classes and Kruskal-Wallis tests were run to determine if there were significant differences in these physical variables between abundance classes. Correlations between physical parameters and all fish abundance indices, by species, were investigated using Spearman rank correlation. Principal component analyses (PCA) using varimax rotation were conducted on the physical habitat and KRTemp variables to derive habitat factors. We used varimax rotation to allow for easier interpretation of the derived factors. We ran PCA for all 1,826 reaches, but excluded latitude, longitude, and KRTemp variables because values for these variables were missing for 348 reaches. We also ran PCA for only those 1,478 reaches where latitude, longitude, and KRTemp values were available. Since KRTemp was predicted using elevation and latitude, we were concerned that inclusion of this variable might force the PCA to create a factor that heavily weighted latitude, elevation, and predicted July air temperature. We removed the variable KRTemp from the variable set for the 1,478 reaches to assess the impact this variable had on derived PCA factors.

Discriminant analysis, logistic regression, and classification tree analyses were conducted to explore how physical habitat and ranked abundance of nonnative fish species related to ranked abundance of westslope cutthroat trout. Since latitude, longitude and KRTemp estimates were missing for 348 reaches, we removed these 348 reaches and analyzed the remaining 1,478 reach data set. We separated the 1,478 reach data set into a training subset that contained a randomly selected 75% of the data (1,113 reaches) and a test subset that contained the remaining 25% (356) of the reaches using SYSTAT's (version 7.0.1) uniform random number generator (SYSTAT 1997). The training data subset was used to develop predictive models through discriminant, logistic regression, and classification tree analyses. These predictive models were then applied to the test data subset to observe how well the model fit the remaining data.

Discriminant analyses were done using estimates of habitat variables. We used discriminant analyses to discover which, if any, habitat variables could be used to discriminate between the three ranked abundance levels of westslope cutthroat trout abundance (absent = 0; rare = 1; or abundant = 2). Discriminant analyses used numerous subsets of the data:

1) the full 1,826 reach data set;
2) the 1,478 reach data set that excluded those reaches where no latitude or longitude data were available;
3) a "high quality data" subset of the data containing only those reaches having data quality ratings of "5" and higher for fish abundance estimates;
4) a "non-hybrid" subset of the data containing only those reaches that supported westslope cutthroat trout that either tested as at least 95% genetically pure by electrophoretic techniques, or were classified as "pure" based on the presence of potentially hybridizing species within the reach; and

5) a "genetically pure" subset of the data containing only those reaches that supported westslope cutthroat trout where electrophoretic tests indicated those populations were at least 95% genetically pure.

Forward and backward stepwise discriminant analyses were first done using only habitat variables on the training subset. Next, we added relative abundance estimates for nonnative brook, rainbow, and brown trout to the habitat variables and repeated the forward and backward stepwise discriminant analyses on the training data subset. We then tested classification success for the relative abundance of westslope cutthroat trout using the habitat and nonnative fish abundance variables retained in this discriminant analyses on the test data subset. We also evaluated "jackknifed" classification matrices to understand the effect of sampling on classification results on all stepwise discriminant analyses. We used SYSTAT (version 7.0.1; 1997) with the tolerance set to 0.001 and probabilities to enter or remove variables set at 0.15 to conduct all discriminant analyses.

Logistic regression analyses were conducted using presence (1) or absence (0) of westslope cutthroat trout versus physical habitat variables and an effects variable to indicate if any of the three nonnative species (brook, rainbow, or brown trout) were present (1) or not present (0) within the reach. Logistic regression analyses were conducted using only the data set containing the 1,478 reaches for which all habitat data were available. We followed Hosmer and Lemshow's (1989) suggestion of conducting univariate logistic regression models and selecting those variables that showed some association to the dependent variable as covariates in multiple logistic regressions. We used forward and backward stepwise logistic regression within the program SYSTAT (version 7.0.1; 1997) to determine which main effects were retained on the training data subset. After determining which main effects were retained we again used forward and backward stepwise logistic regression model building within SYSTAT with those retained main effects and all possible two-way interactions on the training data subset to obtain a final model. We used McFadden's Rho-squared and Hosmer-Lemeshow statistics (Hosmer and Lemeshow 1989) to evaluate how well the final model performed.

This final model was then applied to the test data subset after selecting a "cut-point" for assigning probabilities to indicate whether westslope cutthroat trout were present or absent. This "cut-point" was set by equalizing error rates for model predicted probabilities. We compared logistic regression model predictions of presence/absence on the test data subset with actual presence/absence data to determine rate of successful classification.

We also ran forward and backward stepwise logistic regressions using the five PCA factors and presence/absence of nonnative salmonids on the 1,478 reach data set. After determining which main effects were retained we again used forward and backward stepwise logistic regression model building within SYSTAT with those retained main effects and all possible two-way interactions. Probabilities to enter or remove variables were set at 0.15 and 0.20, respectively.

A classification tree analysis employing the "Phi coefficient" loss function fitting methodology was used to classify the reaches that contained no, low, and abundant populations of westslope cutthroat trout (Kass 1980). We included all habitat variables and relative abundance of the three nonnative species as potential independent variables. We initially classed the training data subset and then cross-validated the classification tree developed from the training data subset on the test data subset. SYSTAT (version 7.0.1; 1997) was used with both the minimum proportion reduction in error allowed at any split, and split value allowed at any node, set to 0.01 and the minimum number of reaches retained at a terminal node set at 10.

Results

Relative Fish Abundance and Genetic Status

A total of 2,884 reaches existed in the MRIS database for the upper Missouri. Of these 2,884 reaches, 1,826 reaches (63%) were used in the final analysis after excluding reaches that covered lakes or reservoirs (62 reaches); or for which fish abundance information was not available (937 reaches) or no or poor (single cell) DEM coverage was found for the entire reach (59 reaches). A total of 837 of these 1,826 reaches supported westslope cutthroat trout with 357 reaches supporting relatively abundant populations (rated as common or abundant). The remaining 480 reaches supported relatively low populations (rated as rare or uncommon).

Only 184 reaches contained populations of westslope cutthroat trout that had been electrophoretically tested as at least 95% genetically pure. Another 537 reaches contained untested populations that were designated as westslope cutthroat trout based on the absence of potentially hybridizing species, while 116 reaches contained suspected hybridized or tested introgressed populations less than 95% pure.

Habitat Information

Latitude and longitude data were missing for 348 of the 1,826 reaches used in the final analyses. Of the 1,478 reaches that had latitude and longitude information, 680 supported westslope cutthroat trout with 280 supporting common or abundant populations. Frequency histograms of the raw data showed that the distributions of latitude, longitude, and mean elevation data for the sample reaches exhibited some central tendency (Figure 14). Distributions of data for valley slope and standard deviations of mean valley slope were highly skewed to the left, distribution of latitude data was slightly skewed to the left, and the distributions of KRTemp and elevation data was skewed to the right (Figure 15). Sine and arcsine transformations of degree data resulted in distributions where the majority of observations fell near 1.0 and - 1.0 (Figure 15), however, we found that using these transformations on 10,000 uniform random numbers between 0 and 360 resulted in similar distributions. No clear differences in distributions between reaches that did and did not contain westslope cutthroat trout were obvious from these plots, however, it appeared that disproportionately more reaches with low gradient and lower standard deviation of gradient contained westslope cutthroat trout (Figure 14).

