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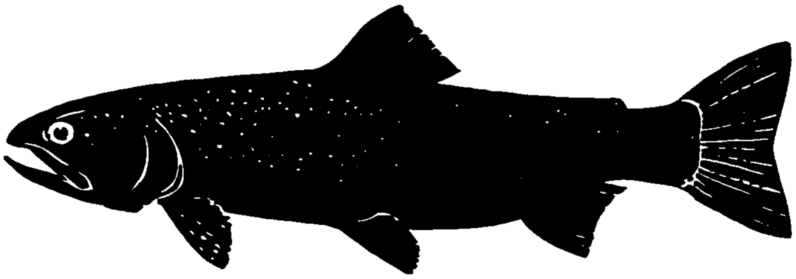
INFLUENCE OF NON-NATIVE TROUT AND GEOMORPHOLOGY ON DISTRIBUTIONS OF INDIGENOUS TROUT IN THE YELLOWSTONE RIVER DRAINAGE OF WYOMING



by
Carter G. Kruse

A dissertation submitted to the Department of Zoology and Physiology
and The Graduate School of The University of Wyoming in partial fulfillment
of the requirements for the degree of

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Kruse, Carter G., Influences of Non-native Trout and Geomorphology on Distributions of Indigenous Trout in the Yellowstone River Drainage of Wyoming, Ph.D., Department of Zoology and Physiology, December, 1998.

Abstract - Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (YSC) are declining throughout their historic range in Wyoming due to anthropogenic influences. I intensively studied three watersheds (Greybull River, North, and South Forks of the Shoshone River) in the Yellowstone River drainage in Wyoming that were likely to contain genetically pure YSC in order to define factors limiting their persistence. Native YSC have been extirpated by hybridizing rainbow trout *O. mykiss* and competing brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* from 70% of the perennial streams which currently support a trout. Exotic trout and YSC used similar habitats throughout these watersheds indicating that introduced trout have the ability to invade and displace YSC. Rainbow trout genes were found in the highest elevation sites, evidence that YSC are not biologically isolated from rainbow trout. Four remaining populations of genetically pure cutthroat trout in the study area appear demographically and genetically viable, but genes from Snake River cutthroat trout occur in these fish and they are threatened by exotic salmonids in the watersheds. The YSC has declined primarily due to hybridization and competition with exotic salmonids. Conservation of this native fish will require re-establishment of large, connected populations in relatively large watersheds void of non-native trout.

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PREFACE

This dissertation focuses on the distribution of native, genetically pure Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* in northwestern Wyoming. Declines in several native subspecies of cutthroat trout over the past half-century has brought native fish conservation to the forefront of fisheries management and have galvanized management agencies to gather information and develop conservation strategies for these fishes. The Yellowstone cutthroat trout (YSC) was once the most widely distributed cutthroat trout subspecies in Wyoming, but land-use and management practices have altered and fragmented the environment, restricting this subspecies to a small and declining portion of its native range. My goal was to focus on the conservation biology of genetically pure YSC in the three watersheds where relatively large populations were believed to occur. This dissertation also gives managers predictive and diagnostic tools for YSC management across watersheds.

This dissertation includes seven chapters, five of which were developed independently for submission to scientific journals. Because each stands alone, some redundancy occurs among chapters. Chapter I describes a management tool to assess trout abundance, providing an efficient method for me to sample the large number of streams that required assessment. The results presented in this chapter allowed me to extrapolate one-pass electrofishing estimates of YSC densities for purposes of viability analysis in Chapters IV and V. Chapter II addresses the use of meristic features, spotting patterns, and visual observations for determining hybridization among YSC, the Snake River finespotted form, and rainbow trout. These alternatives to biochemical methods were important tools enabling me to assess hybridization over large areas. Chapter III provides evidence that the presence of exotic trout and poor stream habitat quality have had considerable impact on YSC distributions in the primary study area – Greybull River, and the North and South Forks of the Shoshone River drainage in the Absaroka Mountains. Overlap in habitat use among trout species in the biologically unproductive watersheds of northwestern Wyoming will be a major limitation in the conservation of YSC. Control of non-native trout over large spatial scales will be necessary to insure adequate refugia for YSC persistence. Chapter IV provides a summary of the current status of YSC in the primary study area and assesses the genetic and demographic viability of the remaining YSC populations. Chapter V provides an evaluation of the potential for management of YSC by isolating small populations in high-elevation streams within the primary study area. Chapter VI is a presentation of information on the genetic status of YSC in selected sites outside the primary study area – the upper Yellowstone River, Clark's Fork of the Yellowstone River, and small streams on the west side of the Bighorn Mountains. Chapter VII provides management and conservation recommendations to guide efforts toward preservation of YSC in northwestern Wyoming.

I have developed information of general scientific interest which can be used in management and conservation of YSC and to stimulate future scientific research. However, due to the spatial and temporal limitations of this research, I could not answer all the pertinent ecological questions regarding this declining subspecies. I challenge the readers of this dissertation to improve upon my endeavor and pursue similar research to prevent the extirpation of our native fauna.

Inherent in this dissertation is the assumption that humans have ethical obligations to preserve native fish such as the YSC. While I firmly believe that we must preserve native fishes, others may not agree. While the recreational value of native game fishes, such as cutthroat trout, justify their continued management, the relatively obscure values of unique genetic groups, such as the various subspecies of cutthroat trout, can make it difficult to legitimize their management or conservation. Maintaining biodiversity for utilitarian, aesthetic, and legal purposes, as well as ethical obligations, provides the primary reasoning for preservation of native fish fauna. While we may not all agree on how and why to manage native fish, success can only be insured by establishing clear conservation goals, sharing pertinent information, and cooperating. I feel that this dissertation will be an important component of the conservation process for YSC by providing scientific information to responsible management agencies.

CHAPTER I

Single-pass Electrofishing Predicts Trout Abundance in Mountain Streams with Sparse Habitat

Abstract. - Fish abundances in mountain streams are typically estimated over a reach with multiple-pass-removal electrofishing techniques, but such estimates are time consuming and potentially harm fish. Recent research has indicated that a single electrofishing pass can provide an index of trout abundance in some streams, but applicable circumstances were not clarified. I sampled 30 stream reaches in northwestern Wyoming to determine if the number of trout captured with a single electrofishing pass could be used to predict trout abundance as estimated by a multiple-pass-removal maximum-likelihood model. Stream width, depth, channel slope, instream cover, and substrate were also assessed to determine their possible influences on the relationship between the number of fish captured with a single pass and multiple-pass estimates. I found that trout samples from a single electrofishing pass accurately indexed the abundance of trout in small mountain streams with little instream cover and low fish densities. The relationship between the number of trout captured with a single pass and a multiple-pass estimate was highly significant ($r^2 = 0.94$) and inclusion of stream width in a multivariate model accounted for additional variance ($R^2 = 0.96$). Single pass samples in small mountain streams with little cover and low trout densities can provide accurate estimates of abundance while circumventing problems of differential capture probabilities on subsequent passes, potential harm to trout, and time in the field. Similar relationships may exist within other geographic areas with homogenous habitat, but preliminary testing is required to determine the relationship between abundance and a single-pass estimate.

The attention given to electrofishing in the scientific literature is a testament to its popularity as a stock assessment technique. Electrofishing is commonly used to assess stream fish abundance and biomass (Moore et al. 1983; Bohlin et al. 1989; Riley and Fausch 1992; Schill and Beland 1995) through either mark-recapture (Pederson and Cederholm 1984) or maximum-likelihood removal (Zippin 1956; Otis et al. 1978) approaches. Consequently, research has focused on the reliability of sampling with electrofishing to estimate population metrics (Cross and Stott 1975; Mahon 1980; Schnute 1983; Habera et al. 1992; Riley and Fausch 1992) and on the effects of electrofishing on sampled fish (Mesa and Schreck 1989; Schill and Beland 1995; Habera et al. 1996; Thompson et al. 1997).

Quantitative assessments of trout in streams are an integral part of both management and research in the Rocky Mountains. Jones and Stockwell (1995) suggested that when an abundance estimate is required and logistical constraints allow (stream size is small enough to isolate with block nets, etc.), a removal method is the most commonly applied and is probably the most appropriate technique. The basic premise of a removal estimate is that multiple electrofishing passes through a stream reach isolated with block nets will result in declining catches with each subsequent pass (until a large portion of the population has been captured) allowing fish abundance to be estimated through maximum-likelihood iterations. Certain stipulations are required for a statistically unbiased estimate, including: (1) a closed population, (2) constant fishing effort on all passes, and (3) equal catchability of fish for each capture occasion (see Riley and Fausch 1992; Jones and Stockwell 1995). The first two assumptions are relatively easy to accomplish, but the probability of capture may decrease with each pass due to behavioral changes in fish associated with previous exposure to an electric field (Cross and Stott 1975; Bohlin and Sundstrom 1977; Mahon 1980; Riley and Fausch 1992). A minimum of two passes are required for calculation of a removal estimate, but Otis et al. (1978) advocated at least four passes in order to test the equal catchability assumption.

A time-intensive sampling technique such as multiple-pass abundance estimation limits the ability of field personnel to assess large areas. The trade-off in time and cost between more precise multiple-pass estimates and relatively quick one-pass electrofishing samples argues for a simpler, less-costly method of enumerating stream fish populations. Strange et al. (1989) and Jones and Stockwell (1995) found that a single electrofishing pass could be used to predict three-pass abundance estimates, but accuracy varied among streams. Several conditions may influence the accuracy of one-pass samples as an index of multiple-pass abundance estimates; including the confounding effects of instream cover (Peterson and Cederholm 1984; Thompson and Rahel 1996), stream size (Habera et al. 1992), the potential for higher escapement of smaller fish on the first pass when attention is focused on larger fish (Mahon 1980), and unequal catchability of fish among passes (Riley and Fausch 1992). Thus, one-pass electrofishing samples may be unreliable in streams with complex habitat, but the benefit of such an index is obvious and warrants exploration. Potential for a simplified, one-pass electrofishing sample to index trout population abundance probably occurs in streams that are relatively small (e. g., < 8 m wide) with little instream habitat and low fish densities. These features allow a large proportion of the population to be captured with a single electrofishing pass.

My intent was to determine if a single electrofishing pass could accurately predict multiple-pass-depletion abundance estimates of cutthroat trout *Oncorhynchus clarki*, rainbow trout *O. mykiss*, brown trout *Salmo trutta*, and brook trout *Salvelinus fontinalis* in small mountain streams over a large area of northwestern Wyoming. Measures of stream size and instream cover were obtained to determine their potential influence on the relationship, as well as on estimated capture probabilities.

Methods

I sampled 30 reaches on tributaries to the Greybull, Shoshone, and Clarks Fork rivers in northwestern Wyoming (see Table 1 for reach characteristics). These tributaries drain the Absaroka volcanic field which is geologically young and highly erosive (Minshall and Brock 1991). The tributaries were generally high-elevation streams with steep longitudinal profiles and large, angular, unstable rock substrates.

Multiple-pass electrofishing depletions (Moore et al. 1983; Strange et al. 1989; Riley and Fausch 1992) were conducted with a Smith-Root model 12 backpack electrofisher (400-600 V DC). Three or four electrofishing passes were made through each 100-m stream reach enclosed with block nets (1.5-cm mesh). If the stream was narrow enough to reach bank to bank with the capture net, a single netter was deployed, otherwise two netters were used to more efficiently collect fish. After each pass, fish were counted, measured (total length, mm), and released downstream of the reach. To maintain consistency between sites, age-0 fish (< 60-mm) were not included in the estimates because sampling took place both before and after emergence. At least 20 minutes elapsed between each pass to allow suspended sediments to settle and remaining fish to return to normal activity. Stream width (nearest 0.1 m) and thalweg depth (cm) were measured at five transects equally spaced through each study reach. The proportion of the substrate composed of bedrock, boulder, rubble, gravel, or sand/silt was visually estimated at each transect, but only boulder substrate was used as a variable in the regression analysis because the substrate categories were significantly correlated. The proportion of water surface area with instream cover was measured following Binns and Eisermann (1979) and classified as dam pools, plunge pools, scour pools, large woody debris, undercut banks, and aquatic or overhanging terrestrial vegetation (Bisson et al. 1982). Channel slope (%) through each reach was estimated with a clinometer.

Maximum-likelihood estimates of trout abundance were made using Model $M_{(b)}$ (Zippin estimator, Zippin 1956; Otis et al. 1978) of the program CAPTURE (White et al. 1982) which calculates (and assumes) constant capture probability for all electrofishing passes. Trout densities (age-1+) were calculated based on the estimated number of trout and water surface area in each reach. Simple-linear- and multiple-regression analyses (Neter et al. 1989) were used to assess relationships among one-pass samples and multiple-pass abundance estimates, stream habitat variables, and the probability of capture. Analyses were performed using SPSS/PC+ for Windows version 8.0 (SPSS Inc. 1997). Significance was determined at $P \leq 0.05$ for all tests.

TABLE 1. Site characteristics for the 30 Wyoming stream reaches sampled.

	Population estimation					Probability	Mean	Mean	Channel	Boulder	
	Electrofishing pass			Population	Density	of	wetted	thalweg	slope	substrate	Cover
Reach	1	2	3	estimate	number/m2	capture	width (m)	depth (cm)	(%)	(%)	(%)
Anderson	6	2	1	9	0.017	0.69	5.2	32	2.0	25	20
Brown	16	4	0	20	0.079	0.83	2.5	14	3.6	40	4
Chimney	13	1	0	14	0.043	0.93	3.2	24	4.0	10	16
Clocktower	7	3	2	12	0.022	0.62	5.4	39	7.9	26	15
Cow[a]	2	4	4	12	0.030	0.35	4.1	17	3.0	10	9
Deer	3	0	0	3	0.014	0.99	2.1	14	4.0	0	1
Dundee	1	1	0	2	0.007	0.67	2.9	18	9.9	40	30
Eleanor	14	4	0	18	0.054	0.82	3.4	18	2.4	15	5
Francs Fork	13	5	2	20	0.039	0.68	5.2	26	3.4	10	17
Goff	4	0	0	4	0.015	0.99	2.6	39	8.1	6	19
Greybull 1	21	5	4	31	0.020	0.67	15.8	40	1.0	5	20
Greybull 2	1	0	0	1	0.002	0.99	4.9	31	4.0	30	2
Gunbarrel	19	2	1	22	0.033	0.85	6.7	55	5.0	18	19
Jack	18	5	0	23	0.053	0.82	4.3	33	7.8	50	20
Kitty	10	4	0	14	0.028	0.78	5.1	47	8.3	35	27
Lodgepole	35	4	0	39	0.113	0.91	3.5	26	5.5	8	38
Marquette	44	5	1	50	0.426	0.88	1.2	42	1.4	0	20
MF Wood	11	2	1	14	0.035	0.78	4.0	33	2.0	5	5
Moss	12	1	0	13	0.037	0.93	3.5	31	5.3	11	46
Newton	5	0	0	5	0.028	0.99	1.8	15	5.1	10	12
Oliver Gulch	2	0	0	2	0.013	0.99	1.5	17	5.1	22	16
Pagoda	11	0	0	11	0.085	0.99	1.3	15	6.6	10	9
Pickett[a]	5	2	2	9	0.019	0.60	4.7	14	1.5	40	1
Piney	5	0	0	5	0.015	0.99	3.4	28	5.4	10	22
SF Wood	30	9	2	41	0.064	0.76	6.4	31	1.0	25	25

TABLE 1. Continued.

	Population estimation					Probability	Mean	Mean	Channel	Boulder	
	Electrofishing pass			Population	Density	of	wetted	thalweg	slope	substrate	Cover
Reach	1	2	3	estimate	number/m2	capture	width (m)	depth (cm)	(%)	(%)	(%)
Sheep	16	2	1	19	0.073	0.83	2.6	20	5.5	8	13
Venus	7	0	0	7	0.017	0.99	4.1	49	4.0	20	7
Warhouse	14	0	1	15	0.066	0.88	2.2	18	7.8	60	17
Wood	37	13	5	57	0.049	0.66	11.5	48	2.0	30	11
WF Timber	16	7	1	24	0.082	0.73	2.9	17	2.3	5	26

[a] A fourth pass was completed because of poor depletion after three passes. In these cases, the fourth pass resulted in zero captures.

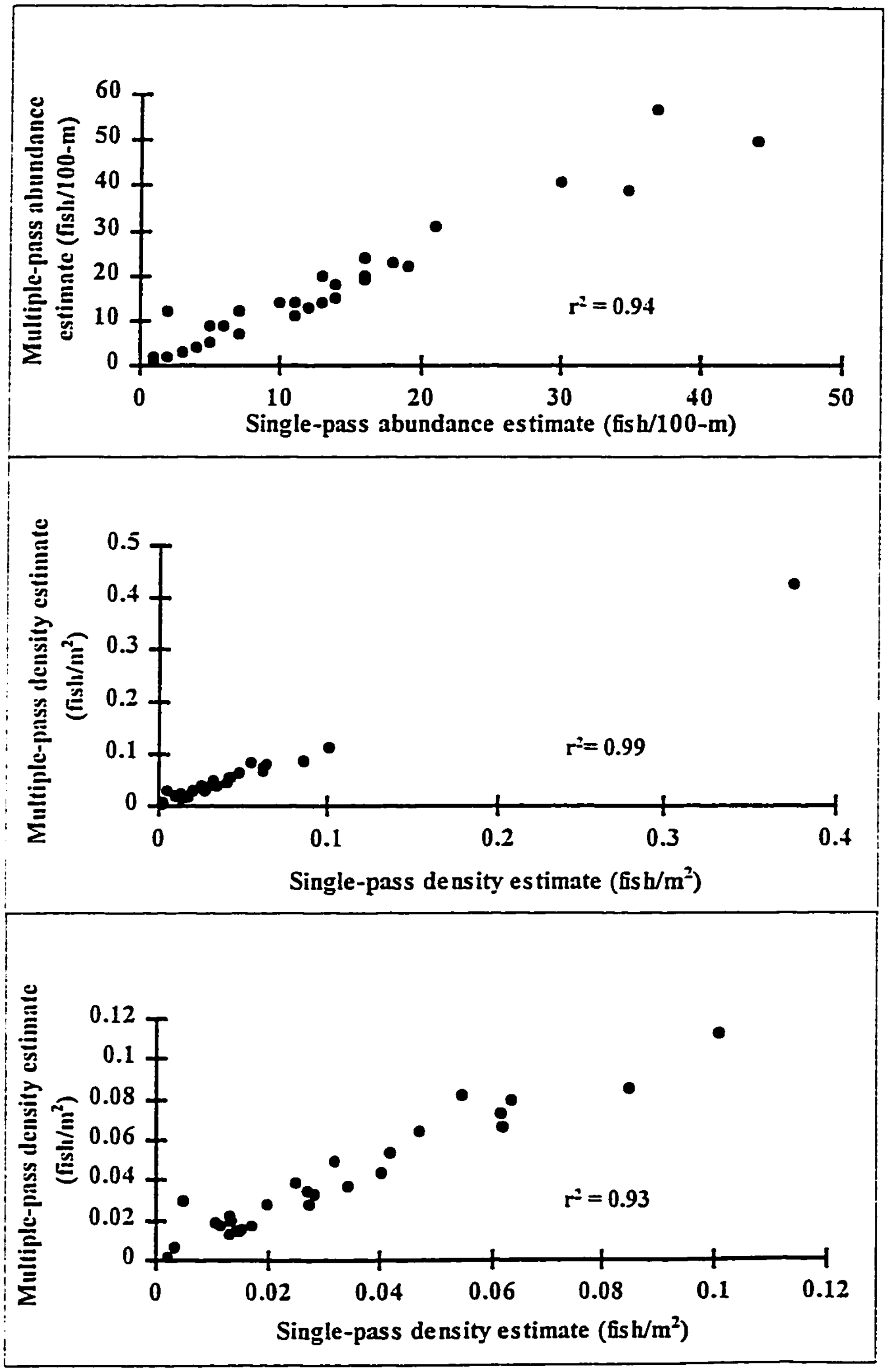
TABLE 2. Regression equations relating one-pass abundance and density to multiple-pass estimates, including significant stream attributes; where MULTIPLE = multiple-pass abundance estimate, PASS1 = one-pass abundance estimate, WIDTH = wetted stream width, MULDENS = multiple-pass density estimate, DENS1 = one-pass density estimate, and PROBCAP = probability of capture. Regression results with the outlier (highest density site) removed are shown in equation (4).

Equation	R^2	*P*
1. MULTIPLE = 0.683 + 1.245 PASS1	0.94	< 0.0001
2. MULTIPLE = -1.863 + 1.181 PASS1 + 0.797 WIDTH	0.96	< 0.0001
3. MULDENS = 0.004 + 1.120 DENS1	0.99	< 0.0001
4. MULDENS = 0.005 + 1.077 DENS1	0.93	< 0.0001
5. PROBCAP = 0.920 - 0.023 WIDTH	0.19	0.017

TABLE 3. Correlations between stream attributes and capture probability, abundance, and density estimates.

Variable	Probability of capture		Multiple-pass population estimate		Multiple-pass density estimate	
	r	P	r	P	r	P
Width (m)	-0.43	0.017	0.44	0.015	-0.24	0.200
Depth (cm)	-0.01	0.954	0.37	0.043	0.11	0.572
Slope (%)	0.26	0.174	-0.43	0.017	-0.24	0.198
Boulder (%)	-0.18	0.356	-0.07	0.700	-0.23	0.228
Cover (%)	0.02	0.912	0.24	0.203	0.14	0.475

FIGURE 1. Relationships between single-pass and multiple-pass estimates of trout abundance (upper panel) and density (middle panel) for 30 stream reaches in northwestern Wyoming . The density relationship after removal of the influential observation is shown in the lower panel (*N* = 29).



Results

Trout population estimates in 100-m reaches ranged from one fish in the upper Greybull River to 57 fish in the Wood River (Table 1). Densities were lowest in the upper Greybull River (0.002/m^2) and highest in Marquette Creek (0.426/m^2). Fish were predominately cutthroat trout, rainbow trout, and hybrids of these two species; however, brown trout predominated in one reach and several others had brook trout present. The number of fish caught with a single pass was significantly related to the corresponding multiple-pass estimate ($P < 0.001$, $r^2 = 0.94$; Figure 1, Table 2). Stream width was significantly ($P = 0.015$, $r^2 = 0.19$) related to multiple-pass estimates and together with the number caught on the first pass accounted for additional variation in multiple-pass estimates ($R^2 = 0.96$). Thalweg depth and channel slope each accounted significantly for variation in estimated abundance (Table 3), but were not significant in a multiple-regression model. Densities computed from first-pass samples were strongly related to the multiple-pass density estimates ($P < 0.001$, $r^2 = 0.99$), but other stream variables did not account for additional variation (Tables 2 and 3). Removal of the highest density observation (see Figure 1, middle panel) reduced the relationship slightly ($P < 0.001$, $r^2 = 0.93$; Table 2).

Estimated constant capture probabilities (Table 1) were high (mean = 0.82) with only one value less than 0.60. Among the measured stream attributes, only stream width had a significant (negative) relation to capture probability ($P = 0.017$, $r^2 = 0.19$, Tables 2 and 3).

Discussion

Several researchers have shown that a one-pass electrofishing sample does not provide a reliable index of fish abundance in streams due to differential catchability of length classes among multiple-passes (more large fish on first pass, Mahon 1980), changing capture probabilities among passes due to behavioral avoidance (Bohlin and Sundstrom 1977; Schnute 1983; Bohlin et al. 1989; Riley and Fausch 1992), or variation in stream size or instream cover (Kennedy and Strange 1981, Peterson and Cederholm 1984, Habera et al. 1992; Thompson and Rahel 1996). However, I observed that in small mountain streams having limited instream cover (defined as absence of undercut banks, instream vegetation, or woody debris) and low trout densities (see Table 1), one electrofishing pass can provide an accurate index of trout (age-1+) abundance. The study streams were typical of those draining the Absaroka volcanic field, being relatively homogenous over each reach with cover occurring predominately as boulder pools. A major difference between this and previous studies was the lack of sampling interference from instream and streamside vegetation or woody debris in our study streams. Trout cover was predominantly boulder pools (> 85% total cover) and categories expected to influence capture ability and population estimates such as undercut banks, vegetation, and woody debris (Thompson and Rahel 1996) were limited. In fact, capture ability was enhanced by the boulder pools which concentrated fish in small areas through the reaches. Strange et al. (1989; $r^2 = 0.52$ for trout and $r^2 = 0.78$ for salmon), Lobon-Cervia and Utrilla (1993; $r^2 = 0.67$ for trout), and Jones and Stockwell (1995; $r^2 = 0.76$-0.86 for trout, including age-0) found significant, but lower coefficients of determination for relationships between one-pass samples and multiple-pass abundance estimates of stream salmonids (age 1+) over a wide variety of stream conditions. While these one-pass assessments indicated the potential to predict abundance, none approached the predictability we observed. However, the habitat complexity and density of fish appeared to be greater in the other studies. Strange et al. (1989) and Lobon-Cervia (1993) may also have compromised their results by using only one netter, increasing the possibility of escapement on the initial electrofishing pass. Jones and Stockwell (1995), who had the highest correlation between single- and multiple-pass estimates, employed multiple netters.

I sampled some streams prior to emergence of age-0 fish, excluding them from capture and subsequent analysis. Upon emergence, age-0 fish were extremely difficult to capture in the swift water amongst large substrate, so capture efficiency was quite variable. Additionally, I wanted to limit their exposure to electric shock and handling stress. Due to these constraints, I limited my analysis to age-1+ fish and made comparisons to values in the previous literature only where age-0 fish were excluded.

I hypothesized that stream size and instream cover would affect the ability to predict multiple-pass estimates of abundance from single pass electrofishing data, but the single pass data predicted abundance and density so well that stream attributes were not necessary to strengthen the relationship.

Similar to Riley and Fausch (1992), but contrary to Peterson and Cederholm (1984), instream cover did not negatively affect our abundance estimates, probably because instream cover and habitat complexity in our study streams were low and actually enhanced capture efficiency. Stream attributes (width, depth, channel slope) were univariately related to estimated fish abundance and stream width significantly explained additional variation when combined with the one-pass index in a multiple-regression equation. However, no stream attribute was significantly related to fish density. This metric includes stream width in its computation, thus I would not expect width to provide more explanatory power in a multivariate setting. Indeed, the equation containing both the one-pass sample index and stream width predicting estimated abundance had a coefficient of determination of 0.96, while the equation predicting estimated density with only the one-pass density index had a coefficient of determination of 0.99, very similar levels of prediction.

The model I used to estimate trout abundance ($M_{(b)}$) calculated a constant capture probability for all passes, thus we could not test for differences in capture probability among passes. However, my mean probability of capture was 0.82, indicating high capture efficiency. Riley and Fausch (1992) mentioned that with high capture probabilities (approaching 0.90) field biologists can become falsely confident in the precision of depletion estimates because high capture probabilities may be the result of reduced catchability on second or third passes due to behavioral avoidance, not depletion of the stock. Because time was allowed between passes and many depletions resulted in zero captures on the second or third passes, I believe my capture probabilities were not inflated by behavioral avoidance. However, as would be expected, the capture probabilities were influenced by stream width (similar to Habera et al. 1992). No other stream variable seemed to affect catch efficiency, probably due to the low habitat complexity among the study streams.

In my study streams with limited cover and low densities of trout, a one-pass sample provided an precise index of trout (age-1+) abundance. Consequently, one pass electrofishing in such streams allows reduced field effort, while limiting potential harmful impacts of electrofishing and handling on the trout. I recommend this approach for watershed-scale assessments of trout populations, but caution its use if rigorous comparisons are needed to detect small changes in trout abundance. This approach has potential for other watershed or geographic areas with simple habitat structure, but a preliminary analysis may be required to assess the relationship between single- and multiple-pass abundance estimates.

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CHAPTER II

Identifying Two Forms of Cutthroat Trout, Rainbow Trout, and Their Hybrids Using Meristic Features and Spotting Patterns: Believe what you see

Abstract. - Identification of genetically pure populations of Yellowstone cutthroat trout *O. c. bouvieri* (YSC) is a management priority as the subspecies become rare due to hybridization with rainbow trout *O. c. mykiss*. I assessed the utility of meristic features and spotting patterns to identify genetically pure YSC, finespotted cutthroat trout, and rainbow trout and their hybrids (YSC x finespotted cutthroat trout and YSC x rainbow trout). Four meristic features (counts of scales in the lateral series and above the lateral line, pyloric caeca, and basibranchial teeth) were significantly different among all three genetically pure trout forms. Discriminate models using meristic features were ineffective in distinguishing between the two forms of pure cutthroat trout, but they classified pure cutthroat trout (of either form) and rainbow trout with 100% accuracy and were able to detect the presence of rainbow trout genes more than 80% of the time in the population. Spotting patterns (size and distribution of spots and color of fin margins) correctly classified genetically pure individuals of all three forms (> 95%), but were of little utility in identifying hybrid individuals. Discriminant models using spotting features were able to detect the presence of rainbow trout genes at a level similar to models using meristic features. Visual classification in the field based on spotting patterns, throat slashes, and white fin margins as diagnostic features performed better than discriminant models with either meristic features or spotting patterns in identifying genetically pure cutthroat trout and rainbow trout, and indicating genetic introgression. Meristic features and spotting patterns can be used as reliable indicators of hybridization, but should be used only as an initial filter. Populations of cutthroat trout appearing to be genetically pure should be further analyzed with biochemical methods prior to their use for conservation populations, reintroduction sources, or translocations.

Genetic introgression among cutthroat trout *Oncorhynchus clarki* and rainbow trout *Oncorhynchus mykiss* is a leading factor in the decline of native cutthroat trout populations (Leary et al. 1987; Marnell et al. 1987; Gresswell 1988; Carl and Stelfox 1989; Young 1995). For example, Varley and Gresswell (1988) estimate that genetically pure Yellowstone cutthroat trout (*O. c. bouvieri*) remain in only 10% of original stream habitat due to genetic introgression (with rainbow trout and other subspecies of cutthroat trout) and habitat alteration. As management agencies initiate preservation and restoration protocols for cutthroat trout subspecies, it becomes imperative to identify the remaining enclaves of genetically pure cutthroat trout.

Differentiation of species, subspecies, or stocks of fishes using meristic and morphological features is common (Marnell et al. 1987; Claytor and MacCrimmon 1988; Melvin et al. 1992; Douglas et al. 1998), but such techniques may be tenuous because these polygenically inherited features are environmentally plastic (Karakousis et al. 1991) and subject to considerable developmental influences (Kwain 1975; Leary et al. 1983; Leary et al. 1985; Leary et al. 1991). In a polytypic species such as the cutthroat trout, subspecies determination based on meristic counts and morphologic comparisons (here defined as external spotting and coloration patterns) has proven difficult, so taxonomists have relied primarily on geographic isolation, with more recent genetic analysis, to discriminate the 14 recognized subspecies (Loudenslager and Gall 1980; Leary et al. 1987; Allendorf and Leary 1988; Behnke 1992; Stearley and Smith 1993). Conclusive subspecies identification has moved to the forefront of management of interior (excluding the coastal subspecies *O. c. clarki*) cutthroat trout as the eight major interior subspecies have experienced precipitous reductions in range and population sizes (Allendorf and Leary 1988; Gresswell 1988; Young 1995). Conservation efforts for individual subspecies have concentrated on locating genetically pure and demographically secure populations. Although the subspecies were originally described based on geographical isolation (see Behnke 1992), assessment of genetic purity is increasingly difficult due to past introductions of various cutthroat trout subspecies and rainbow trout outside their native ranges, resulting in complex hybrid swarms of *Oncorhynchus*.

Multivariate meristic analyses, morphometric comparisons, protein electrophoresis, and deoxyribonucleic acid (DNA) procedures (Ihssen et al. 1981; Leary et al. 1987; Forbes and Allendorf 1991) are being used to determine systematic and clinal differences within a species complex (Qadri 1959; Meng and Stocker 1984; MacCrimmon and Claytor 1985; Claytor and MacCrimmon 1988; Melvin et al. 1992). Hybrid complexes of cutthroat trout subspecies and rainbow trout have necessitated the use of these techniques for discrimination of genetically pure stocks of cutthroat trout. Behnke (1992) provided a comprehensive review of evolutionary, geographic, and typical meristic and coloration differences among fishes in the genus *Oncorhynchus*, and suggested that even subspecies often can be differentiated by meristic counts and spotting patterns. Others have indicated mixed results discriminating subspecies by use of meristic features, often showing better separation occurs among subspecies having large evolutionary divergence (Quadri 1959; Loudenslager and Kitchen 1979; Loudenslager and Gall 1980; Marnell et al. 1987). Assessment of hybridization using meristic features assumes values intermediate to the parents and increased variation in offspring, but recent studies indicate that low levels of introgression, back-crossing, and embryonic developmental conditions can result in values higher or lower than either parent, rendering the intermediate assumption invalid (Leary et al. 1983; Ferguson and Danzmann 1987; Leary et al. 1987; Leary et al. 1991). Thus, while meristic determination of (sub)speciation in cutthroat trout and rainbow trout may be plausible (Behnke 1992), similarity in meristic counts (Kruse et al. 1996) and environmental plasticity of meristic features limit the use of meristic features to differentiate subspecies. Molecular techniques can provide more definitive distinctions than meristic features or morphologic analysis, but differentiation of the most genetically similar forms of cutthroat trout (i.e., finespotted and Yellowstone; Leary et al. 1987) has not been achieved by protein electrophoresis (the more commonly used and less expensive technique).

As cutthroat trout subspecies decline, increasing numbers of populations require analysis of genetic purity before managers can consider preservation options. While the value of electrophoretic information is apparent, analysis of meristic features is a less costly alternative. Some researchers argue that meristic features or morphological comparisons can differentiate subspecies, while others regard such information as inherently faulty. As conservation plans concerning cutthroat trout stocks are developed, acceptable levels of purity and methods to determine the purity of populations are needed. If shown to be reliable, morphological and meristic techniques may be a less costly, less sophisticated alternative to biochemical tests, expediting genetic assessment of populations and allowing field biologists to perform the analysis. Even if these techniques are less than perfect for identifying genetic introgression, any improvement on current options available to conservationists outside of biochemical techniques, will be of value. Techniques that can indicate hybridization in a portion of hybridized populations, can decrease the amount of costly biochemical analyses needed and provide reduced costs, and merit further exploration.

Analysis of stocks of coastal fishes have provided incentive for the use of meristic features to discriminate subspecies and stocks (Dempson and Misra 1984; Meng and Stocker 1984; Beacham 1985; Claytor and MacCrimmon 1988; Melvin et al. 1992). While some systematic information regarding the cutthroat trout complex is based on variation in body coloration and meristic characters (Loudenslager and Gall 1980), these characters can vary as much among disjunct populations within a subspecies as among subspecies, and little work has been done to substantiate proposed differences. Behnke (1992) described meristic differences among cutthroat trout subspecies and rainbow trout. Marnell et al. (1987) indicated good agreement between species identified with both meristic features and electrophoretic analyses. However, most current genetic studies rely entirely on eletrophoretic identification of cutthroat trout subspecies (Reinitz 1977; Loudenslager and Kitchen 1979; Martin et al. 1985; Leary et al. 1987). To my knowledge, only Quadri (1959) has analyzed spotting (morphological) differences among subspecies of cutthroat trout.

Two non-indigenous salmonids, rainbow trout and the genetically similar but morphologically distinct finespotted cutthroat trout, have been introduced and have proliferated through much of the Yellowstone River drainage in Wyoming (Yekel 1980; Wyoming Game and Fish Department files). Conservation prescriptions for Yellowstone cutthroat are dependent on determining the level of hybridization in extant populations. My goal was to determine whether Yellowstone cutthroat trout and the two introduced salmonids, as well as their resultant hybrids, could be identified using meristic features and morphological comparisons (spotting and coloration patterns), expediting assessment of hybridization needed to develop conservation strategies. I also wanted to ascertain whether these approaches improved upon simple visual field assessments of hybridization.

My hypothesis was that the three genetically pure trout forms are meristically distinguishable and can be classified using a multivariate model. If meristic counts were intermediate to parental values in hybrids, I hypothesized that the presence of integration would be detectable, but the presence of hybrid swarms would limit the ability to determine the extent (percentage) of integration. I expected meristic features to be better than morphological patterns to discriminate between cutthroat trout and rainbow trout, but morphology would be more sensitive than meristic counts to differentiate genetically pure individuals of the two forms of cutthroat trout.

My objectives were to: (1) determine if meristic differences existed among genetically pure cutthroat trout from the Yellowstone River drainage (Yellowstone cutthroat trout) and from the Snake River drainage (referred to as finespotted cutthroat trout) and rainbow trout; (2) build discriminating models based on the meristic characters to identify genetically pure fish of each form and their hybrids; (3) compare spotting and coloration patterns among the three trout forms; (4) build discriminating models to recognize genetically pure fish of each form and their hybrids based on spotting and coloration patterns; and (5) compare the results using meristic features and morphological patterns to visual field designations of pure forms and their hybrids. In light of my results, I define the role of meristic features and spotting patterns in genetic assessment of Yellowstone cutthroat trout, more clearly delineate the utility of meristic and morphological comparisons in genetic determination and pacify the debate of their role in conservation decisions.

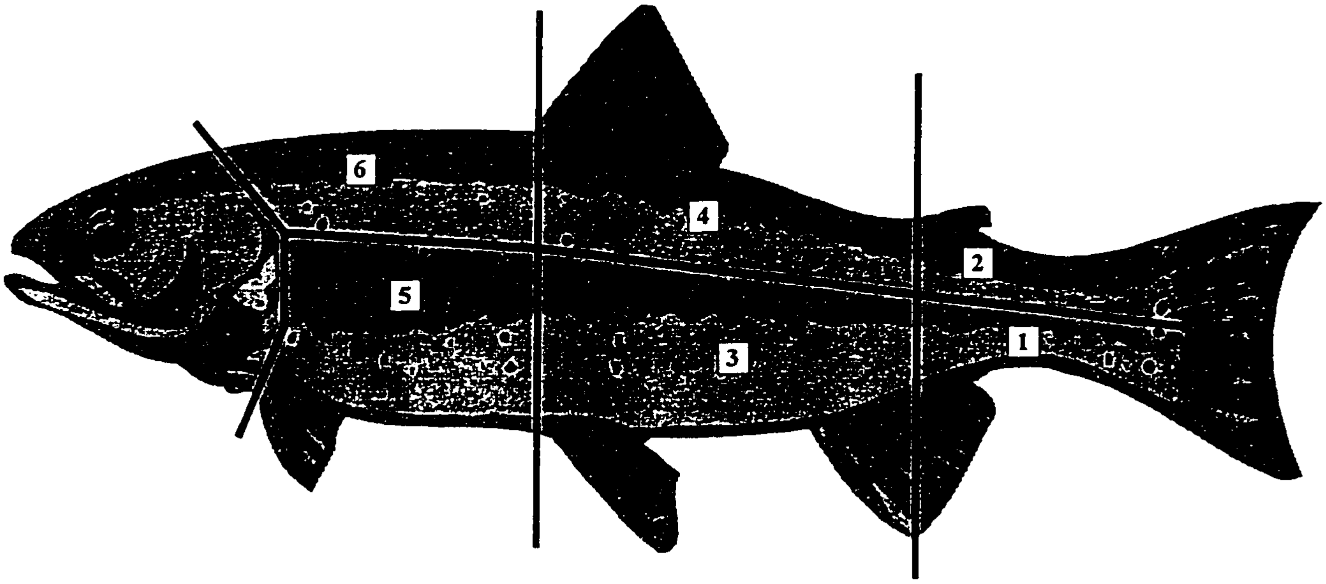
Methods

Analysis of meristic counts and spotting pattern were performed on known genetically pure individuals from each of three trout forms, Yellowstone cutthroat trout, finespotted cutthroat trout, and rainbow trout. Each group of metrics were independently compared to determine mean differences among the three genetically pure forms of trout. Two sets of discriminant models were developed to classify genetically pure fish based on the significant meristic and spotting pattern variables. Models that successfully classified pure forms were validated on other hybrid and genetically pure fish (of unknown genotypes) to assess classification of independent samples. The validation cases were visually identified in order to compare visual classification to model classification.

Counts of meristic features were performed on 50 genetically pure individuals in each of the three groups of trout collected from the Wyoming Game and Fish Department's hatchery system where genetic purity had been confirmed (Alexander and Hubert 1995). Seven commonly assessed meristic features (Schreck and Behnke 1971; Marnell et al. 1987; Behnke 1992) were enumerated on the right side of each fish with the aid of a binocular microscope (up to 20x). Scales in the lateral series (scals) were counted two scale rows above the lateral line from the opercle opening to caudal fin. Scales above the lateral line (scall) were the number of scale rows from the anterior insertion of the dorsal fin down to but not including the lateral line. Pelvic fin rays (pfray), anterior gill rakers on the first arch (raker), and basibranchial teeth (basit) were counted directly. Vertebral counts (verts) were made by filleting the fish and counting exposed vertebrae. Stomachs were excised and stretched so that pyloric caeca (caeca) could be enumerated.

Photographs (35-mm slide) were used to compare morphological patterns (hereafter referred to as spotting patterns, but included coloration of fin margins) of 50 additional specimens determined to be genetically pure by electrophoresis (Alexander and Hubert 1995; Kruse 1995) for each of the three forms of trout. Individual fish were viewed with a projector, measured (total length in mm), and divided into six areas (see Figure 1; similar to Quadry 1959): (1) behind anterior insertion of adipose fin below lateral line, (2) same as area one except above lateral line, (3) behind anterior insertion of dorsal fin below lateral line back to boundary of area one, (4) same as area three except above lateral line, (5) below lateral line forward from boundary of area 3 to opercle, and (6) same as area five except above lateral line. Spots were enumerated in each area and average spot size (mm) in each area was determined based on five

FIGURE 1. Schematic of designated areas used in spotting pattern analysis as described in the methods.



randomly selected spots. To account for differences in slide magnification, spot size was determined as a ratio of measured spot size to projected fish length. Only spots visible to the naked eye on the enlarged picture were counted, connected spots were counted as one, and any spot on the boundary between areas was included in the lower numbered area. The presence of white fin margins (typical in rainbow trout) was noted. Metrics considered in the discriminant analysis were total number of spots, number of spots per area, percentage of total spots per area, average spot size per area, and overall average spot size, as well as the presence or absence of white fin margins.

Counts of meristic features and spotting patterns were assessed for differences among the three trout forms using simultaneous multivariate discriminant function analysis which detects the maximum amount of variation (relative variation within- and across-groups) among the set of all variables used to predict group membership. Discriminant analysis summarizes variability and reduces data multi-dimensionality to *groups - 1* linear combinations of the original variables which can potentially separate previously defined groups (Winans 1984; Hair et al. 1995). Prior probabilities were based on sampled group membership. Analysis of variance (ANOVA) also was used to assess mean differences in meristic features and spotting patterns among the three groups of trout. Only those meristic characteristics significantly different among all three groups of trout were considered useable in the discriminant model. Intermediacy of hybrid meristic counts to parental counts was evaluated by comparing counts from sampled hybrids (origin from field described below) to known pure forms of trout (from hatchery) with ANOVA.

Multiple discriminant models were built separately for each of the two groups of variables (meristics and spotting) by including each entire variable set in a discriminant model and systematically deleting unsuitable variables until one or two appropriate models were developed based on significance (Wilks' lambda), the percent of variation explained by each discriminant function, and the proportion of cases correctly classified. One variable in any highly colinear variable pair was removed from the model. Models with the fewest, unrelated variables were considered to be better than those containing numerous variables when classification rates were similar. Statistical significance of the resultant functions discriminant power was assessed with Wilks' lambda, while the overall fit of the function was indicated by the percent of cases classified correctly. The assumption of equal covariance among groups was tested with Box's M (Hair et al. 1995) and case classification was based on group-specific covariance matrices when the assumption was violated. Once a model was considered appropriate, the discriminant equation was recorded and discriminant functions were characterized by the structure matrix (discriminant loadings) and potency index of individual variables. The potency index was defined by Hair et al. (1995) as a measure of a single variable's discriminating power relative to all other variables. Because the white-fin variable was a dichotomous measure with no variation within a pure trout form, random dummy values (0 - 0.5 = no white fin, 1 - 1.5 = white fin) were entered to allow the computer program to accept it as a legitimate variable.

To verify the discriminatory power of the model(s), test specimens identified to the *Oncorhynchus* genus, but otherwise genetically unknown, were collected from tributaries in the Shoshone River drainage of northwestern Wyoming. Specimens ($N = 52$) were preserved in 95% ethanol and returned to the lab for enumeration of meristic features, while photographs were taken in the field for spotting pattern analysis ($N = 50$). Eye, liver, and muscle tissue was extracted, frozen, and shipped to the University of Montana Wild Trout and Salmon Genetics Laboratory for electrophoretic analysis. Allelic variation at diagnostic loci was used to determine the genetic makeup of individual fish (Leary et al. 1987); these results were considered to reflect the true genetic identity of each fish (see Table 1 for diagnostic loci). The previous introductions of rainbow trout and finespotted cutthroat trout into the Yellowstone River drainage allowed me to collect individual fish that were potential genetically pure or hybrid forms of any two or all three groups of trout. This design allowed me to evaluate model performance in identifying hybrids.

Each test fish was coded separately and analyzed, thus I was able to determine allele composition at each diagnostic locus and calculate the percentage introgression (at tested loci) for individual fish as well as the entire population. For example, if an individual had Yellowstone cutthroat trout genes at six of

TABLE 1. Diagnostic loci between Yellowstone cutthroat trout and rainbow trout.

	Yellowstone Cutthroat Trout	Rainbow Trout
Locus	Alleles	Alleles
sAAT-1*	165	100, 0
CK-A2*	84	100, 76
CK-C1*	38	100, 150, 38
mIDHP-1*	-75	100
sIDHP-1*	71	100, 114, 71, 40
sMEP-1*	90, 100	100
sMEP-2*	100	100, 75
PEPA-1*	101	100, 115
PEPB*	135	100
PGM-1*	*null*	100, *null*

Yellowstone cutthroat trout (allele 100) and finespotted cutthroat trout (allele 300) are currently separated by allele differences on a single loci (AK-1*).

eight loci and rainbow trout at the other two, it was classified as a hybrid predominately Yellowstone cutthroat trout (hysc). Thus, I was able to determine hybrid presence with a measure of the level of introgression. Level of genetic introgression (e.g. 75% Yellowstone cutthroat trout) was regressed against probability of group membership (0 - 100%) indicated by the model to determine if the level of genetic makeup influenced the models ability to distinguish a hybrid.

If a model achieved a reasonable performance level, the test group was applied and potential introgression was assumed to be indicated by a low probability (< 0.80) of fitting into the first group (and high probability of membership in the second group) predicted by the discriminant model. Model output was compared to the actual genetic information to determine validity of results. Model performance was evaluated at two levels, the proportion of fish correctly identified and the ability to indicate the presence of a particular trout form even if classification was incorrect. For example, if the model classified a rainbow trout x cutthroat trout hybrid as a pure rainbow trout, the second level of evaluation considered this an indication of the presence of rainbow trout although first level classification was incorrect.

Model classification also was compared to visual identification of fish genetic makeup when fish were captured in the field. A simple, multiple-character identification based on fin (white margin in rainbow trout), throat (bright red in cutthroat trout, dull red in hybrids, absent in rainbow trout) and body coloration, as well as spot size (largest in Yellowstone cutthroat trout) and distribution (head spots generally lacking or few in Yellowstone cutthroat trout) was recorded in the field for later comparison to results from models using meristic features or spotting patterns.

Based on the correct classification proportion of each model, I calculated the likelihood of detecting at least one hybrid in a sample with differing levels of hybridization present: $A = 1 - B^x$, where A is the detection percent, B is the model detection rate, and x is the number of hybrids in a sample. We evaluated hybrid detection rates at 95 and 99%.

All statistical analysis were performed using SPSS for Windows version 8.0 (SPSS Inc. 1997) and statistical significance was determined at $P = 0.05$. In testing for equality of the covariance matrices,

TABLE 2. Summary statistics for the 28 variables included in the discriminant analysis of meristic features and spotting patterns. Yellowstone cutthroat trout (ysc), finespotted cutthroat trout (fsc), rainbow trout (rbt), hybrids that were predominately Yellowstone cutthroat trout (hysc), and hybrids that were predominately rainbow trout (hrbt) are described. Means not significantly different have the same superscript.