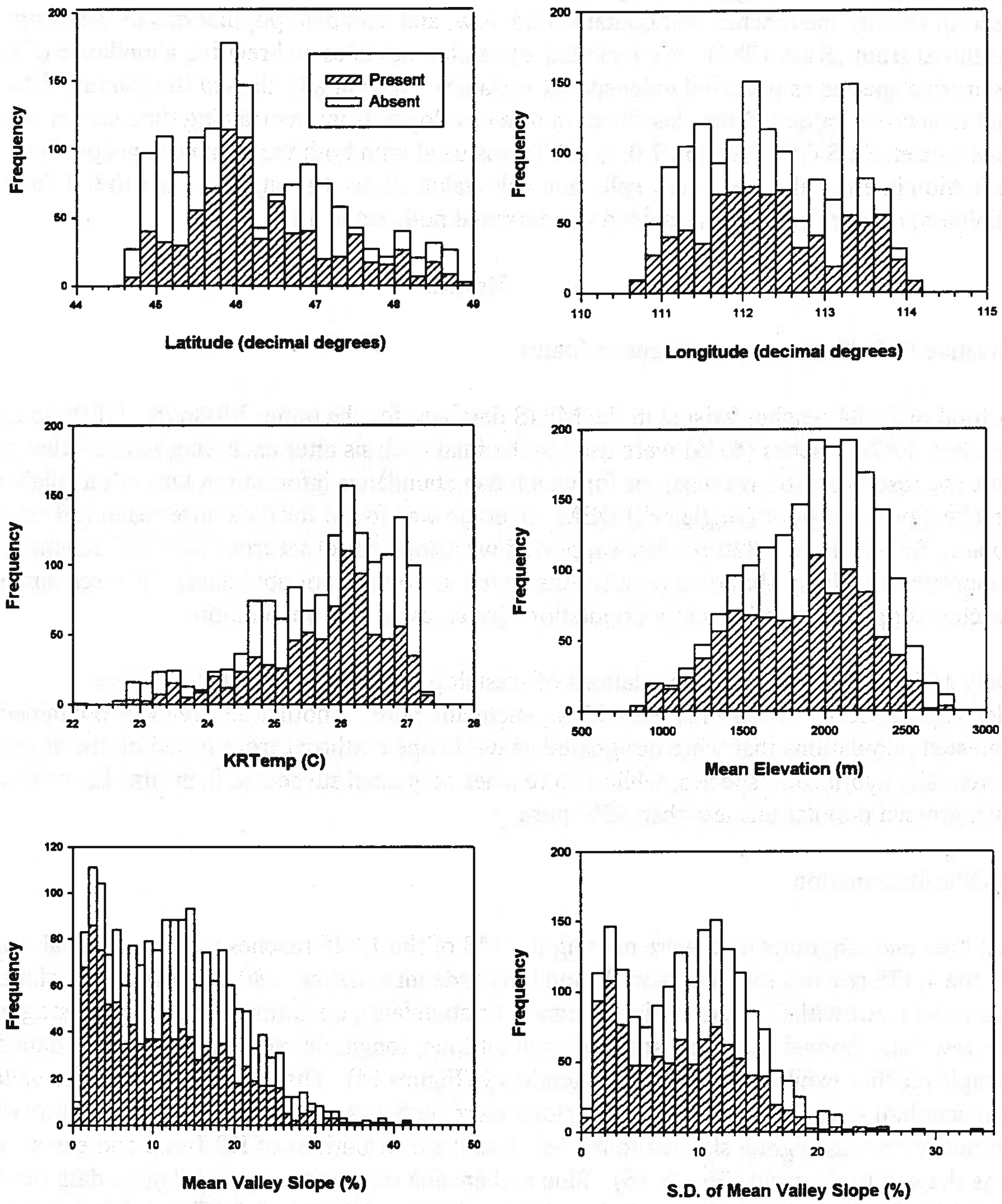

Figure 14. Stacked histograms showing the number of reaches by latitude, longitude, KRTemp, mean elevation, mean valley slope, and S.D. of valley slope where westslope cutthroat trout were present (cross-hatched) and absent (open).

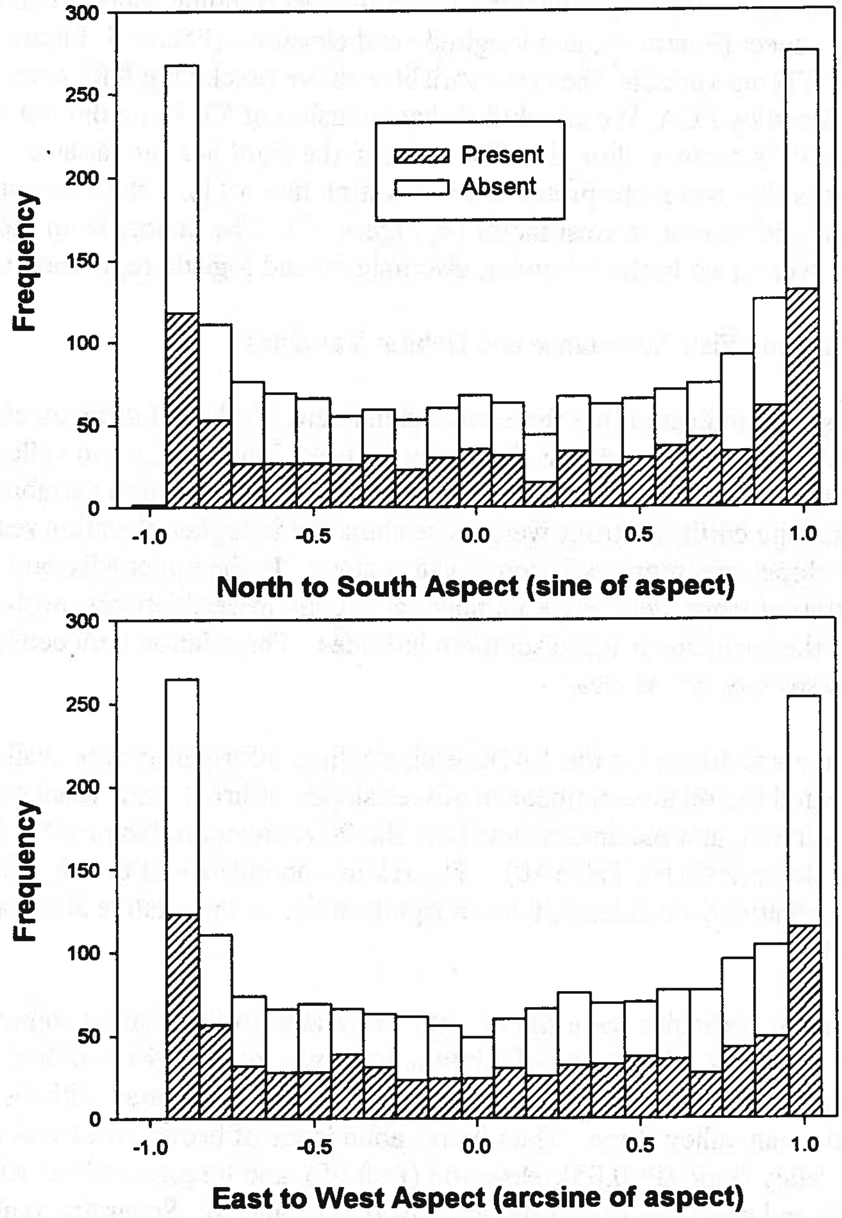

Figure 15. Stacked histograms showing the number of reaches by east to west aspect (arcsine transformation of degrees) and north to south aspect (sine transformation of degrees) where westslope cutthroat trout were present (crosshatched) and absent (open).