Variable	Genetic Status	Mean	Standard Deviation	Minimum	Maximum
			Meristic		
basit	ysc	20.8^{a}	6.2	11	36
	rbt	0.0^{b}	0.0	0	0
	fsc	18.1^{c}	6.3	7	37
	hysc	5.0	3.2	0	9
	hrbt	0.0	0.0	0	0
caeca	ysc	31.6^{a}	5.1	14	41
	rbt	54.7^{b}	7.2	42	79
	fsc	37.3^{c}	5.0	24	47
	hysc	41.3	9.1	31	56
	hrbt	44.9	7.3	33	56
pfray	ysc	9.0^{a}	0.4	8	10
	rbt	9.5^{b}	0.6	8	10
	fsc	9.6^{b}	0.5	8	10
	hysc	9.1	0.4	9	10
	hrbt	8.9	0.7	8	10
raker	ysc	18.4^{a}	1.2	16	21
	rbt	18.8^{b}	1.5	15	22
	fsc	18.1^{a}	1.4	15	21
	hysc	17.5	1.4	15	19
	hrbt	17	1.0	15	18
scall	ysc	37.2^{a}	2.4	31	42
	rbt	27.4^{b}	2.1	24	33
	fsc	38.3^{c}	2.3	33	43
	hysc	37.6	5.3	27	43
	hrbt	29.1	2.3	26	35

TABLE 2. Continued.

Variable	Genetic Status	Mean	Standard Deviation	Minimum	Maximum
scals	ysc	166.5[a]	8.6	149	193
	rbt	135.7[b]	10.2	111	156
	fsc	173.0[c]	8.1	158	189
	hysc	161.6	12.7	146	187
	hrbt	136.3	9.2	116	151
verts	ysc	61.2[a]	1.3	56	63
	rbt	62.1[b]	1.2	56	64
	fsc	61.1[a]	0.8	60	63
	hysc	62.0	1.4	61	65
	hrbt	64.0	1.0	62	65
			Spotting		
spot total	ysc	162.4[a]	78.7	54.0	433.0
	rbt	370.5[b]	132.9	103.0	832.0
	fsc	783.2[c]	449.4	335.0	2730.0
spot size	ysc	7.8[a]	1.9	5.1	14.7
	rbt	6.9[b]	1.6	4.0	12.3
	fsc	3.7[c]	0.9	1.8	5.5
white fin	ysc	0.0[a]	0.0	0.0	0.0
	rbt	1.0[b]	0.0	1.0	1.0
	fsc	0.0[a]	0.0	0.0	0.0
# area 1	ysc	25.8[a]	11.4	8.0	61.0
	rbt	27.2[a]	9.9	6.0	49.0
	fsc	99.7[b]	51.1	39.0	282.0
# area 2	ysc	33.5[a]	15.4	5.0	72.0
	rbt	38.6[a]	13.8	16.0	76.0
	fsc	110.0[b]	52.1	44.0	352.0
# area 3	ysc	24.2[a]	18.2	1.0	83.0
	rbt	62.4[b]	28.0	8.0	126.0
	fsc	178.0[c]	110.6	38.0	576.0

TABLE 2. Continued.

Variable	Genetic Status	Mean	Standard Deviation	Minimum	Maximum
# area 4	ysc	47.2^{a}	25.1	10.0	129.0
	rbt	90.7^{b}	35.2	26.0	219.0
	fsc	196.7^{c}	106.7	93.0	739.0
# area 5	ysc	10.8^{a}	11.2	0.0	42.0
	rbt	59.8^{b}	24.7	5.0	146.0
	fsc	79.0^{c}	70.5	10.0	402.0
# area 6	ysc	21.0^{a}	16.3	0.0	79.0
	rbt	91.9^{b}	36.2	27.0	226.0
	fsc	118.8^{c}	96.8	23.0	567.0
% area 1	ysc	17.0^{a}	6.0	7.7	38.3
	rbt	7.0^{c}	1.0	4.4	11.2
	fsc	13.0^{b}	2.0	8.9	21.8
% area 2	ysc	22.0^{a}	8.0	4.4	45.5
	rbt	11.0^{b}	3.0	6.5	22.3
	fsc	15.0^{c}	3.0	8.4	20.6
% area 3	ysc	14.0^{a}	6.0	1.8	26.1
	rbt	16.0^{b}	4.0	7.8	24.1
	fsc	23.0^{c}	5.0	11.3	31.3
% area 4	ysc	29.0^{a}	7.0	12.3	44.2
	rbt	25.0^{b}	4.0	17.3	32.3
	fsc	26.0^{b}	4.0	18.2	35.8
% area 5	ysc	6.0^{a}	5.0	0.0	17.6
	rbt	16.0^{b}	3.0	4.9	23.5
	fsc	9.0^{c}	4.0	2.7	19.9
% area 6	ysc	12.0^{a}	7.0	0.0	23.8
	rbt	25.0^{b}	4.0	16.0	33.9
	fsc	14.0^{c}	4.0	3.4	22.9
size area 1	ysc	9.0^{a}	2.4	4.8	16.6
	rbt	7.2^{b}	2.1	3.6	14.3
	fsc	3.9^{c}	1.1	1.9	6.9

TABLE 2. Continued.

Variable	Genetic Status	Mean	Standard Deviation	Minimum	Maximum
size area 2	ysc	9.4 ^{a}	3.0	5.7	19.0
	rbt	8.1 ^{b}	2.1	5.7	15.1
	fsc	4.4 ^{c}	1.2	2.1	6.7
size area 3	ysc	7.7 ^{a}	2.1	4.5	17.3
	rbt	6.2 ^{b}	1.6	3.3	9.7
	fsc	3.3 ^{c}	1.0	1.7	5.4
size area 4	ysc	8.0 ^{a}	1.8	5.0	12.8
	rbt	7.6 ^{a}	2.0	3.8	14.6
	fsc	4.1 ^{b}	1.1	2.0	6.7
size area 5	ysc	6.2 ^{a}	1.2	3.5	8.7
	rbt	5.5 ^{b}	1.5	2.7	9.9
	fsc	3.0 ^{c}	0.9	1.6	4.9
size area 6	ysc	6.2 ^{a}	1.2	4.0	8.8
	rbt	6.5 ^{a}	1.7	2.8	12.0
	fsc	3.5 ^{b}	1.0	1.3	5.3

where we want Box's M to exceed the 0.05 level, *P-values* as low as 0.02 were excepted due to the liberal nature of the test (Hair et al. 1995).

Results

Counts of meristic features were significantly different among all three forms of trout for basibranchial teeth, pyloric caeca, and the two scale counts, but at least two trout forms did not differ significantly for the other three meristic features (Table 2). Only the four meristic features with unique means were considered in the discriminant analysis models. Overall measures of the number and sizes of spots were significantly different, as were most comparisons of individual areas (numbers, sizes, and proportions of spots) among the three trout forms. However, in all comparisons of spotting variables, there were no significant differences in at least one area between two of the three trout forms (Table 2). Yellowstone cutthroat trout had significantly larger and fewer spots than rainbow trout, which in turn had significantly larger and less profuse spots than finespotted cutthroat trout. Yellowstone cutthroat trout generally had a larger proportion of spots posteriorly (areas 1 and 2) while rainbow trout had the highest proportion of any trout form in area 6. Bivariate case-wise plots (shown in Figure 2) illustrate the (best variable combination) discriminating utility of meristic and spotting pattern comparisons, but the desired multi-dimensionality of the data required more sophisticated analytical techniques to explain the covariation of the variables and provide a reliable method of classifying individual cases. All pure rainbow trout exhibited a white pelvic fin margin which was absent in all pure cutthroat trout.

The best linear combination of the four meristic variables used in the first discriminant model (m1) correctly classified 83.3% of the three groups. All classification error was between the two cutthroat trout forms (75% correctly); rainbow trout were classified 100% correctly (Table 3). Both discriminant functions were significant, but function 1 contained 97.8% of the explained variance among the four input variables. Scales above the lateral line loaded highest on function 1 and had a greater potency score (0.38) than the other three variables, basit (0.26), caeca (0.23), and scals (0.27), indicating a greater discrimanatory influence.

Due to the limited ability of meristic features to separate Yellowstone cutthroat trout and finespotted cutthroat trout in model (m1), a second model (m2) was developed combining the two forms of cutthroat trout into one group and comparing them to rainbow trout. Model (m2) correctly classified all 150 trout with a single, significant function, providing a tool to separate genetically pure rainbow trout and cutthroat trout. Scales above the lateral line provided the greatest relative contribution to the discriminant function indicated by loading and potency values (Table 3), while pyloric caeca declined in importance when compared to Model (m1). Case-wise scatter plots of the first two canonical axes from model m1 indicated the separation between rainbow trout and cutthroat trout, but the overlap between the cutthroat trout forms (Figure 3).

Meristic counts for hybrid forms were generally intermediate to the parental species (Table 2), but more similar to the pure parental form that dominated the hybrid genome. For example, counts for genetically dominant rainbow trout hybrids were closer to pure rainbow trout than pure Yellowstone cutthroat trout. For the variables used in model (m1), the only variable with counts outside the pure parental range was scall counts of hybrids predominately Yellowstone cutthroat trout (not significantly higher than pure Yellowstone cutthroat trout).

The model (s1) with the best classification results (99.3%) based on spotting patterns contained the white fin, spot total, and spot-size variables. A single Yellowstone cutthroat trout was classified as the finespotted form (Table 3). The first discriminant function, which accounted for nearly 94% of the variation, was dominated by the presence of white on the fin margin (fin white) with extremely high loading (0.996) and potency (0.806) values, indicating this variable was most responsible for discrimination between groups. Model (s2) was obtained after eliminating the white fin variable and did not contain either overall spot total or spot size, but included the proportions and sizes of spots in areas 1 - 4. Model (s2) correctly classified 97.3% of all cases and discrimanatory power was spread relatively evenly among the eight variables with potency ranging from 0.03 to 0.29. Group separation is illustrated with functional plots for each discriminant analysis model (Figure 4). While the rainbow trout form is not as obviously defined by the canonical variates as in model (m2), both spotting-pattern models differentiated all three forms to a much higher degree than the best meristic model.

The 52 individuals used to test the meristic models were classified into five genetic categories based on electrophoretic results: pure Yellowstone cutthroat trout (14), pure rainbow trout (16), 50% cutthroat trout and 50% rainbow trout hybridization at the tested loci (2), rainbow trout x cutthroat trout hybrids predominately Yellowstone cutthroat trout (6), and rainbow trout x cutthroat trout hybrids predominately rainbow trout (14). Model predictions by category are shown in Table 4. Model (m1) correctly classified 33% (17) of the test group, with hybrids between two groups indicated by low group one (< 0.8) and high group two (> 0.2) probabilities. None of the hybrids were correctly identified, but the model did indicate rainbow trout genes in 16 of 22 actual hybrids or 32 of 38 fish containing rainbow trout genes (pure and hybrid fish).

If hybrid restrictions were relaxed and we assumed the models were incorrect only if they classified an individual into a category that did not contain that genetic signature (e.g., a rainbow trout x cutthroat trout hybrid classified as a pure cutthroat or pure rainbow is acceptable, but a rainbow trout classified as a cutthroat trout is not) model (m1) performance increased to 88% (Table 4). The second meristic model (m2) with only two categories improved overall performance to 58% correct classification because all pure rainbow trout and cutthroat trout were correctly identified, but hybrids were misclassified. Rainbow trout genetic presence was detected in 32 of 38 fish containing rainbow genes, but five of the misses were fish predominately cutthroat trout (hysc) .

Visual identification in the field accounted for genetic makeup better than either meristic model correctly identifying 34 (65%) of the test fish and 14 of 22 (64%) hybrids. Most of the hybrid misses (7 of 8) resulted from identifying a hybrid dominated by cutthroat trout or rainbow trout features as a pure individual. Rainbow trout genes were identified in 33 of 38 fish containing at least a partial rainbow trout genome; however, 10 of 16 pure rainbow trout were classified as hybrid rainbow trout.

When considering the ability of any meristic or the corresponding visual identification to indicate the presence of rainbow trout genes (32 or 33 of 38 or about 85% in all three models), 95% detection required two individuals with a rainbow trout genetic signature to be present in a sample of any size (99% certainty would require 3 fish; Table 5). This level of detection requires only 2 fish of a 20 fish sample to be hybridized in order to identify hybridization.

My measure of the level of genetic introgression, or the proportion of alleles specific to each trout form found in each individual test specimen, was not significantly correlated to the predicted probability of group membership. For example, a fish that was 85% Yellowstone cutthroat trout did not have a higher likelihood of being classified as a hybrid that was predominately Yellowstone cutthroat trout (hysc) than a fish that was only 60% Yellowstone cutthroat trout.

Spotting-pattern models were tested with 50 individual fish classified into six categories based on electrophoretic information: pure Yellowstone cutthroat trout (14), pure rainbow trout (7), 50:50 hybrids (1), Yellowstone cutthroat trout dominated hybrids (12), rainbow trout dominated hybrids (7), and Yellowstone x finespotted cutthroat trout hybrids (9). Model (s1) grouped 21 (42%) of test cases correctly, but only four of 29 hybrids (14%). However, it indicated rainbow trout presence in 18 of the 27 fish which had some level of rainbow trout genetic signature and grouped 50 of 50 cases into a group that at least partially contained the genetic signature of the test individual (Table 4). The model did identify four of the nine Yellowstone x finespotted hybrids correctly, but also classified four of the 14 pure Yellowstone cutthroat trout as the finespotted form. Detection of a hybrid with 95% certainty based on the 67% (18 of 27) recognition of rainbow trout, would require four individuals with rainbow trout genes to be present in a sample (99% certainty would require 5). Model (s2) grouped 56% of the test individuals correctly, identified 31% of the hybrids, and indicated 19 of the 27 fish where rainbow trout genetic influence was present. Model (s2) could not distinguish well between Yellowstone and finespotted cutthroat trout forms. Again, a visual evaluation in the field provided the best indication of hybrids with 11 of 29 correctly identified and an overall 56% correct classification. A partially correct genetic signature was indicated in all 50 cases (Tables 3 and 4).

TABLE 3. Discriminant models used to differentiate Yellowstone cutthroat trout, finespotted cutthroat trout, and rainbow trout. Model m2 had only two groups (cutthroat and rainbow), thus only one discriminant function. Discriminant functions for each model indicated by df1 and df2 with the variation described by each function and its significance level shown.

Model	Function loadings		Function coefficients			Variation/significance		Percent correct		Centroids	
variables	df 1	df 2	df 1	df 2	Potency	df 1	df2	classification		df 1	df 2
						Model m1					
basit	0.517	-0.318	0.089	-0.062	0.263	97.88	2.12	ysc	78	2.588	-0.616
caeca	-0.472	0.680	-0.093	0.100	0.228	<0.0001	<0.0001	rbt	100	-4.920	-0.022
scall	0.615	0.514	0.230	0.121	0.376			fsc	72	2.332	0.637
scals	0.511	0.678	0.041	0.059	0.266			overall	83.3		
constant			-11.674	-16.858							
						Model m2					
basit	0.505		0.086		0.255	100		cut	100	2.458	
caeca	-0.437		-0.088		0.191	<0.0001		rbt	100	-4.916	
scall	0.608		0.236		0.369			overall	100		
scals	0.495		0.043		0.245						
constant			-12.445								

TABLE 3. Continued.

Model	Function loadings		Function coefficients			Variation/significance		Percent correct		Centroids	
variables	df 1	df 2	df 1	df 2	Potency	df 1	df2	classification		df 1	df 2
						Model s1					
white fin	0.996	-0.088	6.445	-0.497	0.806	93.9	6.1	ysc	98	-3.268	1.557
spot size	0.078	0.875	0.048	0.465	0.163	<0.0001	<0.0001	rbt	100	6.935	-0.059
spot total	-0.042	-0.735	0.000	-0.002	0.108			fsc	100	-3.667	-1.498
constant			-4.852	-1.683				overall	99.3		
						Model s2					
%area 1	0.603	0.266	17.156	7.699	0.252	62	38	ysc	96	2.249	-0.512
%area 2	0.531	0.046	11.304	2.829	0.175	<0.0001	<0.0001	rbt	98	-1.690	-1.217
%area 3	-0.224	0.490	12.041	16.999	0.031			fsc	98	-0.559	1.783
%area 4	0.225	-0.001	13.652	10.406	0.239			overall	97.3		
size area 1	0.360	-0.692	0.307	-0.035	0.287						
size area 2	0.268	-0.654	-0.160	-0.011	0.262						
size area 3	0.373	-0.726	0.227	-0.104	0.207						
size area 4	0.208	-0.748	0.031	-0.254	0.122						
constant			-12.070	-4.587							

TABLE 4. Model classification based on electrophoretic information. For each category of model, known genetic information was used and model classification in each category is presented. Categories are pysc = pure Yellowstone cutthroat, prbt = pure rainbow trout, h50 = a 50% Yellowstone cutthroat-rainbow trout hybrid, hysc = Yellowstone cutthroat trout dominate hybrid (with rainbow trout), pfsc = pure fine-spotted cutthroat trout, hrbt = rainbow trout dominated hybrid (with Yellowstone cutthroat trout), hfsc = Yellowstone cutthroat dominate hybrid (with finespotted cutthroat trout), pcut = pure, but unidentified cutthroat trout, and cbt = Yellowstone cutthroat-rainbow trout hybrid (genetic level unknown). The total number of correct classification for each model is given in bold, the number of trout with rainbow trout genes present and those identified as such are indicated by (rbt genes), and the number of individuals classified at least partially correct based on genetic makeup are shown by (partial genetic).

	Genetic makeup							
Model	pysc	prbt	h50	hysc	hrbt	hfsc	Total	
				Meristic				
Electrophoresis	14	16	2	6	14	0	52	
Model m1	1	16	0	0	0	0	17	correct
			1-prbt	1-prbt	14-prbt		32/38	rbt genes
	10-hfsc			3-hfsc			46/52	partial genetic
	3-pfsc		1-pfsc	2-pfsc				
Model m2	14	16	0	0	0	0	30	correct
			1-prbt	1-prbt	14-prbt		32/38	rbt genes
			1-pcut	5-pcut			52/52	partial genetic

TABLE 4. Continued.

	Genetic makeup							
Model	pysc	prbt	h50	hysc	hrbt	hfsc	Total	
Visual	14	6	1	1	12	0	34	correct
		10-hrbt	1-hrbt		2-prbt		33/38	rbt genes
				5-pysc			52/52	partial genetic
				Spotting patterns				
Electrophoresis	14	7	1	12	7	9	50	
Model s1	10	7	0	0	0	4	21	correct
				4-prbt	7-prbt		18/27	rbt genes
	4-hfsc		1-hfsc	4-pysc		3-pysc	50/50	partial genetic
				4-hfsc		2-pfsc		
Model s2	13	7	0	4	3	1	28	correct
			1-hrbt	1-prbt	3-prbt		19/27	rbt genes
	1-hfsc			4-pysc	1-pysc	7-pysc	48/50	partial genetic
				2-pfsc		1-hfsc		
				1-hfsc				
Visual	14	3	0	4	7	0	28	correct
		4-cbt					18/27	rbt genes
			1-pysc	8-pysc		9-pysc	50/50	partial genetic

Table 5. Likelihood of detecting one hybrid in a sample of any size given the number of hybrids and model performance. For example, in a model that classified identified 50% of hybrids, we would expect to detect hybridization in 92% of samples (of any size) that contained 5 hybrids.

Number	Model performance									
hybrids	0.10	0.20	0.30	0.40	0.50	0.60	0.70	0.80	0.90	0.95
1	0.100	0.200	0.300	0.400	0.500	0.600	0.700	0.800	0.900	0.950
2	0.190	0.360	0.510	0.640	0.750	0.840	0.910	0.960	0.990	0.998
3	0.271	0.488	0.657	0.784	0.875	0.936	0.973	0.992	0.999	1.000
4	0.344	0.590	0.760	0.870	0.938	0.974	0.992	0.998	1.000	
5	0.410	0.672	0.832	0.922	0.969	0.990	0.998	1.000		
6	0.469	0.738	0.882	0.953	0.984	0.996	0.999			
7	0.522	0.790	0.918	0.972	0.992	0.998	1.000			
8	0.570	0.832	0.942	0.983	0.996	0.999				
9	0.613	0.866	0.960	0.990	0.998	1.000				
10	0.651	0.893	0.972	0.994	0.999					
11	0.686	0.914	0.980	0.996	1.000					
12	0.718	0.931	0.986	0.998						
13	0.746	0.945	0.990	0.999						
14	0.771	0.956	0.993	0.999						
15	0.794	0.965	0.995	1.000						
16	0.815	0.972	0.997							
17	0.833	0.977	0.998							
18	0.850	0.982	0.998							
19	0.865	0.986	0.999							
20	0.878	0.988	0.999							

FIGURE 2. Bivariate plot showing group separation based on only two variables for both meristic (top) and spotting pattern (bottom) variable sets. Variables shown are the two best "grouping" metrics in each data set.

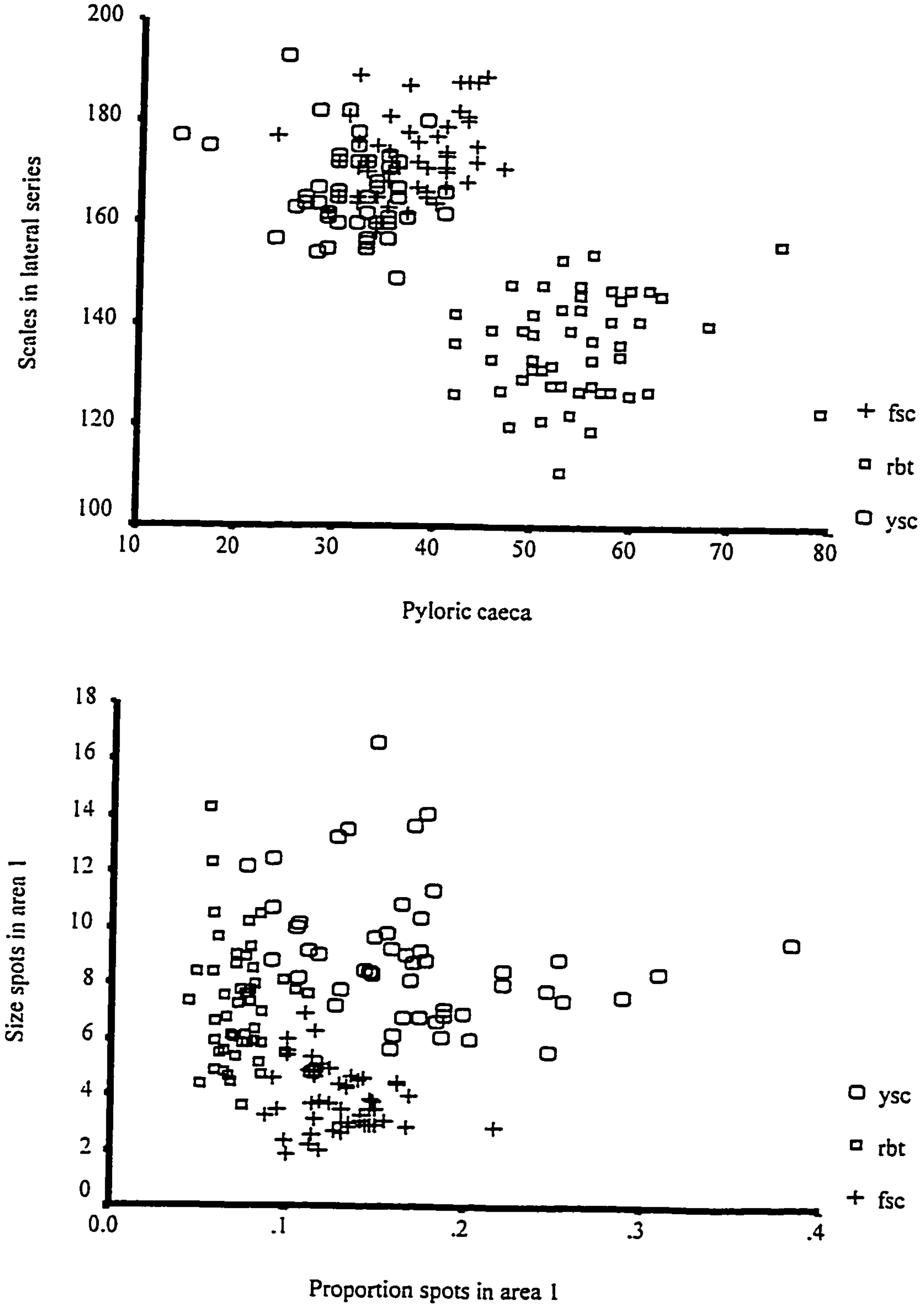


FIGURE 3. Canonical scores for individual cases for model (m1) indicating the inseparability of the finespotted and Yellowstone cutthroat trout forms. Each function corresponds to those shown for model (m1) in Table 3.

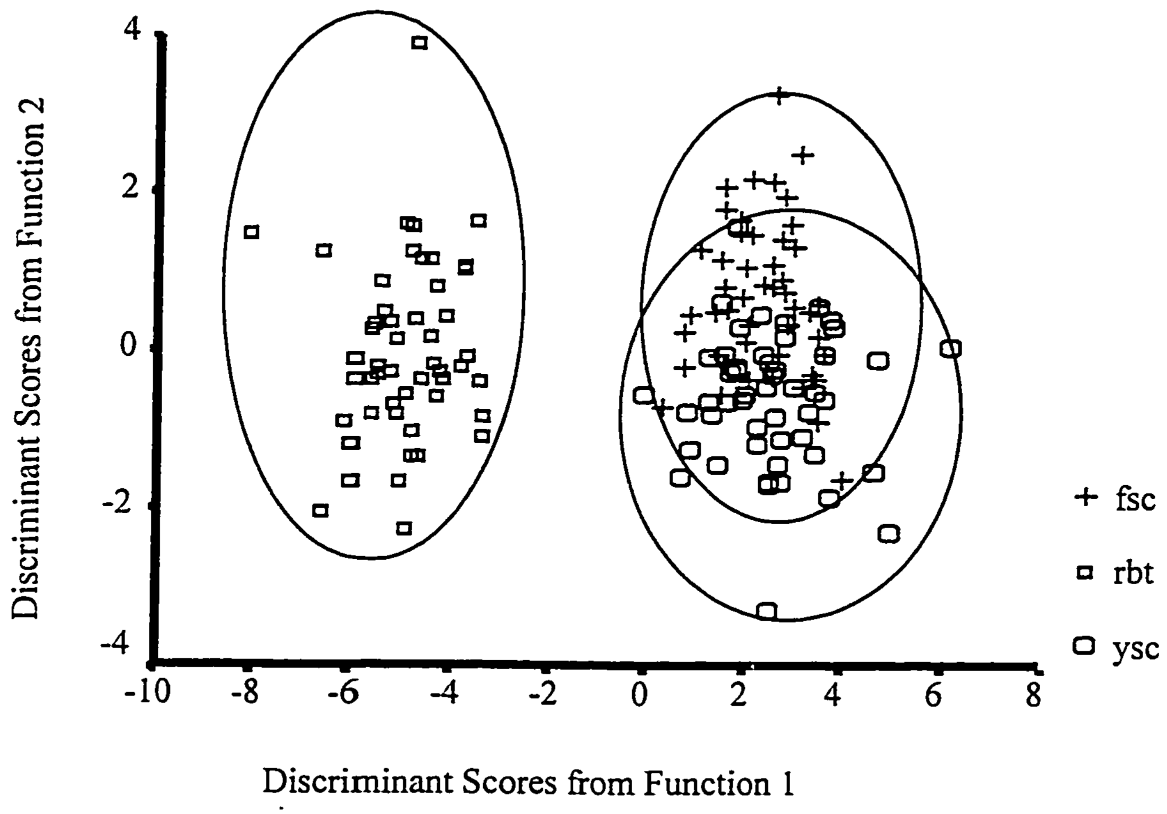
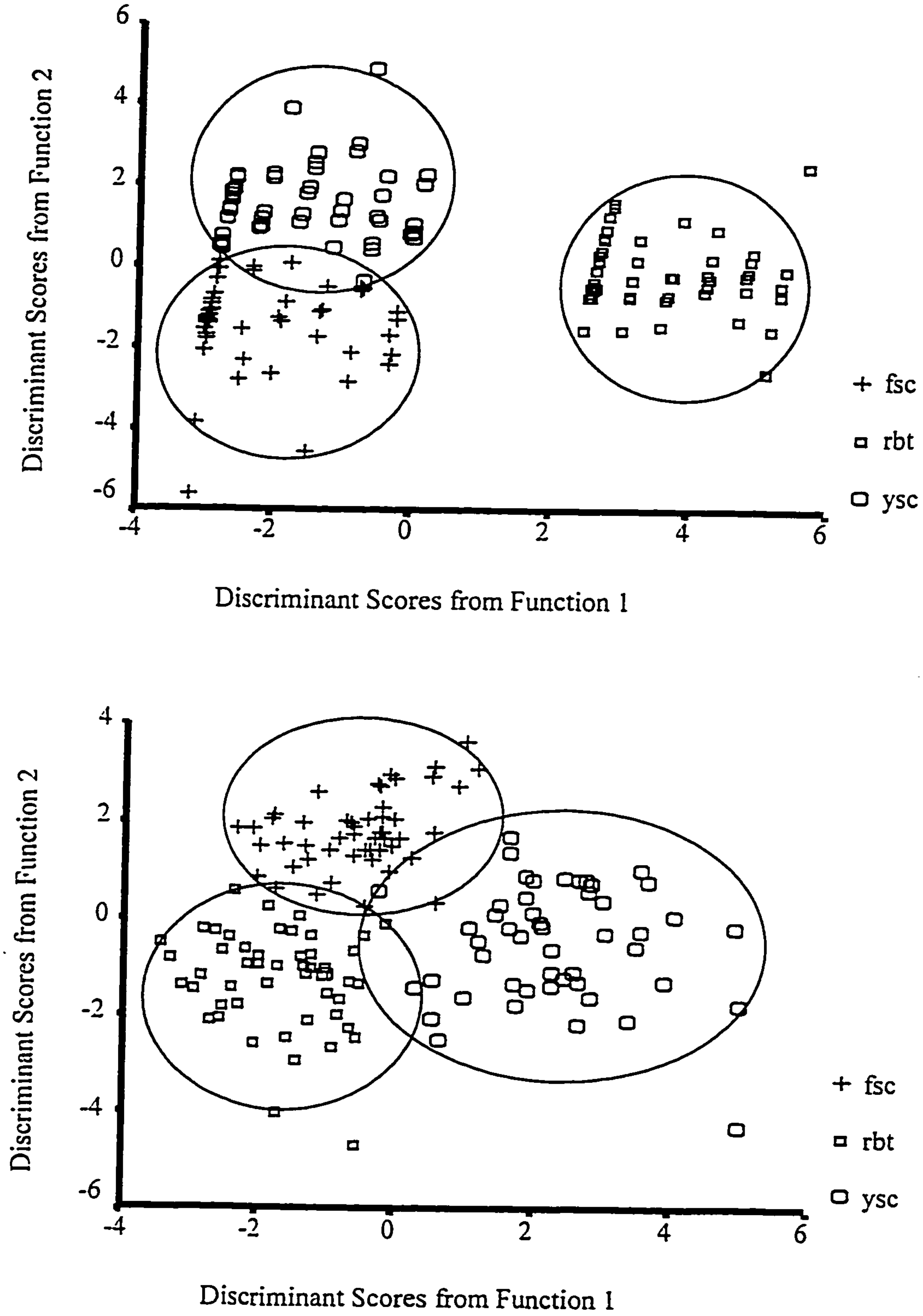


FIGURE 4. Individual canonical scores from spotting pattern analysis models (s1, top) and (s2, bottom) showing relative little overlap between the pure forms of each species. Corresponding model attributes are found in Table 3.



Discussion

The proliferation of rainbow trout and finespotted cutthroat trout across northwestern Wyoming, encompassing most of the native Yellowstone River drainage (Varley and Gresswell 1988), has resulted in myriad populations of trout which require genetic assessment before the current status of Yellowstone cutthroat trout can be determined and conservation options prescribed. While comparison of meristic features and spotting patterns to identify pure individuals of each trout form provides important baseline information, pure forms of these trout are readily recognizable to most biologists familiar with their morphological traits. Thus, the benefit of evaluating meristic features and spotting patterns lies in identifying genetic introgression in extant Yellowstone cutthroat trout populations, not in determining differences among genetically pure individuals of the three forms.

There was considerable overlap in the range of meristic values for each of the three trout forms that I studied (see also Carl and Stelfox 1989; Kruse et al. 1996) suggesting that hybrid assessment with these features alone may not be affective. Meristic features are genetically more stable and more likely to reflect genetic differences than morphologic features, but fish naturally tend to have more variable meristic characters than other vertebrates (Legendre et al. 1972; Leary et al. 1991) and the genetic foundation of variation in meristic traits is poorly understood (Ihssen et al. 1981). Generally, meristic assessments provide significant group differentiation over broad geographic scales, but perform less effectively in localized geographic areas where morphometrics provide finer resolution (Dempson and Misra 1984; Meng and Stocker 1984; Beacham 1985; MacCrimmon and Claytor 1985). Rinne (1985) suggested meristic features are better than morphologic features for separating trout taxa. On the other hand, Behnke (1992), indicated that the Yellowstone and finespotted forms of cutthroat trout were indistinguishable meristically, but easily separated morphologically. Some have shown that differences in meristic features and spotting patterns correspond well to genetic differences (Quadri 1959; Marnell et al. 1987) in cutthroat trout species, but Allendorf and Leary (1988) showed that 40% of westslope cutthroat trout (*O. c. lewisi*) samples considered genetically pure based on meristic and morphological examination were hybridized with Yellowstone cutthroat trout and rainbow trout.

My analysis of meristic differences among genetically pure fish suggested that hybrids of the two cutthroat trout forms were difficult to detect due to similarity in counts, even though several meristic features were statistically different between the pure forms. Cutthroat trout x rainbow trout hybrids could be detected, but not correctly classified, based on large differences in some meristic traits and meristic values intermediate to genetically pure parental species. Hybrid assessment is difficult if progeny do not conform to the intermediacy hypothesis (Leary et al. 1983; Ferguson and Danzmann 1987) or multiple generations develop complex hybrid swarms with wide variation in meristic characteristics. Deviation from meristic intermediacy has been demonstrated for hybrids in many salmonid taxa with offspring often exhibiting counts as high or higher than the parental species (Leary et al. 1983; Leary et al. 1985; Ferguson and Danzmann 1987).

I could not develop a meristic model that discriminated the two pure forms of cutthroat trout, precluding detection of hybridization. Model (m1) based on the four most different meristic characters could not consistently distinguish between pure individuals of the two cutthroat trout forms and classified almost all genetically pure Yellowstone cutthroat trout as hybrid or pure finespotted cutthroat trout. Because the finespotted form is morphologically different from other cutthroat trout it has been designated as a separate subspecies (*O. c. behnkeii*; Montgomery 1995); however, considerable debate surrounds this designation and it is not generally recognized as a separate subspecies due to the lack of genetic differentiation from Yellowstone cutthroat trout (Loudenslager and Kitchen 1979; Loudenslager and Gall 1980; Leary et al. 1987). For purposes of this study, the presence of finespotted hybridization was indicated by the presence of one allele (Table 1) that is common to all finespotted cutthroat trout inside the Snake River drainage and rare in Yellowstone cutthroat trout outside of the Snake River drainage (Robb Leary, University of Montana, personal communication). Regardless of designation, the genetic signature of finespotted cutthroat trout is unknown and we can not be entirely sure of the genetic results reflected by electrophoresis.

Meristic discriminant models (m1 and m2) easily separated pure cutthroat trout and rainbow trout, and correctly classified pure rainbow trout, but were less effective identifying hybrids. Both models missed all levels of hybridization, but they did indicate the presence of rainbow trout genes in the majority of hybrids. Hybrids that had a genome of diagnostic alleles greater than 50% rainbow trout were more likely to be identified as having rainbow trout genes (often classified as pure rainbows) by the models than fish that were only slightly hybridized. Although first level classification (correct identification) of hybrids was incorrect and the level (%) of introgression is impossible to determine, there is value in the second level interpretation of hybrid presence. While it is impossible to accurately determine genetic makeup of a population with a meristic technique, there is value in the models in that they can identify the presence of moderate hybridization between rainbow trout and cutthroat trout.

The inability of the meristic models to classify hybrids is probably a result of trait variation within and overlap in values among the three trout forms. Even though the four meristic traits used in the models had significantly different means, the wide variation in values confounded the ability to categorize hybrid fish. Similar to these results, Douglas et al. (1998) used discriminant analysis and found that meristics could identify pure forms of three chub species (*Gila* spp.) with a high degree of accuracy, but was of limited utility in differentiating hybrids.

Both meristic models were driven by the presence or absence of basibranchial teeth. Because rainbow trout do not express this meristic trait, pure rainbow trout and cutthroat trout can be separated on this trait alone. Leary et al. (1996) suggested that absence of basibranchial teeth indicates pure rainbow trout, while their presence denotes hybridization in fish appearing to be rainbow trout. In my samples, absence of basibranchial teeth did not preclude low-level genetic presence of cutthroat trout, but they did indicate cutthroat trout genetic presence when present.

Because of the similarity in meristic features between the cutthroat trout forms, I expected spotting-pattern analysis would provide better discrimination, but it did not. Typical Yellowstone cutthroat trout have large spots concentrated posteriorly, finespotted cutthroat trout have a larger number of smaller spots scattered across the body, and rainbow trout are intermediate in spotting to the two cutthroat trout forms. Hybrid spotting patterns between the cutthroat trout forms could be expected to very similar to a rainbow trout, but without the characteristic white fin margins of rainbow trout. Most (sub)species descriptions acknowledge spotting pattern differences among *Oncorhynchus* forms, but to my knowledge, only Quadri (1959) had attempted to quantify the differences. He found significant, but highly variable, differences in number and location of spots between coastal and westslope cutthroat trout. Separable spotting patterns did exist among the three trout forms of trout that I studied (substantiating Behnke 1992), but because of widely variable patterns and the fact that morphology is more likely to be affected by nonhereditary factors such as size, sex, and allometrics (Legendre et al. 1972) this type of quantitative assessment has limited utility in absolutely determining genetic makeup in all but the most morphologically dichotomous forms.

A white fin margin was an important variable in the morphological models and always indicated hybridization with rainbow trout in fish otherwise appearing to be cutthroat trout. This provided a key to identifying rainbow trout introgression in remaining Yellowstone cutthroat trout populations. The significance of the fin margin and basibranchial teeth variables suggest that these two easily assessed traits allow identification of a large proportion of hybrids.

Visual field identification provided results similar to the multivariate discriminant models using meristics features or quantified spotting patterns. This suggests a careful field analysis by biologists familiar with the differences among the three forms of trout, can preclude the need for time consuming meristic or spotting pattern analyses when identifying hybridization of Yellowstone cutthroat trout with rainbow trout. Most visual misidentifications occurred when a hybrid was predominately one species or the other. Hybrids containing a genome (at the assayed loci) 85-90% of a parental form were likely to be classified incorrectly as a pure individual. Similarly, Allendorf and Leary (1988) suggest that hybrids with less than a 10% genetic ratio of parental genomes are difficult to detect with any method except biochemical techniques. Smaller fish (< 150-mm) were also more difficult to classify because of fewer discernible coloration and spotting patterns.

Meristic features and spotting patterns can differentiate pure forms of Yellowstone cutthroat trout and rainbow trout; however, visual field identification performs as well in identifying introgression among fish in a hybridized sample. Little can be done to identify Yellowstone x finespotted cutthroat trout introgression. Cutthroat x rainbow trout hybrids were identified if basibranchial teeth were absent or white fin margins were present in a sample from a population that otherwise appeared cutthroat trout. Visual identification provides the capability to filter the numerous Yellowstone cutthroat trout populations requiring genetic evaluation, circumventing the need for more sophisticated biochemical analysis in many cases.

Populations diagnosed as hybridized should be disregarded as potential brood sources, translocation sources, or conservation populations. Because this approach may miss extremely low levels of introgression (i.e., < 1 fish in 10), populations initially diagnosed as pure should be subjected to molecular-based tests to verify genetic status. The inability to quantify the level of genetic introgression (i.e., 90 or 95% pure), a consideration when designating conservation populations, is a limitation of the approach; however, the most important question in Yellowstone cutthroat trout conservation is not how hybridized each population is, but rather if hybridization has occurred with rainbow trout. Because visual identification correctly identified genetic status as proficiently as discriminant models using meristic features or spotting patterns, I suggest foregoing time intensive, complex meristic feature or spotting-pattern analyses when assessing hybridization of Yellowstone cutthroat trout.

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CHAPTER III

The Influence of Habitat Features on the Occurrence of Yellowstone Cutthroat Trout in the Shoshone River Drainage

Abstract. - Non-native trout introductions are a major reason for the decline in indigenous Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (YSC) populations in the North and South Forks of the Shoshone River drainage of northwestern Wyoming. I surveyed 215 sites in 117 tributary basins within the drainages to evaluate habitat use by native and exotic trout species. Yellowstone cutthroat trout, rainbow trout *O. mykiss*, and rainbow trout x cutthroat trout hybrids did not differ in habitats where they were found. Also, habitat use by brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* was similar to that used by the *Oncorhynchus* taxonomic (YSC, rainbow trout, and hybrids of these two species). Native and exotic trout did not segregate habitat spatially. This evidence suggests that YSC can be displaced by introduced trout throughout the drainage. The performance of logistic functions in predicting trout occurrence demonstrated how habitat limits YSC distributions within the drainage. Logistic functions including channel slope and wetted stream width, correctly classified trout presence or absence 79% of the time. At the watershed scale, the length of perennial stream classified trout presence or absence 78% of the time.

The decline in Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (YSC) due to anthropogenic influences over the past half-century (Gresswell 1988; Young 1995; Duff 1996) has resulted in a recent petition to list the subspecies under the Endangered Species Act (Mary Jennings, U. S. Fish and Wildlife Service, Cheyenne, Wyoming, personal communication). Similar to other indigenous salmonids across North America, YSC populations have been negatively impacted by introductions of hybridizing (rainbow trout, *O. mykiss*) and competing (brook trout, *Salvelinus fontinalis*; brown trout, *Salmo trutta*) exotic salmonids, as well as habitat alteration and degradation (Behnke and Zarn 1976; Varley and Gresswell 1988; Young 1995).

Wyoming encompasses much of the native range of Yellowstone cutthroat trout (Behnke 1992; May 1996) and was thought to contain a large proportion of extant YSC populations; however, there was a lack of quantitative information substantiating this claim. A goal of the Wyoming Game and Fish Department (WGFD) is to proactively manage and develop conservation plans for this unique subspecies of cutthroat trout, moderating the necessity for management restrictions commonly required under federal protection.

Persistence of YSC in streams is influenced by their ability to successfully use the limited physical habitat that is present for reproduction, food acquisition, and cover, and to moderate competition with other species (Bozek and Hubert 1992). Constraints imposed by physical habitat limiting persistence of the subspecies are important to identify. Stream habitat includes the physical (e.g., width, depth, velocity) and biological (e.g., community structure and interaction, food availability) components required to support fish populations and communities. Although poorly understood mechanistically and difficult to define, poor instream habitat often corresponds to impoverished fish communities, both in numbers and diversity (Binns and Eiserman 1976; Fausch et al. 1988; Herger et al. 1996).

Yellowstone cutthroat trout have successfully utilized relatively poor quality habitat in the Shoshone River drainage for reproduction, cover, and procuring food since subspecieation; however, only recently have they been required to share and spatially segregate the limited habitat with introduced trout species. The inability of YSC to successfully interact and persist when other exotic salmonids is believed to be the predominate reason YSC populations have declined (Fausch 1988; Fausch 1989; Marcus et al. 1990; Wang and White 1994).

Persistence of YSC has been greatest in high-elevation, low-order streams in remote areas protected by public ownership (U. S. Forest Service and Bureau of Land Management) and limited access (Hanzel 1959; Scarnecchia and Bergerson 1986; Gresswell 1988; Young 1995). Such streams tend to be small, have cold water temperatures, high channel slopes, and limited habitat (Platts 1979; Bozek and Hubert 1992). It has been hypothesized that YSC may have physiological or behavioral advantages over non-native salmonids in these harsh habitats (Behnke and Zarn 1976; Fausch 1989) allowing them to persist in streams where there are no barriers to upstream invasion by exotic salmonids. Baltz and Moyle (1993) suggested that native species are resilient to invasion by exotic fishes in unaltered habitats, but this assertion is largely untested for cutthroat trout (Young 1995). Even though the mechanisms are largely undetermined, studies have suggested distributional segregation among habitats by cutthroat trout and brook trout, rainbow trout, or brown trout (Hartman and Gill 1968; Vincent and Miller 1969; Fausch 1988; Fausch 1989; Kozel and Hubert 1989; Bozek and Hubert 1992).

Although biologists have traditionally characterized habitat or its use by a species (i.e., preference, selection, segregation) through small-scale, stream reach or habitat-unit inventories (Binns and Eiserman 1976; Heggenes 1991; Rieman and McIntyre 1995; Herger et al. 1996), it is important to understand large-spatial-scale geomorphic processes that link habitat and fish distributions (Nelson et al. 1992; Rieman and McIntyre 1995). Recent studies have demonstrated that species distributions and persistence (often one and the same) are linked to spatially large-scale variables, such as basin size, arrangement of streams, connection among streams, and elevation (Rieman and McIntyre 1995). Lanka et al. (1987) predicted trout standing stocks as well with large-scale geomorphic variables as with stream-reach variables and Nelson et al. (1992) found that trout distributions were clearly related to watershed geology. While habitat features characterizing trout distributions have been a focus of research (see Fausch et al. 1988), only recently have biologists shown that elevation, channel slope, and stream size are clearly linked to landscape form and process (Platts 1979; Beschta and Platts 1986) and are useful indicators of trout distributions.

The ability to predict YSC distributions over broad spatial scales can be of considerable value to management agencies responsible for development of conservation protocols for this subspecies. In order to accurately determine current YSC distributions, large tracts of remote, headwater stream habitat remain to be surveyed within Wyoming, so development of tools useful in focusing these efforts can aid the conservation process. Logistic models relating presence and absence of trout to site- and watershed-scale variables can be useful tools, predicting trout presence in areas where little detailed habitat or population information is available (Nelson et al. 1992; Rieman and McIntyre 1995; Rich 1996). These models can also elucidate physical factors effecting persistence of trout over large geographical areas (Rich 1996).

Although generalized distributions of YSC are known in Wyoming, accurate knowledge of current locations, habitat limitations, and interactions with non-native salmonids was lacking. My goal was to determine the effects of physical habitat quality and biological interactions with exotic salmonids on the presence (used as a surrogate for persistence) of YSC in the Shoshone River drainage. I estimated the probability of YSC presence at two scales: the small-scale stream reach and within an entire drainage basin. I wanted to determine if trout presence was predictable at these scales and whether similar processes influenced trout presence at both the reach and watershed scales. Because cutthroat trout are commonly found at the highest elevation sites in other locations, I determined if YSC may persist at sites that are inaccessible to non-native trout and whether these sites are unique (in terms of physical habitat) when compared to sites occupied by non-native trout in the drainage. I hypothesized YSC would not be isolated at high elevation sites and both rainbow trout and brook trout would also occur at such sites with similar habitat features.