For the 1,478 reaches where information was available for all variables, varimax rotated PCA reduced the 11 habitat variables to five factors. These factors described elevation, latitude, and KRTemp (Factor 1); valley slope (Factor 2), east to west trending aspect (Factor 3), north to south trending aspect (Factor 4), and longitude and elevation (Factor 5; Figure 16). When we removed the KRTemp variable, the same variables above (excluding KRTemp) were included in the factors retained by PCA. We concluded that inclusion of KRTemp did not unduly influence the selection of PCA factors. For all 1,826 reaches, the eight habitat variables were reduced to four PCA factors that were interpreted as an elevation factor (1), a slope factor (2), and a north to south factor (3) and an east to west factor (4; Figure 17). The factors from the above varimax rotated PCA's were used in the following discriminant and logistic regression analyses.

Relationships among Fish Abundance and Habitat Variables

Kruskal-Wallis tests indicated that there were significant ($P<0.001$) differences between the three westslope cutthroat trout abundance classes for latitude, longitude, mean valley slope, median valley slope, standard deviation of valley slope, and the three elevation variables (Table 9). It was clear that westslope cutthroat trout were more abundant in higher elevation reaches that had steeper valley slopes and more variation in valley slope. In the upper Missouri River basin, westslope cutthroat trout were more abundant at slightly lower latitudes, probably because the headwaters of the basin are at more southern latitudes. The relation between longitude and abundance classes was not as clear.

Spearman rank correlations for the 1,478 reaches where information was available for all habitat variables indicated the relative abundance of westslope cutthroat trout was positively correlated with mean, minimum, and maximum elevation, the PCA elevation factor ($P<0.05$), and mean and S.D. of valley slope ($P<0.10$; Table 10). The relative abundance of brook, rainbow, and brown trout were all negatively correlated, but not significantly, to the relative abundance of westslope cutthroat trout.

None of the habitat variables were significantly correlated to the relative abundance of brook trout (Table 10). The relative abundance of rainbow trout was positively ($P<0.001$) correlated with the relative abundance of brown trout, and negatively ($P<0.05$) correlated with elevation variables, longitude, and mean valley slope. The relative abundance of brown trout was negatively correlated to valley slope ($P<0.05$), elevation ($P<0.05$), and longitude ($P<0.10$) variables and slope ($P<0.05$) and elevation ($P<0.001$) PCA factors (2 and 5). Spearman rank correlations for those variables estimated for all 1,826 reaches and the relative abundance of each trout species were similar to correlations for the 1,478 reaches that included all variables.

Stepwise discriminant analysis to classify the relative abundance of westslope cutthroat trout (absent = 0; rare = 1; abundant = 2) using habitat variables on the random 75% training subset of the 1,478 reaches resulted in an overall correct classification rate of 55% (Table 11). The jackknifed overall correct classification rate was the same. Retained variables were latitude, longitude, standard deviation of slope, minimum elevation, mean elevation, and KRTemp.

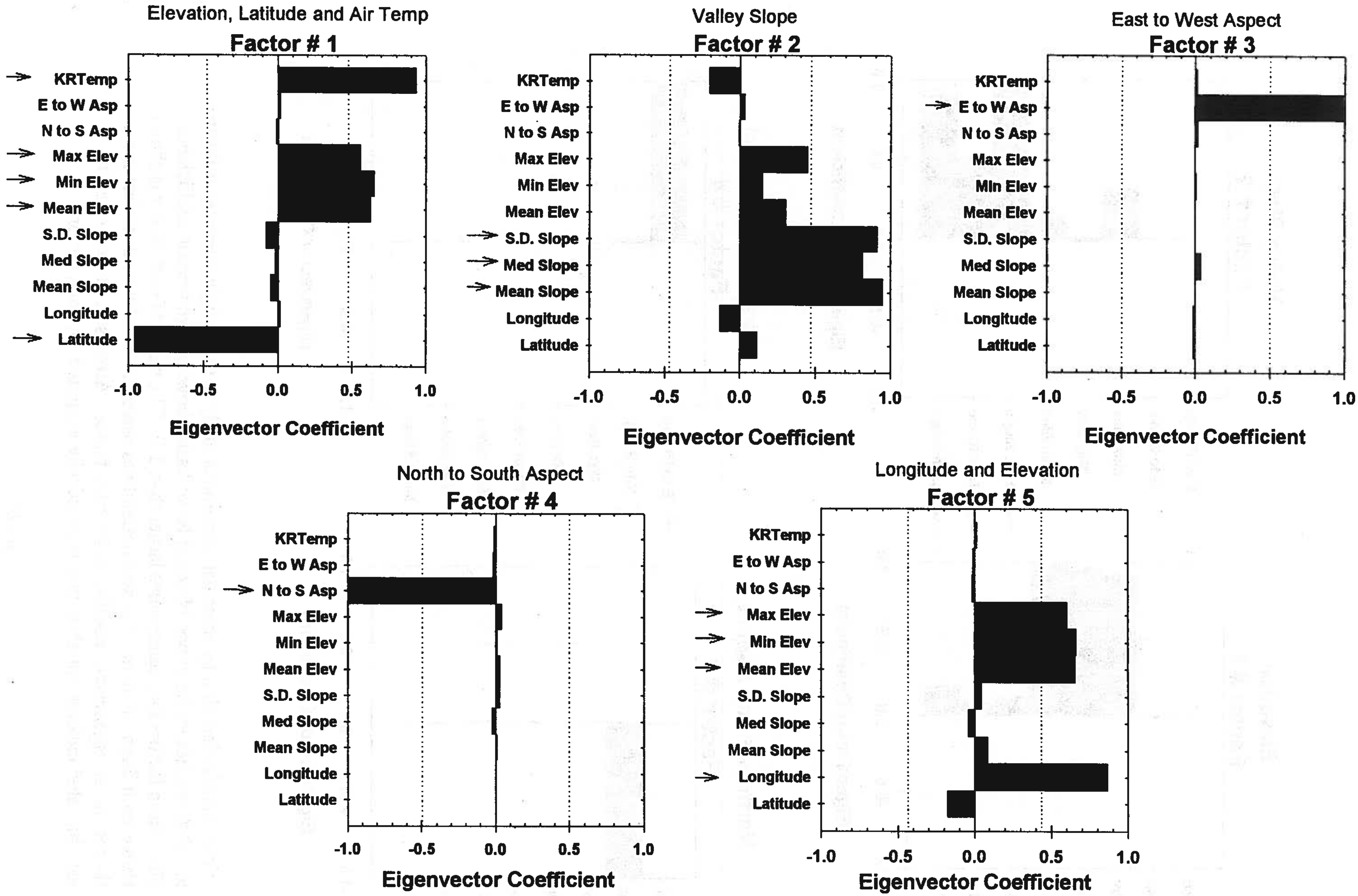

Figure 16. Five factors identified by principal component analysis using 12 variables estimated in 1,478 reaches in the upper Missouri River basin showing eigenvector coefficients. Only these factors had eigenvalues larger than 1.0. The name of each factor is shown above each factor number. Vertical dotted lines represent absolute values that are half the maximum eigenvector coefficient for each factor. Arrows to the left of each variable label indicate variables that were heavily weighted for each factor.

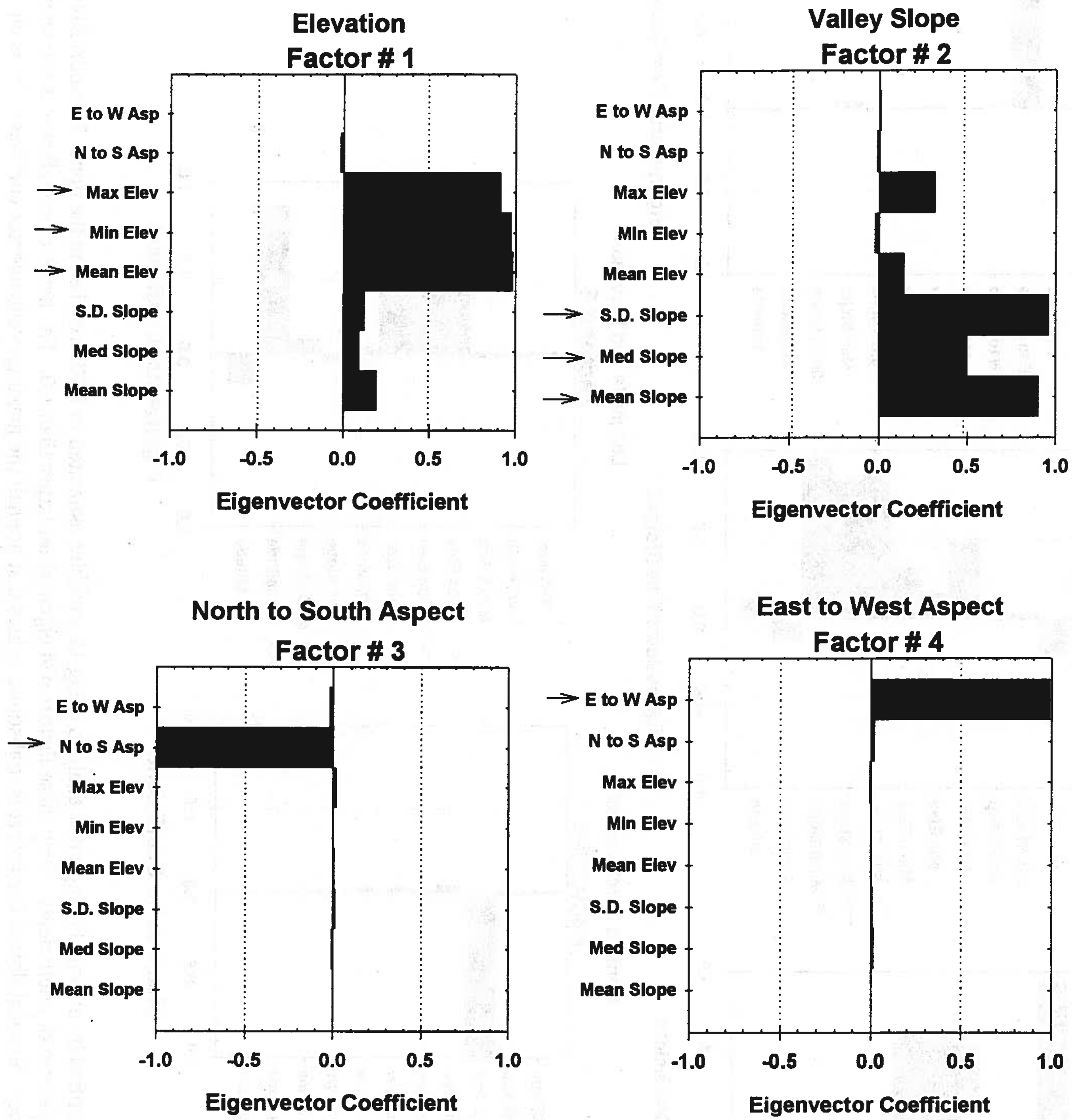

Figure 17. Four factors identified by principal component analysis using eight variables estimated in 1,826 reaches in the upper Missouri River basin showing eigenvector coefficients. Only these factors had eigenvalues larger than 1.0. The name of each factor is shown above each factor number. Vertical dotted lines represent absolute values that are half the maximum eigenvector coefficient for each factor. Arrows to the left of each variable label indicate variables that were heavily weighted for each factor.

Table 9. Means and medians by abundance class of westslope cutthroat trout (WCT) for parameters estimated from GIS layers in the upper Missouri River basin. Kruskal-Wallis test results between abundance classes are shown (* indicates P<0.001).

	Mean by WCT Abundance Class			Median by WCT Abundance Class			Kruskal-Wallis Test
Parameters	Absent	Rare	Abundant	Absent	Rare	Abundant	
Latitude	46.11	46.04	45.91	45.87	45.76	45.61	20.71*
Longitude	112.16	111.97	112.23	112.09	111.91	112.15	20.03*
Mean Elevation	1738	1893	1985	1800	1910	2016	115.87*
Minimum Elevation	1649	1779	1852	1707	1786	1889	94.12*
Maximum Elevation	1853	2036	2153	1867	2009	2158	123.35*
Mean Slope	10.2	12.9	13.3	9.1	12.5	12.7	77.84*
Median Slope	9.7	12.6	13.1	7.0	10.5	10.5	55.17*
S.D. Slope	7.3	9.4	9.25	7.1	9.3	9.51	76.23*
KRTemp	25.6	25.5	25.6	25.8	25.7	25.9	4.54
N to S Aspect	0.002	0.060	0.025	0.022	0.115	0.026	1.80
E to W Aspect	0.019	-0.008	0.007	0.081	0.012	0.052	0.44

Table 10. Spearman rank correlations for habitat variables and PCA factors versus abundance rankings for westslope cutthroat (WCT Score), brook (EBT Score), rainbow (RB Score), and brown (BT Score) trout in 1,478 reaches of the upper Missouri River basin. Significance levels are shown by *** = P<0.001; ** = P<0.05; and * = P<0.10.

	WCT Score	EBT Score	RB Score	BT Score
WCT Score	1.0000			
EBT Score	-0.1771	1.0000		
RB Score	-0.1512	-0.0189	1.0000	
BT Score	-0.1890	-0.1267	0.5584 ***	1.0000
Latitude	-0.1138	0.0894	0.1047	-0.0467
Longitude	-0.0215	0.2110	-0.2744 **	-0.2512 *
Mean elev	0.3143 **	0.0707	-0.4125 **	-0.4530 ***
Min elev	0.2822 **	0.0878	-0.3414 **	-0.3761 **
Max elev	0.3260 **	0.0601	-0.4539 ***	-0.5001 ***
Mean slope	0.2568 *	0.0150	-0.2476 *	-0.3720 **
Med slope	0.2094	0.0058	-0.1613	-0.2662 *
S.D. slope	0.2351 *	0.0123	-0.2054	-0.3319 **
July temp	0.0385	-0.1231	0.0034	0.1968
N to S asp	0.0035	0.0105	-0.0130	0.0252
E to W asp	0.0023	-0.0325	0.0140	0.0319
FACTOR(1)	0.1466	-0.1362	-0.0732	0.0622
FACTOR(2)	0.2850 **	-0.0124	-0.2194	-0.3529 **
FACTOR(3)	-0.0154	-0.0263	0.0225	0.0403
FACTOR(4)	-0.0055	-0.0177	0.0222	-0.0182
FACTOR(5)	0.1496	0.2268	-0.4058 **	-0.4889 ***

Table 11. Discriminant analysis results for classifying abundance classes of westslope cutthroat trout in the upper Missouri River basin using habitat variables for a random 75% of 1,478 reaches showing classification coefficients of retained variables by abundance class of westslope cutthroat trout and the number and proportion of correct classifications by abundance class and jackknifed classification matrix.