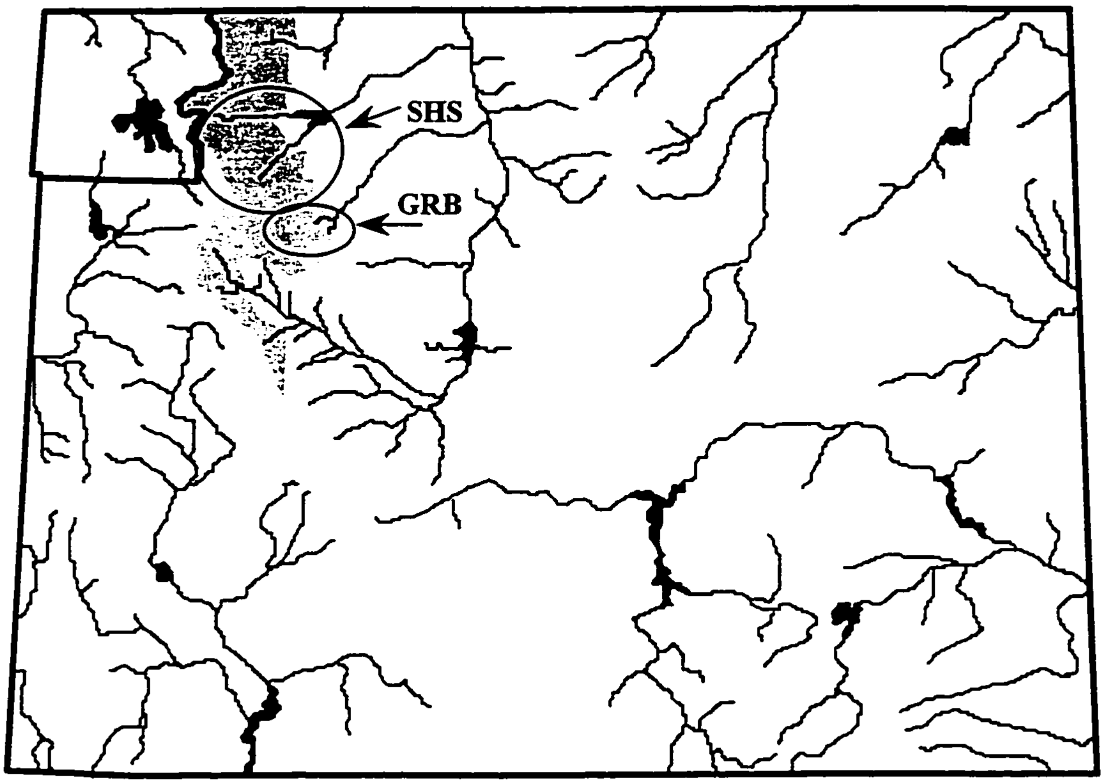
Study Area

Several watersheds in northwestern Wyoming were believed to have a high likelihood of containing genetically pure, native populations of YSC, including the North (NF) and South Fork's (SF) of the Shoshone River drainage (Ronald McKnight, WGFD, personal communication). These watersheds originate in the Absaroka Mountain Range and eastwardly drain that portion of the Greater Yellowstone Ecosystem immediately east and southeast of Yellowstone National Park. The NF and SF of the Shoshone River drain over 3,600 km^2 of the Shoshone National Forest and private lands before joining at Buffalo Bill Reservoir west of Cody, Wyoming (Figure 1). Watershed elevations range from 1,660 m at the NF - SF Shoshone River confluence to 4,010 m at headwater divides.

The Absaroka Mountains were formed during the Laramide orogeny nearly 75 million years ago. Intense volcanic activity (Wilson 1964; Breckenridge 1975) resulted in vast accumulations of volcanic debris (Nelson et al. 1980) and a steep, rugged landscape with uplifted peaks and deep valleys. Geologic history, as well as climatic and environmental weathering of the porous brecca (volcanic rock) and lava deposits, has resulted in geologic instability throughout the region (Keefer 1972; Kent 1984). Stream systems draining these materials tend to be steep and torrential with unstable substrates and large annual fluctuations in discharge (Hansen and Glover 1973; Breckenridge 1975; Kent 1984). Channel classifications, according to Rosgen (1994), are predominately A and B types, typical of high-gradient, straight, entrenched mountain streams. Channel substrates and banks are largely erodible volcanic material (Hansen and Glover 1973; Zafft and Annear 1992), which, coupled with high spring flows and steep channel profiles, result in channels that shift regularly (Kent 1984), are strewn with large angular rocks, are poorly defined, and provide limited, relatively homogenous fish habitat.

Climate is typical of high-mountain environments with mean annual precipitation exceeding 50 cm, predominately in the form of snowfall (Martner 1982). Wetted width during late summer of the mainstem of the NF and SF of the Shoshone River range from a few meters near headwater sources to

FIGURE 1. Major drainage basins of Wyoming with the study watersheds indicated by ellipses. Drainages are abbreviated as SHS = North and South Fork's of the Shoshone River drainage and GRB = Greybull River drainage. The Shoshone National Forest is indicated in gray shade.



more than 30 m at the downstream boundaries of the study area and tributary streams range from 1 to 18 m in width.

The earliest documented introductions of non-native salmonids in the Shoshone River drainage occurred in 1919 (WGFD records, Wyoming State Archives). Brook trout, brown trout, and rainbow trout were commonly introduced until the 1970's. From 1972 to 1975, non-indigenous finespotted cutthroat trout *O. c. behnkeii* from the Snake River drainage were introduced into the watershed. More recently, as native fish conservation has come to the forefront and the problems of hybridization and competition have become apparent, only YSC have been stocked. However, resident populations of brown trout, rainbow trout, and cutthroat trout x rainbow trout hybrids dominate the mainstem trout fauna in the NF and SF of the Shoshone River. Other fish common to the drainage include: mountain whitefish *Prosopium williamsoni*, mountain sucker *Catostomus platyrhynchus*, longnose sucker *Catostomus catostomus*, and longnose dace *Rhinichthys cataractae*. The WGFD currently manages both the NF and SF watersheds as native sport fisheries with focus on conserving YSC (Yekel 1980; Steve Yekel, WGFD, personal communication).

Anthropogenic influences are wide ranging throughout the study area. The upper SF Shoshone River drainage (upstream of Deer Creek), as well as many NF Shoshone river tributaries, are within the Washakie Wilderness Area and are accessible only by hiking or horseback and are relatively pristine. The lower SF Shoshone tributaries and mainstem are affected by roads, agriculture, and irrigation withdrawals, often to the point of stream dewatering. The lower NF Shoshone is paralleled by a highway accessing Yellowstone National Park from Cody, Wyoming, making it subject to erosion and sediment deposition. Fishing pressure is relatively low throughout the study area, except along the Cody to Yellowstone conduit. Even with substantial mainstem impacts in the NF and SF of the Shoshone River watersheds, most headwater tributaries remain relatively inaccessible to humans and can be considered pristine in terms of fish habitat.

Methods

Streams were sampled during summer low flow periods (early July to mid September) from 1994 to 1997. Tributary streams were selected based on the presence of perennial flow (U. S. Geological Survey, USGS, 1:24,000 topographic maps) and a high likelihood of containing trout populations (WGFD file data). Survey sites on tributary streams ranged from 1,713 m to 3,250 m in elevation. Channel slopes ranged from 0.5% to 25.0% with a mean (6.6%) that is generally considered steep (Kondolf et al. 1991; Rosgen 1994). Starting at the confluence of each tributary with the mainstem river and progressing upstream, single-pass, 100-m electrofishing bouts were performed every 1.5 km along the tributary profile until trout were no longer captured. To insure trout absence, an additional 100-m reach was sampled 1.5 km upstream if habitat that could possibly contain trout was present. At each sampling site captured trout were identified and released. Visual field assessment of trout morphology, spotting pattern, and coloration (described in Chapter II) was used to identify rainbow trout, YSC, and their hybrids. Tissue was removed from a subset of *Oncorhynchus* samples to electrophoretically verify the field genetic assessment.

A variety of stream habitat (site-scale) features were measured at each sampling site. Wetted stream width (nearest 0.1 m), thalweg depth (1 cm), and bankfull width (0.1 m) was measured perpendicular to stream flow at five transects spaced equally throughout the 100-m reach. Bankfull flows were estimated based on high water marks indicated by bank erosion or depositional areas. Channel slope was estimated with a clinometer based on the thalweg distance. Instream substrate was visually categorized as proportion of bedrock (solid bed material), boulder (> 30.5 cm, longest diameter), rubble (7.6 - 30.5 cm), gravel (< 7.6 cm), or sand/silt (fines) at each transect. Trout cover (Bowlby and Roff 1986; Herger et al. 1996) was measured over a randomly selected (upper, middle, or lower) 50-m reach within the 100-m sampling reach following Binns and Eisermann (1979). Channel units were identified similar to Bisson et al. (1982). Run, chute, and cascade habitat was grouped into a single category called run, so all channel units not classified as cover was considered either riffle or run. Cover was measured as a linear distance (nearest 0.1 m) and classified as overhanging vegetation, large woody debris, undercut banks, or pools. Pool habitat was further separated into scour pools or plunge and dam pools formed by either boulders or large woody debris.

Reach location (latitude-longitude) and elevation (m) were recorded using a global positioning system and USGS 1:24,000 topographic maps. Watershed-scale geomorphic variables were measured directly from USGS 1:24,000 topographic maps. Each tributary basin was delineated along the hydrologic divide and the following variables were measured:

(1) Basin area - measured with a compensating polar planimeter and including all sub-basins within the catchment area (km^2, Horton 1945);

(2) Drainage aspect - orientation of basin in compass direction with 90° indicating a tributary draining directly north to south, measured by angle of straight line between points at 15% and 90% of the longest stream corridor on the map;

(3) Highest basin elevation - elevation (m) at the highest point on hydrologic divide of basin;

(4) Mid-high basin elevation - elevation (m) at beginning of perennial stream flow in the watershed;

(5) Mid-low basin elevation - elevation (m) at 10% of perennial stream length measured upstream from the outlet;

(6) Outlet basin elevation - elevation (m) at tributary outlet or confluence with mainstem river;

(7) Midrange basin elevation - (highest basin elevation + outlet basin elevation) / 2;

(8) Basin relief - highest basin elevation - outlet basin elevation (Schumm 1956);

(9) Total stream length - the longest watercourse on the map including both perennial and ephemeral segments measured with an electronic map wheel (km);

(10) Perennial stream length - the longest perennial watercourse indicated on the map measured with an electronic map wheel (km);

(11) Relief ratio - basin relief / stream length (m/km, Schumm 1956);

(12) Basin slope - (stream elevation at 90% of stream length - stream elevation at 10% of stream length) / length of stream between these two points (%, modified from Lanka et al. 1987);

(13) Link number - total number of feeder streams flowing into the tributary from headwaters to outlet (following Shreve 1967).

Site- and watershed-scale variables were compared across drainages with analysis of variance (ANOVA) to evaluate inherent differences in habitat characteristics. Sites occupied by trout were partitioned into taxonomic groups based on the species present. For sites containing more than one species of trout the variables were used to calculate means for each of the species present. For example, if brook trout and cutthroat trout were both found in the same 2.4-m-wide reach, the width measurement was used to calculate an overall width for both species, which were then compared across species for statistical differences. The initial categorization compared habitat at sites containing (1) pure Yellowstone cutthroat trout, (2) rainbow trout, (3) rainbow trout x cutthroat trout hybrids, (4) brook trout, and (5) brown trout. There was no significant difference between the cutthroat trout, rainbow trout, or hybrid groups, so they were combined into a single taxonomic group, *Oncorhynchus*, for my analysis. Tukey's multiple-comparison test was used to assess differences among the three taxonomic groups (*Oncorhynchus*, brook trout and brown trout) when significant differences were found. Once habitat use was evaluated for each group, sites containing trout of any taxonomic group (referred to as present) were compared to sites with no trout (referred to as absent) with independent sample *t-tests* (Steel and Torre 1980) to determine whether site-scale habitat variables influence trout presence given a suite of habitat. Because of similarities among all three taxonomic groups, I considered the presence of any trout to identify ites that YSC occupied historically.

At the watershed-scale, sub-basins where trout were absent were compared to those supporting trout where trout were present (*t-test*) to assess differences which might influence trout distributions across entire watershed(s). Because the three taxonomic groups were ubiquitous across the spatial scale of the variables, it was not possible to assess the effect of basin characteristics on individual species.

Analyses were performed only on those sites unaffected by fish migration barriers. Because fish migration barriers restrict trout movement and eliminate the possibility of natural colonization above a barrier, all reaches above fish migration barriers were removed from analyses. Similarly, drainage basins which included a mainstem barrier within 1 km of the outlet were eliminated from consideration; however, basins with large fishless areas upstream from barriers were included if fish were present for more than 1 km below the barrier. Barriers were defined as geologic structures at least 1.5 m high (Stuber et al. 1988) or reaches of very high channel slope or water velocity.

Logistic regression was used to develop incidence functions or probabilistic predictions regarding trout presence at both spatial scales. Logistic regression is an appropriate choice for modeling these binomial data because normality assumptions are not required and the form of the model is consistent with the anticipated probabilistic function reflecting the underlying relationship between habitat and trout presence (Rieman and McInytre 1995). The logistic function form is

$$P = e^{u} / (1 + e^{u}),$$

where P = probability of trout presence (≥ 0.5) or absence (< 0.5), e = the inverse natural logarithm of 1, and u = linear model:

$$u = f + b_1X_1 + b_2X_2 + \ldots + b_n X_m,$$

where f = regression constant, b_n = regression coefficients, and X_m = independent variables. The goodness-of-fit of each model was evaluated with several statistics, including (-2) log-likelihood, model chi-square (χ^2), and the logistic coefficient of determination (R^2, Menard 1995). The log-likelihood statistic is analogous to the error sum of squares in linear regression analysis and is used as an indicator of how poorly the model fits, larger values indicate poorer prediction of the endogenous variable. Model chi-square, similar to the regression sum of squares, tests whether the model significantly explains variation in the dependent variable. The logistic R^2 is the proportional reduction in model χ^2 or in the absolute value of the log-likelihood measure and is calculated by dividing the model χ^2 with the initial (-2) likelihood function. Accuracy of prediction was assessed with the classification efficiency and lambda-p. Lambda-p measures the proportional reduction in error, similar to the logistic R^2, but can be negative if the model predicts worse than the model (Hosmer and Lemeshow 1989; Menard 1995). Significance of lambda-p was calculated according to Menard (1995).

Trout presence-absence probabilities predicted by the logistic models were compared to observed values to determine the classification percentage. Models showing significant reductions in error over mode prediction (lambda-p) were compared to observed fish presence in an independent data set from the Greybull River drainage (from Kruse et al. 1996) and reported as a percentage correct classification. Predicted probabilities equal to or greater than 0.5 indicated trout presence at the site (site-scale) or within the sub-basin (watershed-scale) being tested, while all values under 0.5 were considered to represent the absence of trout. Statistical analyses were performed with SPSS 8.0 for Windows (SPSS 1997) and Minitab 11 for Windows (Minitab 1996). Significance was determined at $P \leq 0.05$ for all tests.

Results

Site or stream scale - A total of 215 sites in 117 tributary basins were surveyed. Fish migration barriers isolated and eliminated 22 headwater sites from analysis. Trout were present in 139 of the remaining 193 sites, including 107 of 135 sites in the NF Shoshone River drainage, and 32 of 58 sites in the SF Shoshone River drainage. *Oncorhynchus* were found in 86% (113) of the 139 occupied sites or 59% of all survey sites. Genetically pure YSC were captured in only 9% (10) of the 113 sites containing *Oncorhynchus* or 7% of the sites containing trout. Brook trout and brown trout were captured in 47% (65) and 12% (16) of all occupied sites (139), respectively.

None of the measured habitat variables were significantly different between the NF and SF of the Shoshone River allowing me to pool the data for further analyses. Comparisons of habitat availability between sites where pure YSC were found and sites containing rainbow trout or rainbow trout x cutthroat trout hybrids indicated no differences in the site-scale variables between the two groups (Table 1). I pooled these taxa (*Oncorhynchus*) for comparison to sites containing either brook trout or brown trout. Significant differences among the three groups (*Oncorhynchus*, brook trout, and brown trout) were detected for seven of the 23 habitat variables (Table 2), but habitat use overlapped for at least two groups at each of these seven significant variables. Brook trout were found in significantly higher elevations with less boulder plunge pool habitat than brown trout, but brook trout occupied wider sites with lower channel slopes than *Oncorhynchus*. Total cover was limited (mean 20%) in all areas occupied by any species of trout.

Presence or absence of trout at each site was analyzed for each of the three taxonomic groups and all trout combined (Tables 3 and 4). Similar patterns were observed between *Oncorhynchus* and brook trout (the two largest groups). Presence of these two groups was significantly influenced by channel slope, measures of stream size, and amount of rubble substrate (Figure 2). Brook trout occupied sites with significantly more scour pools and large woody debris cover, whereas *Oncorhynchus* were found at sites with more pool cover (Table 3). Brown trout were found in larger streams with more cover.

When all taxonomic groups were considered together (overall trout presence, Table 4), lower channel slopes and larger stream channels significantly influenced trout presence, as well as the amounts of scour pool, run, and total cover. Most individual cover components were not significantly different among sites where trout were present or absent; however, in sum there was significantly more cover at sites where trout were present.

Logistic models were developed to predict overall trout presence (all taxonomic groups pooled) based on the site-scale variables observed to be significantly different where fish were present or absent (Table 4). A suite of significant incidence functions were developed (Table 5). Although most models based on site-scale variables had significant chi-square values and provided similar levels of classification (72-79%), only five significantly reduced prediction error over a model based on the mode as indicated by lambda-p values (Table 5). Although channel slope was not a significant univariate predictor of trout presence, all five significant functions, indicated by the highest correct classification and lowest log-likelihood values, contained the channel slope variable in a multivariate form. Model 5, with the inclusion of wetted stream width and total instream cover in addition to channel slope, had the lowest log-likelihood (158.8), highest model chi-square (69.4), highest logistic R^2 (0.30), and the best classification ratio (79%); however, Model 1 (channel slope and wetted stream width) classified cases equally well (79%) and had the highest lambda-p value (0.259) or error reduction of any model.

Site-scale logistic models which significantly reduced prediction error had good agreement between observed and predicted fish presence when tested on sites from the Greybull River drainage (Table 6). Because cover attributes were not collected in the Greybull River drainage, models 3 and 5, which included the total cover variable, could not be tested. Agreement rates approached 81% for models 1 and 2, even though model performance statistics (Table 5) for model 2 were poorer than model 1. Agreement for model 4, which had classification rates lower than both model 1 and 2, was slightly lower (79%). The error rate was similar for all three models -- one model did not consistently misclassify one category (absence or presence) more than another model.

Watershed scale - Five of the 117 sub-basins in the two watersheds contained fish migration barriers within 1 km of the basin outlet. Of the remaining 112 sub-basins, 36% (40) did not contain trout -- 16 of 65 in the NF Shoshone and 24 of 47 in the SF Shoshone. Watershed-scale variables did not differ significantly among drainages.

Because taxonomic groups used similar site-scale habitat (Tables 2-4) and distributions were ubiquitous across drainages, overall trout presence was assessed (Table 7). All geomorphic variables measured at the watershed-scale, with the exception of basin aspect, had significant differences between sites where trout were present and absent. Tributaries where trout were present tended to drain significantly larger areas. Streams in these basins were longer, had lower channel slopes, and significantly more hydrologic input (link number).

Several univariate and multivariate watershed-scale incidence functions predicting trout presence had significant chi-squares and significantly improved (lambda-p) estimates of the dependent variable (Table 8). Classification efficiency of significant (lambda-p) watershed-scale models (72-81%) was higher than non-significant watershed models (67-70%) and slightly higher than site-scale classification efficiencies (77-79%). Model 9 included the length of perennial stream and was the best univariate exogenous variable, correctly classifying 78% of all sites with a proportionate reduction in the log-likelihood of 0.32. Several two-variable models produced similar results (Table 8), but always included the length of perennial stream as a variable. Perennial stream length coupled with mid-range basin elevation (# 16) proportionately reduced the log-likelihood value by 35% to the lowest level for a two-predictor model (93.8); however, model 16's classification rate (78%) was less than the 81% efficiency produced by the perennial stream length and hi elevation model (# 12). The best two-variable model without an elevation element was a toss-up among models containing perennial stream length and basin area, basin slope, or link number -- all of which had virtually identical log-likelihood, R^2 and classification rate values. Models 18-21 included three variables and resulted in slightly lower log-likelihood and higher R^2 values than the best two-variable model, but ultimately did not improve classification efficiencies over one- or two-variable models (Table 8).

When applied to the data set from the Greybull River drainage, agreement rates varied widely among the best logistic watershed-scale models (Table 6). The best univariate function (# 9) correctly classified 86% of the basins, perfectly classifying the barren basins (20/20), and incorrectly categorizing 6 of 23 basins where trout were present. Surprisingly, efficiency dropped to 78% for the best two-variable model (# 16) and was surpassed by the other "good" two-variables models (# 10, 12-14) at 86%. Three of these four models classified absence (19 or 20/20) and presence (17 or 18/20) in basins at similar rates, but model 14 incorrectly classified more basins where trout were absent (16/20), creating a bias towards basins were trout were present. Test agreement rates were poorest for three-variables models (67-83%), all of which incorrectly categorized several barren basins.

TABLE 1. Comparison of sites where rainbow trout, genetically pure Yellowstone cutthroat trout, and their hybrids were found. Bold indicates a significant difference between the species groups.

Site variable	Rainbow trout and hybrids ($N = 103$)	Yellowstone cutthroat trout ($N = 10$[a])
	Mean	Mean
Elevation (m)	**2072**	**913**
Channel slope (%)	6.05	5.45
Width (m)	6.6	4.4
Depth (cm)	40	37
Boulder (%)	22	18
Undercut Bank (m/50 m)	0.70	2.00
Large Woody Debris (m/50 m)	0.62	0.30
Total Pool Cover (%)	14	8
Total Cover (%)	19	17

[a] Five of the ten sites were sampled on Marquette Creek, the lowest elevation tributary in the South Fork Shoshone River drainage, protected by a fish migration barrier.

TABLE 2. Comparison of occupied sites for three species categories of trout. Due to a small sample of cutthroat trout, no significant differences were found between rainbow trout and cutthroat trout, thus rainbow trout, cutthroat trout, and rainbow trout x cutthroat trout hybrids were grouped together as *Oncorhynchus*. Significant differences ($P > 0.05$) among species groups are indicated by a different letter designation following the sample size column. A significant P indicates that at least one of the three categories is different.

	Oncorhynchus			Brook trout			Brown trout			
Site variable	Mean	N		Mean	N		Mean	N		*P*
Elevation (m)	2079.0	107	ab	2171.0	65	b	1993.0	15	a	0.000
Channel slope (%)	6.0	113	a	4.8	65	b	5.7	16	ab	0.026
Width (m)	6.5	113	a	7.9	65	b	7.6	16	ab	0.038
Depth (cm)	40.2	113	a	44.1	65	ab	50.0	16	b	0.045
Bankfull (m)	16.2	113		17.7	65		17.3	16		0.556
Width:Depth	15.7	113		18.3	65		15.6	16		0.054
Bedrock (%)	1.0	113		1.0	65		1.0	16		0.962
Boulder (%)	22.0	113		20.0	65		28.0	16		0.111
Rubble (%)	36.0	113		37.0	65		37.0	16		0.692
Gravel (%)	34.0	113		35.0	65		30.0	16		0.432
Sand/Silt (%)	7.0	113		7.0	65		4.0	16		0.382
Boulder Dam Pool (m/50 m)	0.03	112		0.04	65		0.06	16		0.785
Log Dam Pool (m/50 m)	0.09	112		0.30	65		0.00	16		0.191
Boulder Plunge Pool (m/50 m)	6.47	112	ab	4.88	65	a	7.66	16	b	0.042
Log Plunge Pool (m/50 m)	0.75	112		0.81	65		0.69	16		0.957
Scourpool (m/50 m)	0.56	112	a	1.95	65	b	1.44	16	ab	0.020
Total Pool Cover (%)	13.0	112	ab	10.0	65	a	15.0	16	b	0.042
Undercut Bank (m/50 m)	0.82	112		0.99	65		0.38	16		0.502
Large Woody Debris (m/50 m)	0.59	112		1.11	65		0.72	16		0.064

TABLE 2. Continued.

Site variable	*Oncorhynchus*		Brook trout		Brown trout		*P*
	Mean	N	Mean	N	Mean	N	
Overhanging Vegetation (m/50 m)	0.27	112	0.12	65	0.31	16	0.781
Run (m/50 m)	34.4	112	32.9	65	33.5	16	0.471
Riffle (m/50 m)	6.0	112	6.9	65	5.3	16	0.589
Total Cover (%)	19.0	112	21.0	65	23.0	16	0.448
Oncorhynchus presence	1.00	113	0.65	65	0.56	16	0.000
Salvelinus presence	0.37	113	1.00	65	0.44	16	0.000
Salmo presence	0.07	113	0.10	65	1.00	16	0.000

TABLE 3. *P*-values for comparison of sites where each species group was present or absent. If significant differences occurred among sites where each species was present or absent a (+) indicates that present sites had a significantly higher value, while a (-) indicates that absent sites had a higher mean value for the measured habitat variable. N = the total number of sites used in the analyses and P = the number of those sites that contained each species of fish.