Variable	Classification coefficients By WCT abundance class 0	1	2	Class	Classification Matrix 0	1	2	Total (%)
Constant	-1612447	-1611901	-1611306	0	397	105	108	610 (65)
Latitude	46415.1	46408.5	46399.5	1	73	122	110	305 (40)
Longitude	342.4	341.6	341.8	2	44	56	98	198 (49)
Mean elev	-	-	-	Total	514	283	316	1113 (55)
Min elev	16.51	16.51	16.50					
Max elev	11.85	11.85	11.85					
Mean slope	-	-	-					
Med slope	-	-	-	Jackknifed Matrix				
S.D. slope	-89.81	-89.71	-89.73	0	394	107	109	610 (65)
KRTemp	39105	39099	39091	1	73	119	113	305 (39)
N to S asp	-	-	-	2	44	57	97	198 (49)
E to W asp	-	-	-	Total	511	283	319	1113 (55)

When the ranked abundance for the three exotic species were added to habitat variables the final discriminating functions contained the variables latitude, longitude, standard deviation of slope, KRTemp and the relative abundance of brook and rainbow trout (Table 12). The overall correct classification rate was 60%. These discriminating functions correctly classified 68% of the reaches where westslope cutthroat trout were absent, 47% of the rare abundance reaches, and 57% of the abundant reaches. The overall jackknifed correct classification rate was 59%. It was interesting to note that minimum and mean elevation variables were dropped from the habitat model and replaced by variables indicating abundance of rainbow and brook trout. Using these discriminating functions to classify abundance classes of westslope cutthroat trout on the test data subset resulted in an overall correct classification of 63% (Table 12).

For all 1,826 reaches a stepwise discriminant analysis yielded a model containing the variables standard deviation of slope, mean elevation, and maximum elevation. The overall correct classification success of this model was only 47% and the jackknifed classification rate was the same. When relative abundance scores for the three nonnative species were added to the physical habitat variables a stepwise discriminant analysis resulted in a model containing the variables standard deviation of slope, mean elevation, relative abundance of brook trout, and relative abundance of rainbow trout. The overall correct classification rate was 53% with the jackknifed correct classification rate being the same.

When we eliminated all reaches that did not have a "data quality rating" of at least "5" (see Methods and Table 8) from the 1,478 reaches data set, 748 reaches were retained. We called this the "high quality data" subset. Forward and backward stepwise discriminant analyses using the "high quality data" retained all seven variables (latitude, longitude, and standard deviation of valley slope, KRTemp, and abundance of brook and rainbow trout) that had been retained in the original discriminant analysis, as well as minimum elevation. The overall rate of correct classification increased to 64% with a jackknifed overall correct classification rate of 63% (Table 13).

A "non-hybrid" westslope cutthroat trout data set was created by eliminating all reaches from the original 1,478 reaches that contained westslope cutthroat trout that tested as less than 95% genetically pure. This resulted in a data set containing 1,386 reaches. Forward and backward stepwise discriminant analyses using this "non-hybrid" data subset retained the variables latitude, longitude, standard deviation of slope, maximum elevation, KRTemp, and abundance of brook and rainbow trout (Table 14). The overall rate of correct classification was 61% with a jackknifed overall correct classification rate of 60%. When reaches that contained westslope cutthroat trout that had not been electrophoretically tested as at least 95% pure were eliminated, 924 reaches were retained in a data subset called "genetically pure". Stepwise discrimination resulted in discriminating functions that contained the variables mean and minimum elevation, KRTemp, and abundance of brook and rainbow trout. The difference between these functions and

Table 12. Discriminant analysis results for classifying abundance classes of westslope cutthroat trout in the upper Missouri River basin using habitat variables and relative abundances of nonnative fish species (brook trout = EBT; rainbow trout = RBT; and brown trout = BT) for a random 75% of 1,478 reaches showing classification coefficients of retained variables by abundance class of westslope cutthroat trout and the number and proportion of correct classifications by abundance class and jackknifed classfication matrix. Classification matrix for a random 25% test data set using the final model is also shown.

	Classification coefficients by WCT abundance class				Classification Matrix			Total
Variable	0	1	2	Class	0	1	2	(%)
Constant	-142931	-142501	-142478	0	412	101	97	610 (68)
Latitude	3332.6	3327.5	3326.8	1	76	144	85	305 (47)
Longitude	456.13	455.44	455.65	2	34	52	112	198 (57)
Mean elev	-	-	-	Total	522	297	294	1113 (60)
Min elev	-	-	-	Jackknifed Matrix				
Max elev	-	-	-	0	408	103	99	610 (67)
Mean slope	-	-	-	1	79	141	85	305 (46)
Med. slope	-	-	-	2	34	55	109	198 (55)
S.D. slope	32.17	32.23	32.22	Total	521	299	293	1113 (59)
KRTemp	3168.2	3163.5	3162.9					
N to S asp	-	-	-	Test Case Classification Matrix				
E to W asp	-	-	-	0	138	29	21	188 (73)
EBT abun	0.582	0.442	-0.161	1	25	44	26	95 (46)
RB abun	-180.65	-180.20	-180.83	2	18	16	48	82 (59)
LL abun	-	-	-	Total	181	89	95	365 (63)

Table 13. Discriminant analysis results for "High Quality Data" subset of the upper Missouri River basin data set showing classification coefficients of retained variables by abundance class of westslope cutthroat trout and the number and proportion of correct classifications by abundance class and jackknifed classification matrix.

Variable	Classification coefficients by WCT abundance class 0	1	2	Class	Classification Matrix 0	1	2	Total (%)
"High Quality" Data Set								
Constant	-821013	-820692	-820251	0	310	62	47	419 (74)
Latitude	23313.7	23310.9	23303.9	1	64	106	58	228 (46)
Longitude	360.16	359.01	359.40	2	23	17	61	101 (60)
Mean elev	-	-	-	Total	397	185	166	748 (64)
Min elev	13.885	13.887	13.883					
Max elev	-	-	-					
Mean slope	-	-	-	Jackknifed Matrix				
Med slope	-	-	-	0	309	62	48	419 (74)
S.D. slope	89.733	89.821	89.792	1	66	101	61	228 (44)
KRTemp	19742.7	19740.0	19734.0	2	23	20	58	101 (57)
N to S asp	-	-	-	Total	398	183	167	748 (63)
E to W asp	-	-	-					
EBT abun	-475.39	-475.98	-476.63					
RBT abun	-392.68	-392.10	-392.61					
BT abun	-	-	-					

Table 14. Discriminant analysis results for "Non-hybrid", "Genetically Pure", and "Genetically Pure and High Quality Data" westslope cutthroat trout subsets of the upper Missouri River basin data set showing classification coefficients of retained variables by abundance class of westslope cutthroat trout and the number and proportion of correct classifications by abundance class and jackknifed classification matrix.

	Classification coefficients by WCT abundance class				Classification Matrix			Total
Variable	0	1	2	Class	0	1	2	(%)
"Non-hybridized" Data Set								
Constant	-605168	-604516	-604467	0	537	135	126	798 (67)
Latitude	16534.4	16526.2	16525.0	1	95	179	86	360 (50)
Longitude	636.85	636.13	636.46	2	46	57	125	228 (55)
Mean elev	-	-	-	Total	678	371	337	1386 (61)
Min elev	-	-	-					
Max elev	7.695	7.693	7.693	Jackknifed Matrix				
Mean slope	-	-	-	0	534	138	126	798 (67)
Med slope	-	-	-	1	97	176	87	360 (49)
S.D. slope	-102.79	-102.71	-102.74	2	47	59	122	228 (54)
KRTemp	14228.4	14221.0	14219.8	Total	678	373	335	1386 (60)
N to S asp	-	-	-					
E to W asp	-	-	-					
EBT abun	-198.34	-198.44	-199.15					
RBT abun	56.584	57.094	56.334					
BT abun	-	-	-					

Table 14. (Continued).