	Oncorhynchus	Brook trout	Brown trout
Site variable	N = 193 P = 113	N = 193 P = 65	N = 193 P = 16
Elevation (m)	0.212	0.000+	0.268
Channel slope (%)	0.006-	0.000-	0.264
Width (m)	0.001+	0.000+	0.014+
Depth (cm)	0.006+	0.000+	0.006+
Bankfull (m)	0.002+	0.000+	0.146
Width:Depth	0.019+	0.000+	0.490
Bedrock (%)	0.127	0.132	0.208
Boulder (%)	0.437	0.276	0.031+
Rubble (%)	0.014+	0.010+	0.350
Gravel (%)	0.288	0.869	0.241
Sand/Silt (%)	0.205	0.378	0.000-
Boulder Dam Pool (m/50 m)	0.051-	0.372	0.950
Log Dam Pool (m/50 m)	0.058	0.370	0.000-
Boulder Plunge Pool (m/50 m)	0.007+	0.075	0.129
Log Plunge Pool (m/50 m)	0.526	0.453	0.995
Scourpool (m/50 m)	0.123	0.009+	0.414
Total Pool Cover (%)	0.011+	0.068	0.123
Undercut Bank (m/50 m)	0.673	0.283	0.176
Large Woody Debris (m/50 m)	0.559	0.004+	0.803
Overhanging Vegetation (m/50 m)	0.308	0.494	0.575
Run (m/50 m)	0.632	0.158	0.654
Riffle (m/50 m)	0.156	0.737	0.315
Total Cover (%)	0.290	0.081	0.051+

TABLE 4. Differences between sites where trout (all species pooled) are present and absent in the North and South Fork Shoshone River drainages.

	Absent			Present			
Site variable	Mean	SD	N	Mean	SD	N	*P*
Elevation (m)	2128.0	245.6	139	2114.0	188.0	51.0	0.727
Channel slope (%)	8.8	3.0	139	5.7	2.8	54.0	0.000
Width (m)	3.3	2.2	139	6.6	3.8	54.0	0.000
Depth (cm)	30.4	16.0	139	40.3	15.6	54.0	0.000
Bankfull (m)	10.3	8.7	139	16.0	9.6	54.0	0.000
Width:Depth	11.0	3.4	139	16.2	7.2	54.0	0.000
Bedrock (%)	3.4	10.4	139	0.6	3.3	54.0	0.057
Boulder (%)	22.0	15.0	139	21.0	15.7	54.0	0.665
Rubble (%)	31.9	11.5	139	34.9	11.0	54.0	0.098
Gravel (%)	33.1	13.2	139	35.7	15.2	54.0	0.244
Sand/Silt (%)	9.4	11.1	139	7.8	9.7	54.0	0.348
Boulder Dam Pool (m/50 m)	0.11	0.4	138	0.05	0.3	54.0	0.289
Log Dam Pool (m/50 m)	0.22	0.8	138	0.20	1.0	54.0	0.897
Boulder Plunge Pool (m/50 m)	5.13	3.6	138	5.97	4.8	54.0	0.196
Log Plunge Pool (m/50 m)	0.41	1.2	138	0.80	1.7	54.0	0.079
Scourpool (m/50 m)	0.19	0.7	138	1.15	3.5	54.0	0.003
Total Pool Cover (%)	10.5	7.0	138	12.0	9.0	54.0	0.237
Undercut Bank (m/50 m)	0.24	0.6	138	0.97	2.1	54.0	0.000
Large Woody Debris (m/50 m)	0.43	1.3	138	0.73	1.4	54.0	0.150
Overhanging Vegetation (m/50 m)	0.06	0.3	138	0.25	1.7	54.0	0.216
Run (m/50 m)	37.3	6.9	138	33.0	8.9	54.0	0.001
Riffle (m/50 m)	6.0	6.3	138	6.9	7.1	54.0	0.383
Total Cover (%)	14.0	8.0	138	20.0	12.0	54.0	0.000

TABLE 5. Logistic regression analysis using site variables for trout (all species pooled) presence and absence in the North and South Fork Shoshone River drainages. A series of models and their parameters along with the classification efficiency are presented using those site-scale variables shown to be significant univariate predictors of trout presence (Table 4). Initial log-likelihood values for sample sizes 192 and 193 are 228.15 and 228.80, respectively. Unreported *P*-values for lambda-p are > 0.05.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lambda-p	*P*
Model 1	192		0.000	169.5	58.7	50/79/91	0.26	0.259	0.018
Channel slope		-0.289 (0.07)	0.000						
Width		0.320 (0.09)	0.000						
Constant		1.600 (0.70)	0.023						
Model 2	192		0.000	180.4	47.8	46/78/91	0.21	0.222	0.035
Channel slope		-0.341 (0.07)	0.000						
Depth		-0.032 (0.01)	0.013						
Constant		2.289 (0.72)	0.001						
Model 3	192		0.000	169.1	59.1	48/78/89	0.26	0.204	0.046
Channel slope		-0.397 (0.07)	0.000						
Total cover		9.015 (2.41)	0.000						
Constant		2.330 (0.61)	0.000						
Model 4	193		0.000	169.5	59.3	46/77/89	0.26	0.204	0.046
Channel slope		-0.273 (0.07)	0.000						
Width		0.438 (0.14)	0.002						
Depth		-0.020 (0.02)	0.308						
Constant		1.688 (0.72)	0.019						

TABLE 5. Continued.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lambda-p	*P*
Model 5	193		0.000	158.8	69.4	54/79/88	0.30	0.241	0.024
Channel slope		-0.322 (.08)	0.000						
Width		0.253 (0.09)	0.004						
Total cover		7.349 (2.48)	0.003						
Constant		0.915 (0.76)	0.227						

TABLE 6. Agreement (percent) between actual and predicted fish presence when testing logistic models on sites in the Greybull River drainage. Only models with significant lambda-p values are shown. Model numbers correspond to those models listed in Tables 5 and 8. Models 13 and 15 which included a total cover variable were not tested because cover variables were not collected in the Greybull River drainage.

Model number	Overall correct classification (%)	Proportion of absent sites correctly classified	Proportion of present sites correctly classified
1	80.5	19/38	84/90
2	80.5	19/38	84/90
3	not tested		
4	79	18/38	83/90
5	not tested		
6	86	17/20	20/23
7	53	0/20	23/23
8	53	0/20	23/23
9	86	20/20	17/23
10	86	20/20	17/23
11	60	4/20	22/23
12	86	19/20	18/23
13	86	20/20	17/23
14	86	16/20	21/23
15	86	20/20	17/23
16	78	14/20	19/23
17	53	0/20	23/23
18	67	8/20	21/23
19	76	13/20	20/23
20	76	13/20	20/23
21	83	16/20	20/23

Table 7. Differences between watershed variables where trout (all species pooled) are present and absent in the North and South Fork Shoshone River drainages.

Watershed variable	Trout absent			Trout present			*P*
	Mean	SD	N	Mean	SD	N	
Basin area (km2)	13.1	11.8	40	90.1	299.4	72	0.033
Aspect (degrees)	172.5	105.7	40	200.9	120.2	70	0.201
Hi elevation (m)	3105.9	439.5	40	3402.8	273.5	70	0.000
Mid hi elevation (m)	2652.5	337.7	40	2829.1	221.3	70	0.004
Mid low elevation (m)	1965.9	252.9	40	2070.4	218.5	70	0.032
Low elevation (m)	1918.4	229.9	40	2011.8	213.9	70	0.039
Mid range basin elevation (m)	2512.1	303.0	40	2707.3	195.3	70	0.001
Basin relief (m)	1187.5	352.9	40	1391.0	297.8	70	0.003
Relief ratio (m/km)	191.1	84.2	40	136.9	51.9	70	0.001
Basin slope (m/m)	13.9	7.3	40	9.4	4.2	70	0.001
Perennial stream length (km)	4.7	4.0	40	11.4	5.6	70	0.000
Total stream length (km)	7.10	3.2	40	11.80	5.2	70	0.000
Link number	10.50	9.6	40	36.00	45.7	70	0.000

TABLE 8. Logistic regression analysis using watershed variables for trout (all species pooled) presence and absence in the North and South Fork Shoshone River drainages. A series of models and their parameters along with the classification efficiency are presented using watershed variables shown to be significant univariate predictors of trout presence (Table 7). Initial log-likelihood values for sample sizes 112 and 110 are 146.0 and 144.2, respectively. Unreported *P*-values for Lambda-p are > 0.05.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lamda-p	*P*
Model6	112		0.000	117.6	28.4	60/72/79	0.19	0.225	0.049
Basin Area		0.071 (0.02)	0.001						
Constant		-0.866 (0.39)	0.026						
Model7	110		0.000	127.4	16.8	38/75/96	0.12	0.300	0.017
Hi Elevation		0.002 (0.00)	0.000						
Constant		-7.170 (2.11)	0.001						
Model8	110		0.000	129.1	15.1	40/73/91	0.10	0.250	0.035
Mid Range Basin Elevation		0.003 (.00)	0.000						
Constant		-7.774 (2.33)	0.001						
Model9	110		0.000	98.2	46.1	68/78/84	0.32	0.400	0.004
Perennial stream length		0.388 (0.08)	0.000						
Constant		-2.332 (0.62)	0.000						
Model 10	110		0.000	98.0	46.1	67/79/86	0.32	0.425	0.003
Basin area		0.005 (0.02)	0.733						
Perennial stream length		0.374 (0.09)	0.000						
Constant		-2.329 (0.62)	0.000						

TABLE 8. Continued.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lamda-p	*P*
Model 11	110		0.000	110.3	33.9	55/73/83	0.23	0.250	0.035
Basin area		0.051 (0.02)	0.010						
Hi elevation		0.002 (0.00)	0.012						
Constant		-6.753 (2.42)	0.005						
Model 12	110		0.000	95.8	48.4	60/81/93	0.34	0.475	0.000
Perennial stream length		0.342 (0.09)	0.000						
Hi elevation		0.001 (.00)	0.133						
Constant		-6.084 (2.64)	0.021						
Model 13	110		0.000	97.9	46.3	65/77/84	0.32	0.375	0.005
Perennial stream length		0.370 (0.09)	0.000						
Basin slope		-2.280 (5.07)	0.639						
Constant		-1.910 (1.07)	0.073						
Model 14	110		0.000	116.4	27.9	58/73/81	0.19	0.250	0.035
Basin area		0.059 (0.02)	0.009						
Basin slope		-5.170 (4.73)	0.275						
Constant		-0.029 (0.84)	0.972						
Model 15	110		0.000	97.9	46.32	68/78/84	0.32	0.400	0.004
Perennial stream length		0.370 (0.09)	0.000						
Link		0.009 (0.02)	0.616						
Constant		-2.332 (0.62)	0.000						

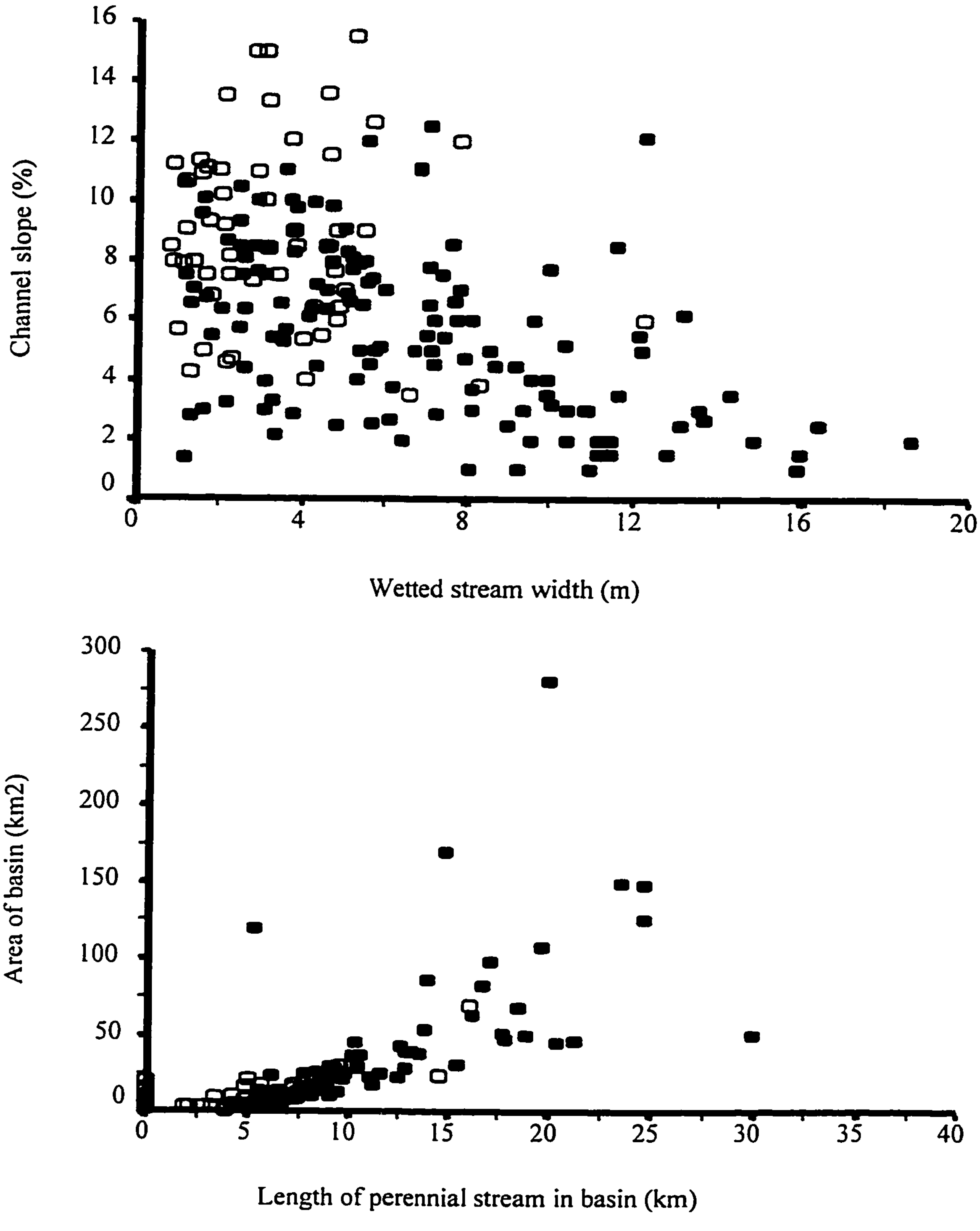
TABLE 8. Continued.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lamda-p	*P*
Model 16	110		0.000	93.8	50.4	60/78/89	0.35	0.400	0.004
Perennial stream length		0.349 (0.08)	0.000						
Mid range basin elevation		0.002 (0.00)	0.043						
Constant		-7.994 (2.96)	0.007						
Model 17	110		0.000	111.3	32.9	60/79/90	0.23	0.425	0.003
Mid range basin elevation		0.003 (0.00)	0.006						
Link		0.055 (0.02)	0.009						
Constant		-7.473 (2.55)	0.003						
Model 18	110		0.000	92.8	51.8	60/79/90	0.36	0.425	0.003
Perennial stream length		0.379 (0.09)	0.000						
Mid range basin elevation		0.005 (0.00)	0.092						
Hi elevation		-0.002 (0.00)	0.333						
Constant		-7.974 (2.92)	0.006						
Model 19	110		0.000	93.7	50.5	60/77/87	0.35	0.375	0.005
Perennial stream length		0.338 (0.09)	0.000						
Mid range basin elevation		0.002 (0.00)	0.048						
Link		0.004 (0.02)	0.782						
Constant		-7.911 (2.98)	0.008						
Model 20	110		0.000	92.9	51.34	63/79/89	0.36	0.425	0.003
Perennial stream length		0.301 (0.09)	0.001						
Mid range basin elevation		0.002 (0.00)	0.029						
Basin slope		-5.271 (5.65)	0.351						
Constant		-7.539 (2.90)	0.009						

TABLE 8. Continued.

Model and Parameter	N	Value (SE)	*P*	-2 Log - likelihood	Model Chi-square	Classification % (absent/overall/present)	R^2	Lamda-p	*P*
Model 21	110		0.000	94.8	49.4	63/79/89	0.34	0.425	0.003
Perennial stream length		0.290 (0.10)	0.003						
Basin slope		-5.441 (5.63)	0.333						
Hi elevation		0.002 (0.00)	0.081						
Constant		-5.838 (2.58)	0.024						

FIGURE 2. Locations where trout were present (solid) and absent (empty) based on site-scale (top panel) and watershed-scale (bottom panel) variables.



Discussion

Habitat Segregation

Possible persistence of some YSC populations in high-elevation sites has intrigued researchers and focused conservation efforts in these areas. Cutthroat trout concede to competition in low-gradient streams at low elevations, but several works have alluded to a possible physiological or biological superiority of cutthroat trout over other trout species at high-elevation sites (Behnke and Zarn 1976; Fausch 1989; Young 1995). However, no quantitative research supported this hypothsis.

I found that YSC were not utilizing a unique component of high-elevation habitat. Habitat did not differ among sites where genetically pure YSC, rainbow trout, or rainbow trout x cutthroat trout hybrids were present. The small number of sites where YSC were found and the presence of genetically pure rainbow trout and hybrid rainbow x cutthroat trout at the highest elevation sites suggests that pure rainbow trout can invade high-elevation headwater habitats and displace YSC through hybridization. Other studies have suggested that rainbow trout and cutthroat trout spatially segregate on habitat gradients, such as channel width, channel slope, and elevation (Hartman and Gill 1968; Vincent and Miller 1969; Fausch 1989; Bozek and Hubert 1992), but the ubiquitous distribution of swarms of cutthroat trout x rainbow trout hybrids in the Shoshone River drainage indicates that these two *Oncorhynchus* species do not segregate spatially.

The *Oncorhynchus* taxonomic group and brook trout showed substantial overlap in habitat suggesting habitat segregation does not occur and that YSC displacement by brook trout is possible throughout the Shoshone River watershed. In sympatry, brook trout commonly eliminate cutthroat trout in western waters (Cunjak and Green 1986; Fausch 1989; DeStatso and Rahel 1994), especially in low-gradient reaches with diverse cover.

Brown trout was the only trout species not found in high elevation sites corresponding to the temperature limitations discussed by Vincent and Miller (1969); Gard and Flittner (1974) and Fausch (1989). Cutthroat trout and cutthroat trout x rainbow trout hybrids were rarely found with brown trout suggesting an ability by brown trout to displace YSC (Fausch 1989; Wang and White 1994; Dunham et al. 1997).

While Bozek and Hubert (1992) described segregation among cutthroat trout, rainbow trout, brook trout, and brown trout, they stated that all species were capable of existing over the entire range of habitat measured. My evidence corroborates that YSC can be displaced by hybridization with rainbow trout or competition with brook trout throughout all high-elevation sites in the Shoshone River watershed where YSC may occur.

Cover for trout was limited and homogenous (predominately in the form of boulder pools) within the Shoshone River watersheds. Instream cover is commonly correlated with trout abundance (Fausch et al. 1988). Binns and Eisermann (1979) classified streams with 10 - 25% of the water surface areas having cover as having limited potential to support trout. The limited cover among streams in the Shoshone River drainage was similar among sites used by all taxonomic groups of trout. The lack of cover required all trout to use what was.

The limited amount of instream cover among streams in the Shoshone River watershed has considerable conservation implications for YSC. Because lower elevation, higher order streams within the historic YSC range have been affected by introductions of exotic trout, the best opportunity for conservation of YSC lies in preserving populations in high-elevation, relatively pristine streams. However, many of these streams are physically unable to support YSC. Additionally, because of overlap in habitat use, streams with adequate habitat to support YSC can also support rainbow trout and brook trout, thereby leading to hybridization or displacement of YSC. Hearn (1987) suggests that habitat segregation is a mechanism by which sympatric species may coexist, with habitat diversity allowing for increased species diversity. The homogenous habitat in these watersheds does not provide opportunity for YSC to segregate and persist when watersheds where they occur are invaded by exotic salmonids.

Predicting trout presence

Physical attributes such as channel slope and channel size (width and depth) were important predictors of trout presence at the site-scale. Estimated cover was also different among sites with and without trout. Channel slope and stream width are considered to be closely linked to watershed processes and have considerable impact on instream habitat (e.g., cover). Channel slope, often controlled by basin morphology and geology (Beschta and Platts 1986), is a measure of stream energy or the force of flowing water and directly influences the availability and type of habitat which ultimately determines the presence or absence of trout (Chisholm and Hubert 1986; Bozek and Hubert 1992; Rosgen 1994). Because wider streams tend to have lower channel slopes, wetted width is also indicative of stream energy and affects the availability of physical habitat (Kennedy and Strange 1982; Bisson et al. 1988; Kozel and Hubert 1989), which tends to increase in complexity and support a more diverse ichthyofauna as streams widen in a downstream direction (Gorman and Karr 1978; Schlosser 1982). Because channel slope and channel width were correlated to one another, it is difficult to assess their independent affects on trout distributions.

At the watershed scale, the entire array of variables had a significant influence on trout presence. The slate of significant relationships indicated a strong linkage between watershed-scale measures and trout distributions. Lanka et al. (1987) showed that measures of basin elevation, basin area, channel slope, and drainage density were good predictors of trout abundance. Likewise, Rieman and McIntyre (1995) predicted bull trout *Salvelinus confluentus* distributions based on patch size (i.e., basin area). Similarily, Nelson et al. (1992) suggested that trout distributions were correlated to landtype association which differed in elevation and geology.

Trout presence was predictable on both spatial scales; however, different processes seemed to control trout presence at each scale. Combinations of the channel slope, wetted width, and cover variables were most significant when predicting trout present at the site scale, while the length of perennial stream in the basin consistently appeared in watershed-scale models which provided good classification efficiency. Multivariate watershed models were only slightly better than a univariate model containing perennial stream length, indicating that the majority of explainable variation at the watershed-scale was accounted for by perennial stream length. The length of perennial stream is not the single factor influencing trout distributions (Lanka et al. 1987; Nelson et al. 1992; Rich 1996), but it appears to play a major role and can be conceptually linked to both watershed- and site-scale attributes. Larger basin areas have a higher likelihood of supporting trout populations and longer, wider perennial conduits. High-elevation drainages with consistent water sources (glacial- and snow-melt) will also support an increased length of perennial stream. Longer water courses will reduce basin, and corresponding site-scale slopes, and tend to have a larger link number indicating a larger drainage network. A greater number of links and increased perennial flow suggests the presence of many low-order feeder streams and larger mainstem areas important as spawning and rearing habitat (Heggenes et al. 1991), as well as refugia during catostrophic events (Lamberti et al. 1991), increasing probability of trout persistence. Thus, while the amount of perennial stream and its relationship to other watershed attributes appears to dictate the ability of trout to persistent in a basin, other characteristics (channel slope, wetted width, and cover) define trout presence at each site within a basin.

The transferability or generality of models is an important consideration for their utility in conservation planning (Bowlby and Roff 1986; Fausch et al. 1988). Tests on an independent, but geologically similar, volcanically derived watershed (Greybull River), indicated that my models can be judiciously applied to similar areas. All site-scale models, and most watershed-scale models, correctly classified the majority of test sites. While still providing adequate levels of classification, watershed-scale models which included elevational variables classified fewer test sites correctly due to the significantly higher basin elevations in the Greybull River drainage. The respectable, but poorer model performance resulting from the discrepancy in elevations between the watersheds for which the models were developed and tested, illustrates the limitations of these models and the necessity for careful application. As Fausch et al. (1988) and Nelson et al. (1992) caution, habitat features affecting trout may vary across broad land classes and models may perform poorly if applied in areas structurally different from where they were developed. Small differences among watersheds may impact model performance and without additional testing and ground-truthing, application of these models to areas other than volcanically derived watersheds within YSC native range is not advised.

Models at both scales classify sites where trout were present with more efficiency than sites where they were absent. By misclassifying absent sites, the models actually error conservatively, occasionally directing survey efforts to basins with a low probability of supporting trout -- a more cautious and appropriate approach than the alternative when considering sensitive species.

Conservation of YSC is predicated on successfully understanding factors governing their persistence and identifying the distributional extent of extant populations. To this end, site-scale models are valuable in identifying variables critical to survival of YSC on a localized scale. Watershed-scale models performed as well or better than the site-scale models in predicting trout distributions, evidence that watershed-scale variables can be used for identifying basins which potentially contain trout without extensive field surveys. Unsurveyed basins where YSC may persist can be identified using my models, as well as potential reintroduction and reclamation sites. Knowledge gained from these models can be merged with analytical tools, such as geographic information systems, allowing managers to determine potential trout distributions over large spatial scales. Utilizing these diagnostic tools and understanding the limitations imposed by non-native trout may will allow managers to more efficiently attain conservation goals developed to perpetuate YSC.