Variable	Classification coefficients by WCT abundance class: 0	1	2	Class	Classification Matrix: 0	1	2	Total (%)
"Genetically Pure" Data Set								
Constant	-480.57	-475.29	-448.92	0	581	144	73	798 (67)
Latitude	-	-	-	1	12	30	15	57 (53)
Longitude	-	-	-	2	3	20	46	69 (67)
Mean elev	0.0147	0.0234	0.0219	Total	596	194	134	924 (71)
Min elev	-0.0791	-0.0859	-0.0807					
Max elev	-	-	-	Jackknifed Matrix				
Mean slope	-	-	-	0	577	144	77	798 (72)
Med slope	-	-	-	1	13	29	15	57 (51)
S.D. slope	-	-	-	2	3	20	46	69 (67)
KRTemp	41.158	40.816	39.570	Total	593	193	138	924 (71)
N to S asp	-	-	-					
E to W asp	-	-	-					
EBT abun	11.229	11.032	9.358					
RBT abun	-5.739	-6.319	-6.213					
BT abun	-	-	-					

Table 14. (Continued).

Variable	Classification coefficients by WCT abundance class 0	1	2	Class	Classification Matrix 0	1	2	Total (%)
"Genetically Pure and High Quality Data" Set								
Constant	-3329.2	-3359.9	-3423.9	0	343	60	16	419 (82)
Latitude	135.1	135.7	136.9	1	9	7	6	22 (32)
Longitude	-	-	-	2	0	4	16	20 (80)
Mean elev	-0.459	-0.416	-0.392	Total	352	71	38	461 (79)
Min elev	0.579	0.550	0.541					
Max elev	0.181	0.170	0.161	Jackknifed Matrix				
Mean slope	-	-	-	0	341	60	18	419 (81)
Med slope	-	-	-	1	9	6	7	22 (27)
S.D. slope	-	-	-	2	0	4	16	20 (80)
KRTemp	-	-	-	Total	350	70	41	461(79)
N to S asp	-	-	-					
E to W asp	-	-	-					
EBT abun	-43.108	-43.653	-47.434					
RBT abun	-	-	-					
BT abun	-	-	-					

the original discriminating functions derived from the original training data subset was that the two elevation variables were replaced by the variables latitude, longitude, and standard deviation of slope. The rate of correct classification increased to 71% with the same jackknifed overall correct classification rate (Table 14).

When "genetically pure and high quality data" criteria were applied to the 1,478-reach data set a total of 461 reaches were retained, however, only 44 of these reaches supported westslope cutthroat trout. Forward stepwise discriminate analysis resulted in discriminate functions that retained the variables latitude, maximum elevation, and abundance of brook trout. The overall correct classification rate was 74% with 41% of the rare and 80% of the abundant reaches correctly classified. Backward stepwise discriminate analysis resulted in discriminate functions that retained the above variables along with mean and minimum elevation variables. The overall correct classification rate was 79% with only 32% of rare abundance reaches correctly classified.

Univariate logistic regression analyses indicated that the presence of nonnative salmonids and slope and elevation features were all significantly associated with the presence of westslope cutthroat trout (Table 15). Latitude and longitude had some association with the presence of westslope cutthroat trout, while predicted July temperature and both north to south and east to west aspects had little association. Stepwise logistic regression was run on the training data subset using all variables except KRTemp and both north to south and east to west aspects. The best main effects model used the variables latitude, longitude, mean and maximum elevation, standard deviation of slope, mean slope, and presence of nonnative species (Table 16). Stepwise logistic regression was again run on this training data subset using these main effects and all possible interactions. This stepwise logistic regression procedure resulted in a final model that contained the main effects of mean elevation and standard deviation of slope. This model also included interactions of mean elevation and longitude, latitude and presence of nonnative salmonids, latitude and standard deviation of slope, maximum elevation and mean slope, longitude and standard deviation of slope, mean elevation and standard deviation of slope, mean elevation and presence of nonnative salmonids, and maximum elevation and presence of nonnative salmonids (Table 16). McFadden's Rho-squared equaled 0.191 and the Hosmer-Lemeshow statistic was 19.37 ($P = 0.013$), indicating that the fit of this model was not very good. The probability "cut-point" that resulted in equal error rates of about 29% (correct classification of 71%) occurred at a probability of 0.532. Cross-validation on the test data subset using this final model (Table 16) correctly classified 145 of 188 (77%) reaches that did not have westslope cutthroat trout and 114 of 177 (64%) of the reaches that did contain westslope cutthroat trout.

Using the varimax rotated PCA factors along with the effect of presence or absence of nonnative salmonids yielded a main effects logistic regression model that retained three factors (Factors 1, 2, and 5) and the nonnative salmonids effect (Table 17). When all possible interactions were included, the final model contained the main effects of Factor 2, Factor 5, and presence of

Table 15. Estimated coefficients, standard errors, and ratio of coefficient to standard error for the multivariate logistic regression model containing main effects identified as associated with the presence or absence of westslope cutthroat trout in 1,478 reaches in the upper Missouri River basin from univariate logistic regression analyses. Effects of substituting minimum and maximum elevation for mean elevation and mean and median slope for SD slope on the likelihood ratio test statistic (G) and associated probability of these substitutions significantly improving the model (P).

Variable	Estimated coefficient	Estimated S.E.	Coefficient/ S.E.
Constant	-38.861	9.062	-4.288
Exotic Species	0.802	0.174	4.610
Minimum Elevation	-0.003	0.000	-11.032
S.D. of Slope	-0.037	0.013	-2.903
Latitude	-0.420	0.084	-5.019
Longitude	0.562	0.078	7.233
Log Likelihood = -862.07			
Substituting	Log Likelihood	G	P
Max Elevation for Min Elevation	-895.83	-67.52	-
Mean Elevation for Min Elevation	-869.05	-13.96	-
Mean Slope for SD Slope	-872.61	-21.08	-
Median Slope for SD Slope	-871.98	-19.82	-

Table 16. Multiple step-wise logistic regression results for determining the presence of westslope cutthroat trout using habitat variables and the presence of nonnative salmonids entered as an effect on a randomly selected 75% of 1,478 reaches in the upper Missouri River basin. Results are shown for both a "Main Effects Only" model and a "Main Effects and Interactions" model.

Model Parameter	Estimate	S.E.	t-ratio	Odds ratio
"Main Effects Only"				
Constant	-46.2896	10.6216	-4.3581	
Latitude	-0.4159	0.0991	-4.1955	0.6597
Longitude	0.6356	0.9141	6.9535	1.8882
Mean elevation	-0.0048	0.0007	-6.6714	0.9952
Max elevation	0.0016	0.0006	2.8284	1.0016
Mean slope	0.06183	0.0209	2.9575	1.0638
S.D. of slope	-0.1468	0.0313	-4.6950	0.8635
Nonnative_0	-0.4041	0.0995	-4.0613	0.6676
Log-likelihood: -648.589	McFadden's Rho-squared: 0.1536			
"Main Effects and Interactions"				
Constant	7.0867	0.9248	7.6628	
Mean elevation	-0.0912	0.0118	-7.7000	0.9128
S.D. of slope	13.0032	2.3258	5.5908	443856
Mean elev*Longitude	0.0008	0.0001	7.5039	1.0008
Mean elev*S.D. of slope	0.0001	0.00005	2.1640	1.0001
Mean elev*Nonnative_0	0.0024	0.0006	3.6889	1.0024
S.D. slope*Latitude	-0.0478	0.0110	3.4305	0.9533
S.D. slope*Longitude	-0.0996	0.0207	-4.8042	0.9051
Latitude*Nonnative_0	-0.0343	0.0115	-2.9942	0.9663
Max elev*Nonnative_0	-0.0017	0.0005	-3.0832	0.9983
Log-likelihood: -619.941	McFadden's Rho-squared: 0.191017			

Table 17. Multiple step-wise logistic regression results for determining the presence of westslope cutthroat trout using habitat factors generated from PCA and the presence of nonnative salmonids entered as an effect on 1,478 reaches in the upper Missouri River basin. Results are shown for both a "Main Effects Only" model and a "Main Effects and Interactions" model.

Model Parameter	Estimate	S.E.	t-ratio	Odds ratio
"Main Effects Only"				
Constant	-0.1665	0.0848	-1.9700	
Factor(1)	-0.2403	0.0574	-4.1862	0.7864
Factor(2)	-0.5568	0.0589	-9.4495	0.5730
Factor(5)	-0.2211	0.0566	-3.9045	0.8016
Nonnative_0	-0.4775	0.0848	-5.6274	0.6203
Log-likelihood: -919.624	McFadden's Rho-squared: 0.09819			
"Main Effects and Interactions"				
Constant	-0.2622	0.0909	-2.8843	
Factor(2)	-0.5698	0.0612	-9.3148	0.5656
Factor(5)	-0.4732	0.1189	-3.8189	0.6230
Nonnative_0	-0.6027	0.0927	-6.5007	0.5473
Factor(1)*Factor(2)	0.2833	0.0742	3.8189	1.3275
Factor(1)*Factor(5)	0.3014	0.0698	4.3168	1.3518
Factor(1)*Nonnative_0	0.3489	0.0664	5.2500	1.4175
Factor(5)*Nonnative_0	-0.3801	0.1191	-3.1910	0.6838
Log-likelihood: -8.87.768	McFadden's Rho-squared: 0.12943			

nonnative salmonids. Interactions included in this model were (Factor 5)*(Factor 1), (Factor 2)*(Factor 1), (presence of nonnative salmonids)*(Factor 1), and (presence of nonnative salmonids)*(Factor 5). McFadden's Rho-squared was 0.129 for this final model indicating it was not as good a model as the model using relative abundance.

Categorical classification produced a tree that contained 11 terminal nodes (leaves) that classified westslope cutthroat trout abundance using the variables upper reach bound elevation, brook trout abundance, KRTemp, mean elevation of the reach, longitude, latitude, and standard deviation of valley slope for classification. The overall proportional reduction in classification error was 0.244. The classification tree first separated reaches on the basis of maximum elevation (elevation at the top boundary of the reach) into two groups, one with maximum elevations less than 1388 m and one with elevations greater than or equal to 1388 (Figure 18). More reaches with upper elevations of 1388 m and higher had populations of westslope cutthroat trout.

For the higher elevation reaches (the right portion of mobile on Figure 18), the next branch relied on the relative abundance of brook trout. More reaches where brook trout were present did not support westslope cutthroat trout. Where brook trout were present (left side of mobile) longitude was the next variable that classified westslope cutthroat trout abundance, with longitudes less than 111.48 (reaches further east) supporting more reaches that contained westslope cutthroat trout. For reaches located further west than longitude 111.48, latitude was the next split in the tree with more southerly latitudes (less than 44.64) supporting fewer reaches that did not contain westslope cutthroat trout.

For reaches with higher upper elevations (1388 m or higher) where brook trout were absent, predicted July air temperature controlled the next split. The final branch was based on mean elevation of the reach with elevations of 1834 m and higher having a higher frequency of reaches that supported westslope cutthroat trout.

When the 365 randomly selected test cases were cross-validated using this tree, 65% were correctly classified. Many more reaches that did not support westslope cutthroat trout were correctly classified by the tree (174 of 188 or 93%), than either those reaches that supported low (21 of 95 reaches, or 22% correctly classified) or high (37 or 82 reaches, or 45% correctly classified) abundance of westslope cutthroat.

Discussion

Use of the broad-scale MRIS database presented a sample design problem that may have confounded interpretation of statistical results. The MRIS database stores all data on a stream reach basis and fish distribution bounds are not exactly delineated, therefore, there is a lack of resolution on the exact distribution bounds of a particular fish population within and between stream reaches. Lee et al. (1997) documented the same type of scalar resolution problems. The

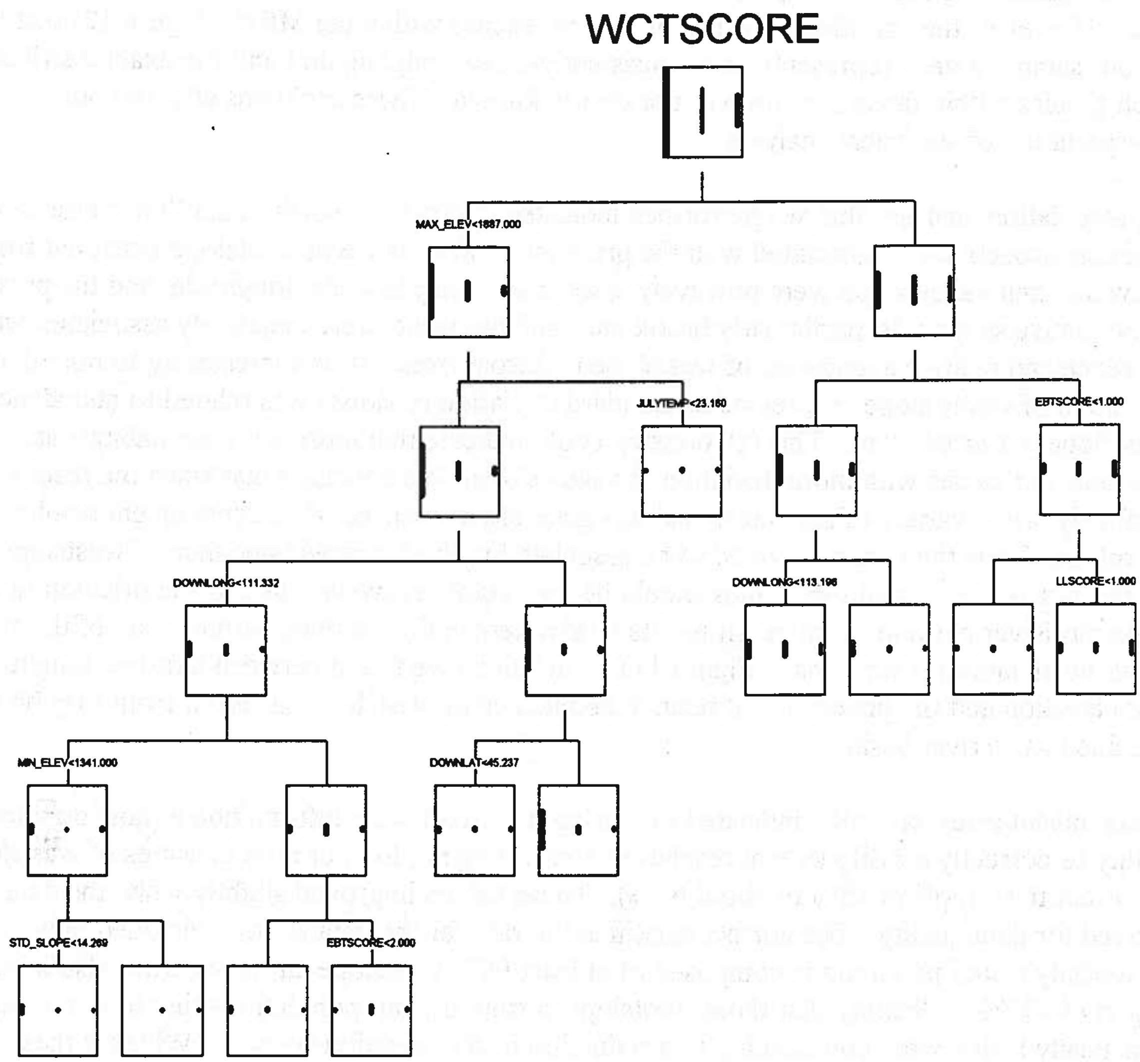

Figure 18. Classification tree for three abundance classes of westslope cutthroat trout (WCTSCORE: absent, uncommon, or common) showing branches, variables that separated branches, and termination nodes (leaves). Dit plots in each box show (from left to right) the number of reaches where westslope cutthroat trout were absent, uncommon, and common for each node.

finest level of analysis they used was the sub-watershed with an average size of about 7,830 hectares. These sub-watersheds often contained more than one tributary stream. Most of the stream reaches we analyzed represented a finer scale than the sub-watershed level defined by Lee et al. However, the variation in length of stream reaches within the MRIS (Figure 12) that made up our sampling units represents an inconsistently-sized sampling unit and the exact distribution of each species within those reaches was not clearly known. These problems affected our interpretation of statistical analyses.