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CHAPTER IV

Status of Yellowstone Cutthroat Trout and Potential for Their Conservation in the Absaroka Mountains of Northwestern Wyoming

Abstract - Introductions of non-native salmonids and habitat alterations over the past half-century have resulted in reductions in the distribution of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*, YSC). I assessed the current status of YSC in three major watersheds of northwestern Wyoming (Greybull River, North and South Forks of the Shoshone River). Only 26% of the 104 streams containing trout still support genetically pure YSC. Extant YSC occupied 245 of 822 km of the perennial streams which contained trout in the Greybull and Shoshone River watersheds, suggesting a 70% loss in native trout from their historic distribution within these watersheds. The four remaining populations in these watersheds have effective population sizes greater than 500 individuals and appear genetically and demographically viable. However, due to potential hybridization and competition by non-native trout, the remaining populations may not be considered secure. Genetically pure rainbow trout (*O. mykiss*) were found at high-elevation sites throughout the study area, indicating that cutthroat trout are not biologically isolated in headwater sites.

Prior to settlement by Europeans, the Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (YSC) occupied the largest geographic range of the 14 recognized cutthroat trout subspecies (Varley and Gresswell 1988; Behnke 1992) with the possible exception of coastal cutthroat trout *O. c. clarki*. The YSC was indigenous to a large portion of the upper Yellowstone and Snake river drainages of Wyoming, Idaho, Nevada, and Utah, but similar to other stocks of cutthroat trout, it has endured population extinction and fragmentation throughout a large portion of its historic range due to anthropogenic perturbations (Gresswell 1995). Varley and Gresswell (1988) estimated 10% of fluvial and 85% (the majority in Yellowstone National Park; Gresswell et al. 1994) of lacustrine historic habitats still contain the subspecies. A recent conservation assessment suggests that viable populations remain in 43% of historic habitat in Idaho, 32% in Montana, and 42% in Wyoming (May 1996). However in Idaho and Wyoming, much of this assessment was based on unsubstantiated information, not scientifically conducted population surveys and genetic analysis. Regardless of potential error in assessments, the evidence of a decline in occurrence and range of endemic cutthroat trout subspecies and subsequent extinction concerns have galvanized discussion regarding appropriate conservation plans and protocols by management agencies. Maintenance and restoration of genetically pure populations of native fish are objectives of state, provincial, and federal agencies (Leary et al. 1993). The American Fisheries Society has designated the YSC as *a species of special concern - class A* (Johnson 1987; also recognized by Montana and Idaho), while the U. S. Forest Service (USFS, Northern and Rocky Mountain Regions) classifies the subspecies as sensitive (Gresswell 1995). Additionally, conservation groups have petitioned the U. S. Fish and Wildlife Service to consider YSC for listing under the Endangered Species Act.

Northwestern Wyoming encompasses a large portion (> 65%) of historic YSC habitat, but little current information verifying the distribution, genetic status, and viability of extant populations was available. Identifying locations of genetically pure YSC and factors affecting their distribution is critical to focus management efforts, understand population fragmentation and viability, preserve genetic variability, and comprehend YSC ecology and habitat requirements (Allendorf and Leary 1988; Krueger and May 1991; Leary et al. 1993). Similar to other native salmonids, the primary agent in the decline of YSC appears to be the introduction of hybridizing and competing non-native salmonids (Leary et al. 1987; Allendorf and Leary 1988; Ferguson 1990; Krueger and May 1991; Rieman and McIntyre 1995). Rainbow trout (*O. mykiss*) were originally introduced to enhance sport fishing, but rainbow trout and cutthroat trout lack reproductive isolating mechanisms and generally, with some exceptions, proliferate and produce hybrids swarms when in sympatry. Brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta*, also introduced as sport fish, have replaced YSC through competitive interactions (Griffith 1972: Fausch 1988; Wang and White 1994). Habitat disturbance (irrigation, logging, mining; Varley and Gresswell 1988; Young 1995) also has displaced YSC and exacerbated competitive interactions by producing conditions that favor introduced species (Benke and Zarn 1976).

Most remaining YSC populations are constricted to headwater environments where public ownership and relative inaccessibility have moderated detrimental anthropogenic impacts, allowing small, highly fragmented enclaves to persist. The stochastic, naturally impoverished nature of the habitat in these systems, coupled with small population sizes and isolation, increases the probability of local population extinction due to environmental or genetic instability (Allendorf and Leary 1988; Ferguson 1990; Rieman and McIntyre 1993; Rieman et al. 1993; Guffey et al. 1998). The persistence and longevity of small, isolated populations continues to confront and frustrate conservation biologists (Harrison 1994). The probability of population extinction (or the minimum viable population size) has received considerable attention in the literature (Schaffer 1981; Boyce 1992) and is generally considered to be the result of stochastic (environmental and demographic), deterministic, or genetic processes (Harrison 1991; Rieman et al. 1993). Small, remnant populations of YSC are temporally more variable in number, have less genetic variation, and can reach fewer refuges as they become fragmented into isolated headwater reaches. As a consequence these populations have higher risks of extirpation from all three extinction processes (Gilpin and Soule 1986; Rieman and McIntyre 1993).

Metapopulation theory has become vogue in conservation biology (Hanski 1991; Rieman et al. 1993; Harrison 1994; Hanski and Gilpin 1997), and while its application to native trout population structure is unknown, the theory is useful to explain the consequences of population reduction, fragmentation, and isolation. Metapopulation dynamics is a mechanism that addresses population organization on a level recognizing connections between discrete subpopulations and the importance of differences in trout life forms and movement patterns (Rieman et al. 1993). Historically, stochastic processes were probably of minor consequence because multiple, separated component populations spread the overall risk of extinction due to an environmental event, while occasional long distance movement by resident fish or straying by migratory fish (e.g., Young 1996; Brown and Mackay 1995; Jakober et al 1998) alleviated the genetic or demographic risks associated with isolated populations, as well as providing propagules for recolonization of extinct subpopulations. The theory suggests that naturally fragmented populations may occur with conduits between subpopulations; however, as artificial fragmentation (habitat loss, biotic introductions) disrupts the network of subpopulations and decreases overall population size, the metapopulation structure breaks down, increasing the extinction probability for each subpopulation. To debate the application of metapopulation dynamics to cutthroat trout may be a useless endeavor as connectivity between most populations has already been lost and will be difficult to restore (Young 1995). Regardless of population structure, small populations isolated in naturally poor habitat (high-elevation streams) with no opportunity for demographic or genetic rescue (Brown and Kodric-Brown 1977) by other enclaves are more likely to succumb to environmental events or reductions in genetic variation through inbreeding and drift (Allendorf and Leary 1988; Rieman and McIntyre 1993; Young 1995).

Remaining YSC populations are primarily found in the most pristine streams remaining (e.g., headwater locations) where native fishes may have the highest resilience to invasion by non-native fishes (Baltz and Moyle 1993); however, this assertion has been largely untested for YSC (see Chapter III). According to Behnke (1992) the resilience of cutthroat trout in headwater habitats may be the result of a competitive advantage (probably due to physiological adaptations) over other fishes in these habitats. Bozek and Hubert (1992), in a study of four trout species, also showed that cutthroat trout were the most likely to be found in small streams at high elevations, suggesting an ecological advantage over other trout species. On the other hand, most direct experimental comparisons of trout interactions have found that cutthroat trout are dominated by other species when in competition for food or habitat (Griffith 1972; Fausch 1988; Wang and White 1994). Managers have assumed that cutthroat trout are biologically segregated from other species in headwater habitats because that is where most genetically pure, intact populations are found, but little research has been done regarding the ability of YSC in high-elevation streams to resist invasion by hybridizing rainbow trout or competition with brook trout. The question remains whether these exotic species are physiologically excluded in perpetuity from small, high-elevation, high-gradient, headwater habitats or if there has been insufficient time since their introduction for them to reach the full extent of their potential range. My results (Chapter III) demonstrate that exotic salmonids can displace YSC in high-elevation habitats, suggesting that YSC are not able to withstand exotic invasion in headwater areas.

My goal was to describe the remaining distributions of genetically pure YSC in a large portion of their historic range in the Absaroka Mountains of Wyoming and to develop understanding of the factors governing distribution and genetic structure of YSC imperative to future conservation efforts. My objectives were to: (1) ascertain the current distributions of genetically pure YSC in the Absaroka Mountains in northwestern Wyoming, (2) determine the effect of non-native salmonids on the distribution of YSC, (3) evaluate the viability of remaining YSC populations, and (4) test the assumption that cutthroat trout are biologically isolated from rainbow trout in headwater habitats. I expected YSC populations to be widespread in headwater streams, but fragmented due to biological interactions with non-native trout. I hypothesized that the remaining fragmented populations of YSC would not be genetically or demographically viable, precluding their long-term persistence. Additionally, I hypothesized that rainbow trout would be physiologically or behaviorally segregated from high-elevation streams and their genetic influence on YSC would decrease from complex hybrid swarms at low elevations to no or minimal presence high in the watersheds.

Study Area

Several watersheds in northwestern Wyoming were identified as having a high likelihood of containing genetically pure, native YSC, including the Greybull, North Fork (NF) Shoshone, and South Fork (SF) Shoshone river drainages (Ronald McKnight, WGFD, personal communication). The headwater tributaries (*N* = 188) forming these watersheds originate in the Absaroka Mountain Range and eastwardly drain that portion of the Greater Yellowstone Ecosystem immediately east and southeast of Yellowstone National Park. The NF and SF of the Shoshone River drain over 3,600 km^2 of Shoshone National Forest and private holdings before meeting at Buffalo Bill Reservoir west of Cody, Wyoming, while the Greybull River drainage encompasses 845 km^2 of headwater habitat immediately south of the Shoshone River drainage (Figures 1-4).

The Absaroka Mountains were formed during the Laramide orogeny nearly 75 million years ago. Intense volcanic activity (Wilson 1964; Breckenridge 1975) resulted in vast accumulations of volcanic rock (Nelson et al. 1980) and a steep, rugged landscape with uplifted peaks and deep valleys. Geologic history, as well as climatic and environmental weathering of the porous brecca (volcanic rock) and lava deposits, has resulted in geologic instability throughout the region (Keefer 1972; Kent 1984). Tributary systems draining these materials tend to be steep, torrential streams with unstable substrates, and large annual fluctuations in discharge (Hansen and Glover 1973; Breckenridge 1975; Kent 1984). Channel classification, according to Rosgen (1994), is predominately type A and B, typical of high-gradient, straight, entrenched mountain streams. Stream substrates and banks are largely erodible volcanic material (Hansen and Glover 1973; Zafft and Annear 1992), which, coupled with high spring flows and steep channel profiles, result in channels that shift regularly (Kent 1984), are strewn with large angular rocks, are poorly defined, and provide limited, homogenous fish habitat.

Watershed elevations range from 1,660 m at the NF - SF Shoshone River confluence to 4,010 m at headwater divides. Survey sites on tributary streams ranged from 1,767 to 3,250 m in elevation. Channel slopes range from 0.5% to 25.0% with a mean (6.6%) that is generally considered steep (Kondolf et al. 1991; Rosgen 1994). Climate is typical of high mountain environments with mean annual precipitation exceeding 50 cm, predominately in the form of snowfall - resulting in extremely high spring flows (Martner 1982). Wetted width of the three mainstem channels range from a few meters near headwater sources to more than 30 m at the downstream boundaries of the study area and, although streamflow is variable from spring to late summer, tributary streams ranged from 1 - 18 m in width (mean 5 m).

The earliest documented introductions of non-native salmonids in the study area occurred in 1915 (Greybull River; 1919 in the Shoshone River drainage; WGFD records, Wyoming State Archives). Brook trout, brown trout, and rainbow trout were all commonly introduced until the 1970's. From 1972-75, non-indigenous finespotted cutthroat trout from the Snake River drainage were introduced into all three watersheds. More recently, as native fish conservation has come to the forefront and the problems of hybridization and competition have become apparent, only YSC have been stocked sparingly. However, resident populations of brown trout, rainbow trout, and cutthroat trout x rainbow trout hybrids dominate the mainstem salmonid community in the North and South Fork's of the Shoshone River. Only the Greybull River still supports mainstem fisheries composed exclusively of cutthroat trout; however, the consequences and genetic effect of stocked cutthroat trout has yet to be determined. Other fish common to the drainages include: mountain whitefish *Prosopium williamsoni*, mountain sucker *Catostomus platyrhychus*, longnose sucker *Catostomus catostomus*, and longnose dace *Rhinichthys cataractae*. The WGFD currently manages all three watersheds as native sport fisheries with focus on conserving YSC (Yekel 1980; Steve Yekel, WGFD, personal communication).

Anthropogenic influences are wide ranging throughout the study area. The Greybull and upper SF Shoshone (upstream of Deer Creek) river drainages are accessible only by hiking or horseback and are considered relatively pristine. The lower SF Shoshone tributaries and mainstem are heavily impacted by roads, agriculture, and irrigation withdrawals. The lower NF Shoshone is paralleled by a highway accessing Yellowstone National Park from Cody, Wyoming, and is subjected to erosion and sediment impacts. Fishing pressure is considered low throughout the study area, except along the Cody to Yellowstone highway. Even with substantial mainstem impacts in the Shoshone River watershed, most headwater tributaries are relatively inaccessible to humans and the habitat can be considered unimpacted.

FIGURE 1. Major drainage basins of Wyoming with the primary study watersheds indicated by the ellipses. Drainages are abbreviated as GRB = Greybull River, and SHS = the North and South Fork's of the Shoshone River. The Shoshone National Forest is indicated by gray shade.

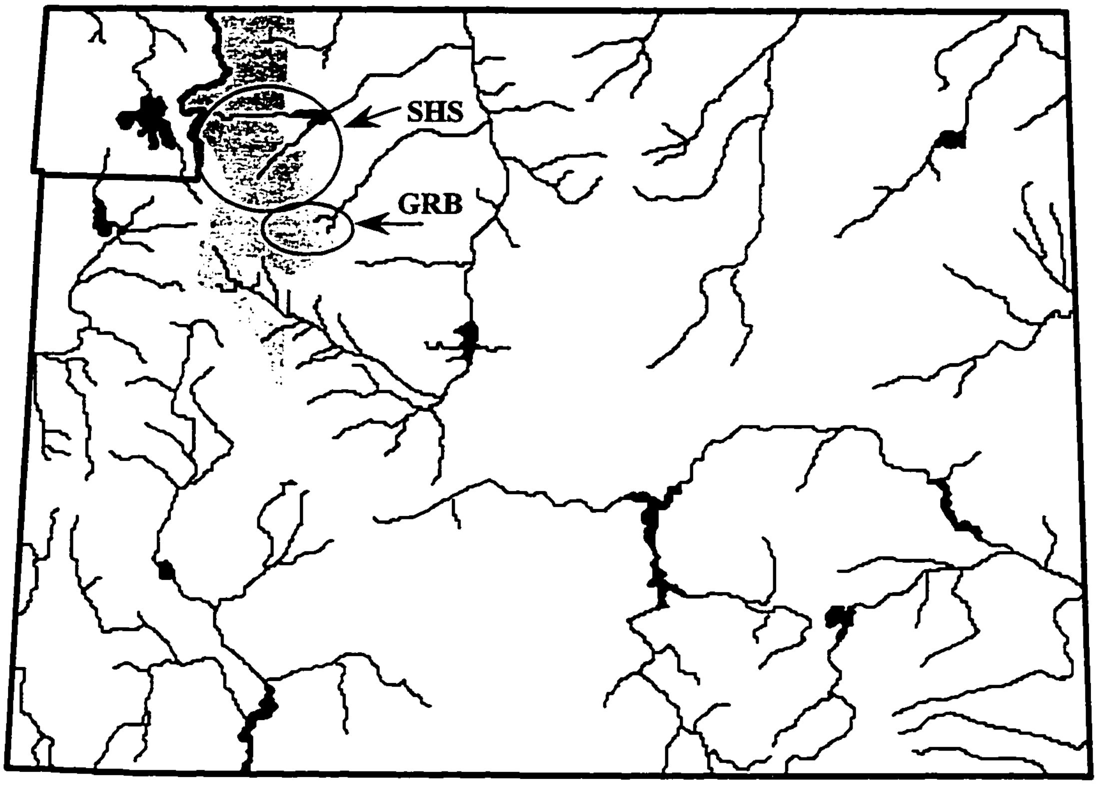


FIGURE 2. Perennial streams in the Greybull River drainage with overall trout distribution indicated in gray shade. Number streams correspond to those listed in Tables 5 and 8.

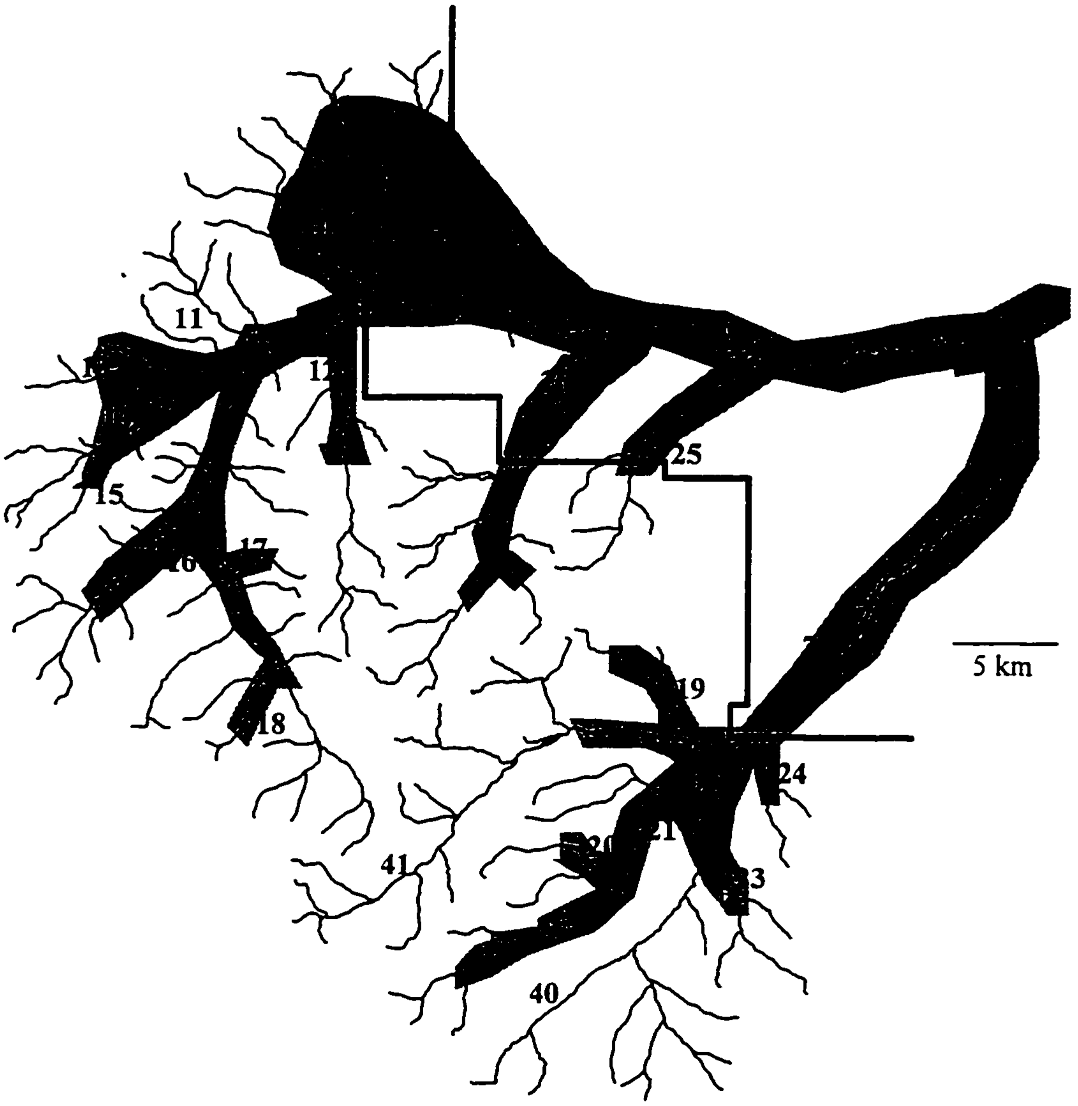


FIGURE 3. Perennial streams in the North Fork Shoshone River drainage with trout distributions indicated in gray shade. Numbered streams correspond to those sites listed in Tables 5 and 8.

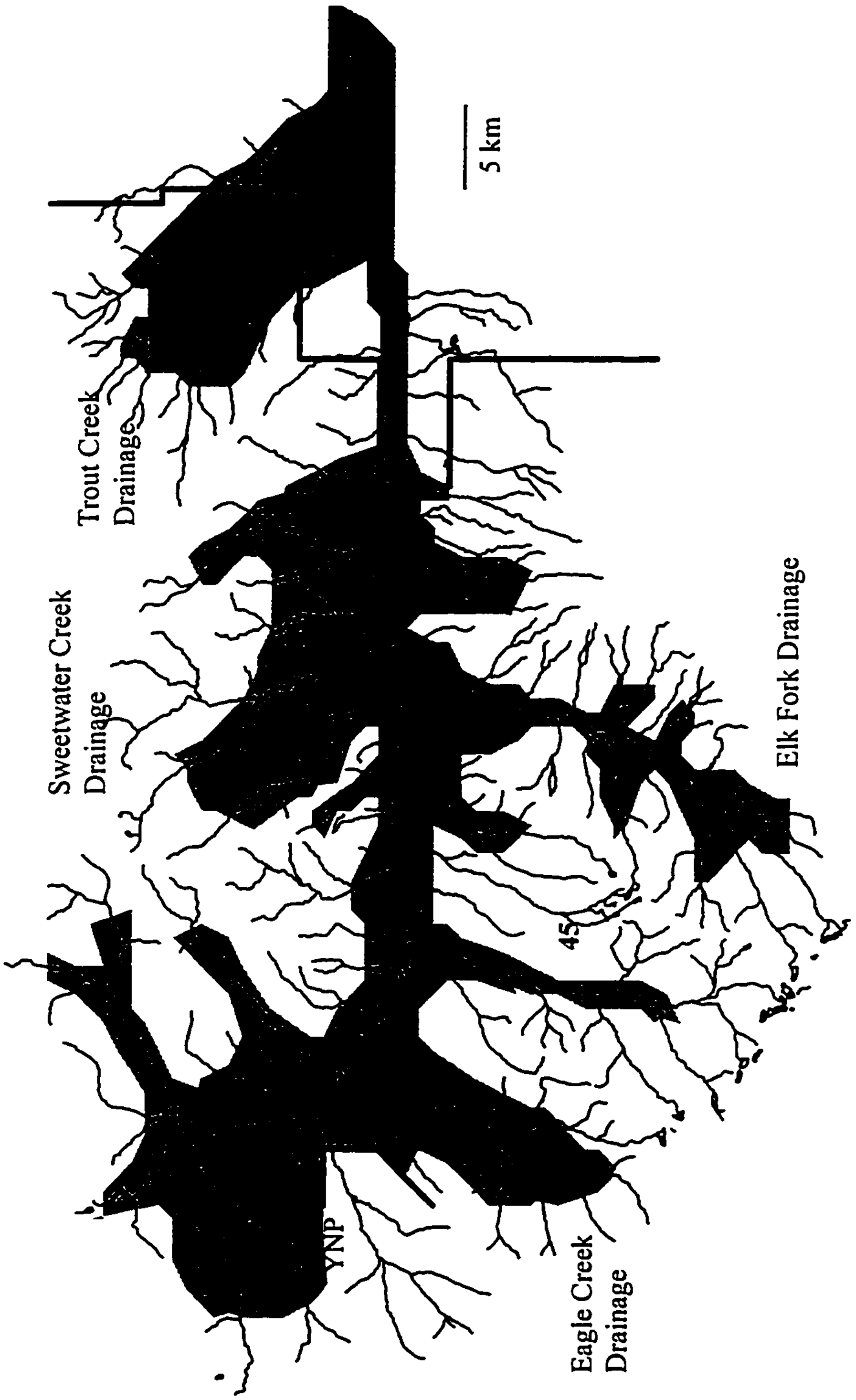
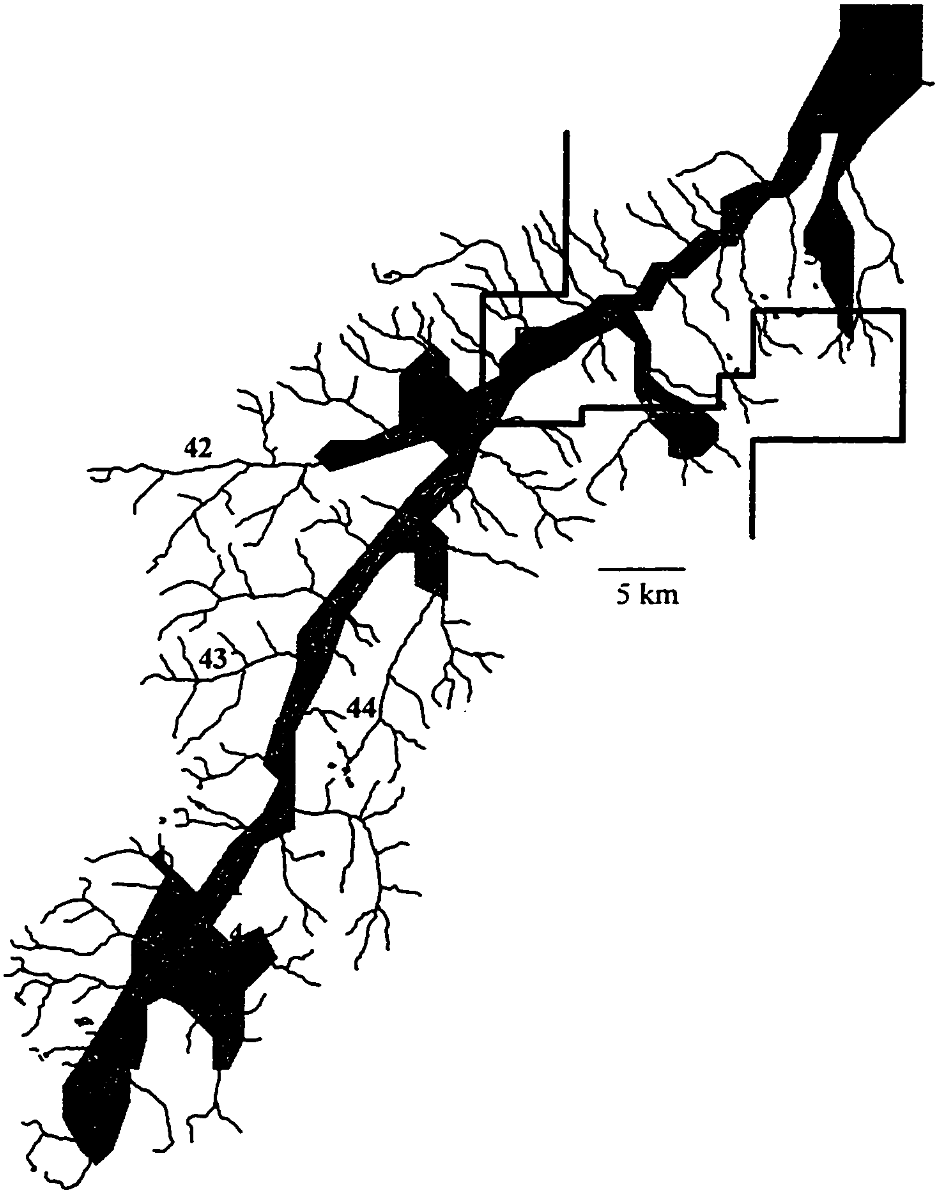


FIGURE 4. Perennial streams in the South Fork Shoshone River drainage with trout distributions indicated by gray shade. Numbered streams correspond to those sites listed in Tables 5 and 8.