All association analyses that we performed indicated that neither north to south nor east to west drainage aspects were associated with the presence or abundance of westslope cutthroat trout. Elevation and valley slope were positively associated, while latitude, longitude, and the presence of nonnative salmonids, particularly brook and rainbow trout, were negatively associated with the presence and relative abundance of westslope cutthroat trout. It was interesting to note that deviation of valley slope (expressed as standard deviation of slope) was related to abundance of westslope cutthroat trout. This relationship could indicate that more complex habitats are available in reaches with more deviation in valley slope. We conclude that since the results from a relatively broad variety of statistical analyses generally concurred, those concurrent results should be robust. Thus the variables found to be associated with presence/abundance of westslope cutthroat trout across all techniques should be important. However, due to the orientation of the Missouri River basin in Montana (it has its headwaters in the southwestern portion of the state, flows north and then flows east; Figure 11) associations we found between latitude, longitude, and elevation and the presence and relative abundance of westslope cutthroat trout may be very specific to this river basin.

Discriminant analysis results indicated that using the broad-scale information almost doubled our ability to correctly classify stream reaches as supporting no, low, or high densities of westslope cutthroat trout (apriori 33% to about 63%). These results improved slightly when the data were filtered for data quality. The correct classification rate for the data set that included only genetically tested populations composed of at least 95% westslope cutthroat trout also increased slightly to 71%, indicating that those westslope cutthroat trout populations that have not been genetically tested were contributing to a reduction in classification success. Whether these untested populations were not genetically pure and/or did not inhabit "typical westslope cutthroat habitats" is unknown. Correct classification rates for logistic regression and classification tree techniques were similar to these discriminant function analyses. These results suggest that as the quality of data entered into the MRIS data base improves and as the genetic status of presently untested westslope cutthroat trout populations is determined the utility of this data base will also improve.

The presence and relative abundance of brown trout was positively correlated to presence and relative abundance of rainbow trout. Rainbow and brown trout are generally found in lower elevation rivers or large streams, and were most often stocked together in these waters to enhance sport fisheries. The negative correlations between these two species and elevation and valley slope also indicate their use of lower elevation mainstem habitats.

Numerous studies have investigated the effects of habitat on salmonids (see Fausch et al. 1988 for a review). One or more studies have shown relationships between trout abundance and at least one of the following variables - geomorphic classification, stream flow, water velocity, fish cover, stream size, pool habitats, stream bank condition, channel substrate composition, channel gradient, woody debris within the stream channel, riparian community and condition, water depth, water temperature, groundwater recharge, and water quality (Elser 1968; Mortensen 1977; Binns and Eiserman 1979; Platts 1979; Cunjak and Power 1986; Conder and Annear 1987; Bozek and Rahel 1991; Pert and Erman 1994; Rieman and McIntyre 1995; Watson and Hillman 1997). Watson and Hillman (1997) studied the relationships between bull trout, Savelinus confluentus, densities and physical habitat variables at site, stream, and basin scales of analysis. They found that at the site scale bull trout occupied sites with alluviated lowlands and valleys, undercut banks, large substrates, pools, and riparian vegetation dominated by trees and shrubs. Bull trout occurrence at the site scale was inversely related to the percentage of canopy cover and vegetation overhang and the presence of brook and rainbow trout. Bull trout densities correlated positively with pool depth, undercut banks and diverse gradients, and indirectly with fine cover at the site scale.

Several studies have applied GIS technology to study the spatial distribution of aquatic species (Goyke and Brandt 1993; Koutnik and Padilla 1994; Parsley and Beckman 1994; Keleher and Rahel 1996; Lee et al. 1997). Of these studies, Lee et al.'s (1997) study of the Upper Columbia River basin is perhaps the most comprehensive look at a large-scale application of GIS technology to investigate relationships between habitat variables and relative abundance of fish species. They used classification trees to investigate relationships between habitat and management variables and status (absent, depressed, strong) and presence/absence of native salmonids, including westslope cutthroat trout. They found that for westslope cutthroat trout, numerous ecological classification, geologic, soil, climatic, land management, stream channel, stream bank, and stream size variables allowed for correctly classifying population status of about 80% of 1,640 sub-watersheds. These variables also correctly classified over 90% of the sub-watersheds as either supporting or not supporting westslope cutthroat trout for their data set. Using classification trees our correct classification rate for population abundance of stream reaches was much lower (error reduction of about 24%), but we utilized far fewer variables.

We believe that the application of GIS technology to obtain consistent estimates of physical and land management variables over broad geographic scales provides a valuable tool for discerning broad-scale relationships between geomorphic conditions and land management activities on aquatic communities. We suggest that reliable data on the distribution and abundance of fish populations will likely be the major factor that will limit the use of GIS technology in broad-scale fish population analyses. We also believe that stream, reach, and site level information will still need to be collected to refine broad-scale relationships. Lotspeich and Platts first (1982) proposed a hierarchical land-aquatic habitat classification system based on geographic scale. Hierarchical studies, as those performed by Watson and Hillman (1997) and Ireland (1996), show much promise for understanding relationships between physical processes, management practices, and aquatic communities. The ability of GIS technology to explore spatial relationships for aquatic communities appears to have great promise and has only recently been applied (Goyke and Brandt 1993; Koutnik and Padilla 1994).

Acknowledgements

This study was made possible through funding provided by the USDA Forest Service, Rocky Mountain Research Station (contracts INT-92682-RJVA and INT-93845-RJVA), USDA Forest Service - Region One; Montana Department of Fish, Wildlife and Parks, and USDI Bureau of Land Management. Bruce Rieman of the Rocky Mountain Research Station provided valuable insight and recommendations that vastly improved this study. Brian Sanborn and Bruce Roberts of the Beaverhead-Deer Lodge National Forest (USDA Forest Service), Mike Enk of the Lewis and Clark National Forest (USDA Forest Service), Carrie Overton of the Rocky Mountain Experiment Station, and Jim Brammer, Dick Oswald, and Ron Spoon of Montana Fish, Wildlife and Parks helped collect fish and habitat data. Cathy O'Conner, Sally Sovey, and Dan Hinkley of the USDI Bureau of Land Management provided background information and logistic support. Rick Stowell, Linda Ulmer, Gloria Flora, and Don Godtel of the USDA Forest Service helped ensure adequate funding was available and provided logistic support. Matt Sloat of the Montana Cooperative Fishery Research Unit helped test the Keleher-Rahel temperature model. Chris Downs, Dale Nixdorff, and Dave Fuller of the Montana Cooperative Fishery Research Unit assisted with field data collection.

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