Methods

Perennial tributary streams in the three intensively sampled watersheds (Greybull, NF Shoshone, and SF Shoshone) were sampled during the low flow months (typically July - September) from 1994 to 1997 with Smith-Root model 12-B electroshockers. All streams designated as perennial on U. S. Geological Survey (USGS) 7.5-minute topographic maps and containing flow at the time of sampling were sampled at least once irregardless of habitat condition or historical information regarding trout distributions. An initial one-pass electrofishing run was performed along a 100-m stream reach at each tributary outlet and was repeated upstream approximately every 1.5 km, or where access allowed, until no fish were captured or visually observed in two consecutive reaches. Additional habitat units were selectively sampled after each barren 100-m reach to verify fish absence.

Locations (latitude, longitude) and elevations (m) of sampling sites were identified with global positioning units and USGS topographic maps. Wetted stream width was measured at each site with a tape perpendicular to stream flow at five transects equally spaced through the 100-m reach. Stream lengths (km) were measured with an electronic map wheel from 1:24,000 scale USGS topographic maps. Cutthroat trout distributions (kilometers of stream occupied) in a given tributary were calculated assuming the subspecies occupied one-half the distance between the last site the species was sampled and the next upstream site. For example if cutthroat trout were sampled at site A and not found 1.5 km upstream at site B, the stream length occupied for cutthroat trout would include an extra 0.75-km, or one-half the distance between sites A and B. Species sampled at a single site along the stream profile were assumed to occupy all other sites downstream to the tributary confluence.

After electrofishing a reach, captured fish were identified, enumerated, measured (total length, TL, cm) and returned to the study reach. Fish in the *Oncorhynchus* genus were classified as rainbow trout, cutthroat trout, or rainbow trout x cutthroat trout hybrids based on morphological characteristics as outlined in Chapter I. Individuals were considered genetically pure rainbow trout when pelvic fin margins were white, numerous spots appeared on the head, and the absence of the characteristic red throat "slashes" of cutthroat trout. Yellowstone cutthroat trout were indicated by the red throat "slashes," lack of white fin margins, and the presence of fewer, larger spots concentrated posteriorly (Behnke 1992). Any fish with a combination of these character sets was classified as rainbow trout x cutthroat trout hybrid. If typical rainbow trout specimens were sampled at any given site, hybridization of cutthroat trout was assumed even if obvious hybrids were not collected. When only fish morphologically typical of YSC were collected at a site, or identification of possible hybridization was questionable, tissue samples were taken for electrophoretic verification of genetic purity. Eye, muscle, and liver tissue were removed from 15-20 specimens, individually coded to identify collection location, and frozen within 1 hr in liquid nitrogen. Electrophoretic analysis was performed by the Wild Trout and Salmon Genetics Laboratory (WTSGL) at the University of Montana, Missoula. Introgression was indicated by the presence of alleles specific to rainbow trout at diagnostic loci (Table 1).

For purposes of viability analysis, I used the concept of metapopulations, defined by Hanski and Gilpin (1997) as spatially structured breeding populations among which migration has some influence on local dynamics, as a biological basis for defining YSC populations. Individual streams may contain multiple groups of resident fish and migratory fish or only partially encompass a single population; thus each stream provides a unique component and all individual streams interact demographically and genetically to form the population. Events which locally decimate part of a YSC population can be offset by rescue individuals from other tributaries. Assessing population viability on this larger scale across groups of connected streams provides a biologically realistic picture of current YSC status. Populations of *Oncorhynchus* were not considered in viability analysis unless they contained only YSC. If rainbow trout were found at the same location as genetically pure YSC, the *Oncorhynchus* population was not considered to be a viable YSC population.

Population size of all genetically pure populations was calculated according to Chapter I. For each 100-m sample, the one-pass electrofishing abundance was converted to an overall population estimate using the equation TA = -1.863 + 1.181 ONE + 0.797 W; where TA is the estimate of total abundance in the 100-m reach, ONE is the number of fish captured with one electrofishing pass, and W is the wetted stream width. For each tributary corrected abundance estimates for each 100-m reach were averaged across all sample reaches containing pure YSC and multiplied by the total occupied stream length to provide an estimate of total population size.

The total in each tributary was summed for the contiguous streams containing genetically pure YSC to estimate population size in the entire group of connected streams. The total estimated population size was converted to an effective population size (EPS) by multiplying the estimate with the proportion of individuals greater than 200 mm in length (TL). Although most fluvial YSC spawners exceed 275 mm (Thurow et al 1988), reproduction is common in fish between 200 and 275 mm (and was observed in fish down to 180 mm); thus all fish greater than 200 mm were considered as part of the effective breeding population. Length structure of *Oncorhynchus* trout within each drainage was pooled across tributaries to give an overall proportion of spawning fish by drainage (Greybull = 0.527, NF Shoshone = 0.223, SF Shoshone = 0.568).

Viability was assessed by comparing EPS's to minimum values necessary to prevent population extinction due to demographic stochasticity or loss of genetic variation presented in the literature. Effective population sizes were defined as the number of sexually mature, spawning adults in the population and compared to minimum values suggested to prevent demographic stochasticity (20 to 30, Rieman and McIntyre 1993, Young 1995), excessive inbreeding (50), and maintain long-term genetic variation (500, 50/500 rule, Soule 1987). Conversion of total population size to effective population size, or the level of genetic variability in the breeding population, is difficult, but estimates of EFP's for populations have ranged from 10 to 75% of the total population size (Reiman and McIntyre 1993). I feel my method of approximating EFP's for YSC is adequate for the intended purpose.

For purposes of conservation priority, I evaluated each remaining YSC population in terms of threats to their continued existence: population size (genetic and demographic considerations), isolation, and the presence of non-native salmonids in the watershed. Risks were assigned to each population to indicate the extinction vulnerability or, conversely, conservation priority of each population. Risk levels were defined as high, moderate, low, or non-existent (see Table 2) and assigned based on what I felt were the most prodigious threats to YSC in the study area according to the literature and my experience. Remaining YSC populations were not considered secure, or having a high probability of long-term persistence, unless risks were either low or non-existence for all categories in Table 2.

Populations with fewer than 20 individuals were considered at high risk (eminently threatened) from demographic and genetic extinction because the population was below excepted minimums for these categories. Demographic and genetic risks decreased as EPS increased (four levels, Table 2) and population size exceeded the levels required to sustain a population. Demographic and short-term genetic risks were considered low (a potential risk, but of limited concern) when EPS exceeded 50. Maintenance of long-term genetic variability was no longer a risk when estimated population size surpassed 500 individuals.

The threat of brook trout was evaluated at two levels: present in the watershed and present in the population. Because of their ability to outcompete YSC, brook trout within the geographical limits of a current YSC population were considered a high risk to all but the largest populations. Large populations have a higher likelihood of sustaining themselves if brook trout are present; however, brook trout are still a moderate risk (threatening long-term survival) and any adverse effects (e.g., a decrease in YSC population size) would shift the risk rating from moderate to high. The presence of brook trout in the watershed outside the geographical extent of the YSC population is less threatening to larger populations which have the potential to withstand or overwhelm a brook trout invasion, but is still a high risk for small populations. If brook trout did invade a small YSC population, their prolific nature may overwhelm the YSC in only a few generations.

The presence of rainbow trout was considered an eminent threat to all population sizes because of the detrimental and additive effects of both hybridizing and competitive interactions with YSC.

Because YSC populations which contained rainbow trout in them were not considered viable, risks were only assigned if rainbow trout were present in the watershed, not in the population.

Isolation was considered highly risky for population survival unless population size was large. Isolation not only amplifies demographic and genetic risks, but also exposes a population to environmental catastrophes with no chance of recolonization. Larger populations, with more individuals and habitat, have a higher probability of surviving environmental catastrophe and are less at risk from isolation. Additionally, isolation of large populations, which are less susceptible to genetic and demographic risks, can protect the population from invasions of exotic salmonids. Thus, large populations which are isolated from exotic immigration receive lower risk rankings than those open to rainbow trout colonization.

Streams with large drops in elevation from headwater to confluence were selected to test the hypothesis of biological isolation. If cutthroat trout can isolate themselves from rainbow trout based on biological differences, I assumed that a large difference in elevation from headwater to outlet, encompassing a wide variation in habitats (e.g. channel slope and water temperature), would provide the best opportunity for cutthroat trout to find physiologically more suitable habitats (i.e. high-elevation sites) and exclude rainbow trout. Elk Fork Creek (elevational range 1806 - 2268 m over 19.9 km), Fishhawk Creek (1937 - 3451 m over 23.6 km), Ishawooa Creek (1843 - 3613 m over 14.9 km), and the mainstem SF Shoshone (1660 - 3466 m over 105 km) were chosen because of their persistent *Oncorhynchus* populations and considerable elevational ranges. Tissue samples were collected from 15-20 *Oncorhynchus* specimens at three points along each stream profile, the tributary outlet or confluence with Buffalo Bill reservoir for the mainstem SF Shoshone (low-elevation), the highest elevation at which fish were collected (high-elevation), and mid-way between the previous two (mid-elevation), to assess the level of rainbow trout introgression. Samples were electrophoretically analyzed by the WTSGL. The proportion of rainbow trout alleles at the analyzed diagnostic loci was used to assess changes in the level of introgression in each sample along the elevational profile.

TABLE 1. Diagnostic loci which separate Yellowstone cutthroat trout and rainbow trout.

Locus	Yellowstone Cutthroat Trout Alleles	Rainbow Trout Alleles
sAAT-1*	165	100, 0
CK-A2*	84	100, 76
CK-C1*	38	100, 150, 38
mIDHP-1*	-75	100
sIDHP-1*	71	100, 114, 71, 40
sMEP-1*	90, 100	100
sMEP-2*	100	100, 75
PEPA-1*	101	100, 115
PEPB*	135	100
PGM-1*	*null*	100, *null*

Results

I sampled 414 sites on 172 streams (including mainstem rivers) throughout the Shoshone and Greybull river drainages. This survey, along with recent (1990 Trout Creek drainage survey, WGFD records) data on 10 additional tributaries, provides information regarding YSC distributions for 182 of 188 (97%) streams in the study area. Native (YSC) or introduced (rainbow, brown, brook) trout were found in 104 (57%) streams, 51 containing only *Oncorhynchus* trout (see Table 3 for a further breakdown of distribution). Genetically pure YSC were found in 27 streams (25 tributaries and the SF Shoshone and Greybull River mainstems), 21 in allopatry.

The 22 streams containing trout in the Greybull River watershed all contained genetically pure cutthroat trout with no indication of rainbow trout, either visually or electrophoretically, in the samples. Thus, 81% of all streams containing genetically pure cutthroat trout were found in the drainage. In the NF Shoshone watershed all the 58 stream samples of *Oncorhynchus* showed hybridization with rainbow trout and most were dominated by pure rainbow trout and rainbow trout x cutthroat trout hybrid swarms. Individual, genetically pure YSC were sampled, but always within a sample that contained hybridized fish. The remaining five streams containing genetically pure YSC were found among the 24 tributaries containing trout in the SF Shoshone River drainage. Brook trout were found in all three drainages, but only rarely in the Greybull River drainage (2 of 22 streams), while brown trout were most common in the SF Shoshone watershed (11 of 24 streams; Table 3). If I singularly base YSC declines on population loss from individual tributaries and assume total trout distribution at the time of survey approximates historic YSC distributions, YSC have been extirpated from 74% (77 of 104 streams) of their historic range in the three drainages.

The study area included 1,735 km of perennial tributary and mainstem river, 1,585 km for which information was gathered during this survey. A 1990 survey of the Trout Creek watershed (WGFD records) provided species composition data on an additional 104 km, leaving only 46 km (or about 3%) of stream in the three watersheds unsampled (6 streams). The six streams not surveyed were in the NF

Shoshone watershed where no pure YSC were found in nearby streams and all were connected to other streams with prolific populations of rainbow trout and rainbow trout x cutthroat trout hybrids, thus I assumed YSC probably did not exist in these unsurveyed waters. Because the previous survey of the Trout Creek drainage only described species composition and not the distributional extent (km) of trout, for purposes of distributional computations, I assumed that trout occupied a percentage of the watershed similar to other watersheds of equal size (65% or 68 km). Yellowstone cutthroat trout were found in 244 km of stream habitat throughout the entire study area, none in the NF Shoshone River drainage, 53 km (27% of total occupied habitat) in the SF Shoshone River drainage, and 192 km (100%) in the Greybull River drainage (see Table 4). Considering the entire perennial drainage of the three watersheds as potential historic YSC range, the data suggest an 85% reduction from past to present day distributions of genetically pure YSC. If drainage area above barriers blocking trout movement into these potential habitats is removed, loss declines to 82%. If the historic range of YSC is based on the current distribution of all trout species, YSC have been displaced from about 70% of their historical distribution in the Shoshone and Greybull River drainages (Table 4).

The 27 tributaries and mainstem rivers containing genetically pure YSC were found in four populations. The 22 streams in the Greybull drainage were split between two populations: the Greybull River watershed (15 streams) and the Wood River watershed (7 streams). These two populations are separated by a segment of river containing large populations of exotic salmonids and impacted by irrigation withdrawals and diversion dams, likely proving impassable to cutthroat trout and effectively isolating the two populations of YSC. Four of the five SF Shoshone streams containing YSC form a headwater population, while the fifth stream is an isolated tributary, Marquette Creek (see Figures 2 and 4).

Viability analysis suggested that all four populations had breeding populations large enough to withstand demographic and genetic pressures. The Greybull River population (12,300), the Wood River population (5,300), and Marquette Creek (1,600) all had estimated EPS's exceeding a thousand individuals. The lowest EPS (500), in the upper SF Shoshone population, was severely underestimated because numbers of YSC in the mainstem river which connected the other three tributaries could not be estimated due to high water. Regardless, the SF Shoshone population also exceeds the minimum number required to preserve long-term genetic variation and adaptability (Table 5)

Because of its large population size and the presence of an irrigation diversion low on the mainstem which acts as a fish migration barrier, the Greybull River drainage population has the lowest risk ranking of the remaining populations. Although the presence of rainbow trout in the watershed is troubling, they provide a moderate risk to the YSC due to the barrier presence. Marquette Creek, also protected by irrigation diversions, is threatened by the presence of brook trout and rainbow trout, which provide low and moderate risks, repectively. The Wood River drainage and the SF Shoshone drainage populations have high risks rankings due to the presence of rainbow trout and brook trout. Because of the presence of at least a moderate risk to persistence in all four populations, none should be considered secure (Tables 2 and 6).

Pure rainbow trout and rainbow trout x cutthroat trout hybrids were found at the highest site sampled in three of the four study streams. The percentage of rainbow trout alleles at diagnostic loci in the 15-20 fish samples ranged from 15 - 85% at the low-elevation sites and 0 - 53% at high elevations (Table 7). These levels of genetic introgression indicates that, given the opportunity, rainbow trout can infiltrate high elevation YSC populations.

TABLE 2. Risk factors associated with the vulnerability of remaining Yellowstone cutthroat trout (YSC) populations. A risk rated highly is of immediate concern for population persistence, moderate risks have potential to harm a population in the short-term, while low rated risks are of little concern in the short term, but may have long-term consequences on population persistence. Risk categories include all columns to the right of population size.

EPS	Demographic Risk	Short-term Genetic Risk	Long-term Genetic Risk	Brook trout presence - watershed [a]	Brook trout presence - population [b]	Rainbow trout presence - watershed [c]	Isolation
< 20	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH
21 - 50	MODERATE	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH
51- 500	LOW	LOW	MODERATE	MODERATE	HIGH	HIGH *MODERATE when barrier present*	MODERATE effects on the population directly but protects populations from exotic species
> 500	NONE	NONE	NONE	LOW	MODERATE	HIGH *MODERATE when barrier present*	NO effects on population directly and protects population from exotic species

[a] Indicates that brook trout are present within the watershed where the YSC population is found, but not sympatrically.

[b] Indicates that brook trout are found sympatrically with YSC.

[c] Indicates that rainbow trout are present within the watershed where the YSC population is found, but not sympatrically. When rainbow trout were found in the population it was not considered pure YSC, thus there is no "within population" category.

TABLE 3. Stream occupancy of salmonids in the Greybull (GRB), North Fork Shoshone (NFS), and South Fork Shoshone (SFS) River drainages.

	GRB	NFS	SFS
Total number of perennial streams	53	82	53
Total number streams sampled	53	66	53
Stream information available [a]	53	76	53
Streams with trout	22	58	24
Streams with only brook trout	0	5	6
Streams with brown trout	0	3	11
Streams with only *Oncorhynchus* [b]	20	29	2
Streams with pure YSC	22	0	5[c]
Streams with only pure YSC	20	0	1
Streams with brook trout and *Oncorhynchus*	2	27	8
Streams with brook trout and pure YSC	2	0	4

[a] - Indicates the number of streams for which I had information available. While I may not have sampled all of these, WGFD had information available from other recent surveys.

[b] - *Oncorhynchus* indicates cutthroat trout, rainbow trout, or their hybrids

[c] - Indicates that one of the streams containing pure YSC populations was in the mainstem; pure fish were not found throughout the entire mainstem river.

TABLE 4. Distributional extent (kilometers, km) of Yellowstone cutthroat trout in the study area by drainage, Greybull (GRB), NF Shoshone (NFS), and SF Shoshone (SFS).

	GRB	NFS	SFS	Total
Total stream km	362	834	555	1751
Stream km surveyed	362	684	555	1601
Stream km have information	362	788	555	1705
Stream km occupied by trout	192	432	198	822
Stream km occupied by YSC	192	0	53	245
Stream km unoccupied	170	356	357	883
Stream km above barriers	73	95	172	340
% of watershed occupied by trout	53	55	36	48
% of watershed occupied by YSC	53	0	10	14
% of watershed occupied by YSC removing barrier effects	66	0	14	18
% of occupied km containing YSC	100	0	27	30

TABLE 5. Effective population sizes (EPS) for the four genetically pure Yellowstone cutthroat trout populations. EPS is based on the number of trout per 100-m sample reach, averaged across sampled reaches, and extrapolated to the entire occupied portion of the stream. Populations correspond to those shaded areas shown in Figures 2 - 4.

Population	Mean number of cutthroat trout per 100-m reach	Total stream km containing cutthroat trout	Estimated population size [a]	Estimated EPS [a]
Greybull River	12.9	145.0	23248	12252
Wood River	17.6	46.7	10117	5332
SF Shoshone River	9.2	11.3	942	535
Marquette Creek	18.6	15.5	2883	1638

[a] - Estimated population size and EPS can not be exactly calculated based on the mean number of cutthroat trout and the total stream km containing trout shown here because the actual values are based on weighted averages (occupied length x number per 100-m) for each tributary that was sampled. The mean number of cutthroat trout per 100-m reach is the average for all the tributaries that make up each population.

TABLE 6. Risks threatening the four genetically pure Yellowstone cutthroat trout populations based on population size, isolation, and the presence of non-native salmonids in the watershed. Any population with at least one high risk ranking (see Table 2) can be considered unsecure (long-term persistence is threatened).

	Risk Assessed						
Population	Demographic	Short - Term Genetic	Long - term genetic	Brook trout - watershed	Brook trout - population	Rainbow trout - watershed	Isolation
Greybull River	NONE	NONE	NONE	NONE	NONE	MODERATE	NONE
Wood River	NONE	NONE	NONE	LOW	MODERATE	HIGH	NONE
SF Shoshone River	NONE	NONE	NONE	LOW	MODERATE	HIGH	NONE
Marquette Creek	NONE	NONE	NONE	LOW	NONE	MODERATE	NONE

TABLE 7. Proportion of rainbow trout alleles at the examined diagnostic loci for each 15-20 fish sample at low-, mid-, and high elevation sites in each of the four streams designated to test for isolation between rainbow and cutthroat trout. Length is the distance between the low- and high-elevation samples, while superscript ^{a} denotes those sites where pure rainbow trout were captured. No sample was taken at the high-elevation site on Ishawooa Creek because a barrier was found 12 km upstream; the mid-elevation site was collected at the base of the barrier.

		Percentage rainbow trout alleles		
Stream	Length (km)	Low-elevation	Mid-elevation	High-elevation
Elk Fork (NF)	20.9	74^a	66^a	21^a
Fishhawk (NF)	21.6	85^a	60^a	53^a
Ishawooa (SF)	33.8	15^a	3	No sample
SF Shoshone	84.5	61^a	0	0

Discussion

Assuming that current distributions of indigenous and non-native trout approximate the historic extent of YSC in the Greybull, NF Shoshone, and SF Shoshone watersheds, YSC have become hybridized or been replaced by non-native salmonids in 70% of total perennial stream habitat in the three drainages. However, the definition of finespotted cutthroat trout endemic to the Snake River drainage is a major caveat in assessment of YSC status. Behnke (1992) described the finespotted cutthroat trout as an unnamed subspecies based on morphological and geographical differences between them and other cutthroat trout subspecies. Recently, finespotted cutthroat trout have been designated as a separate subspecies (*O. c. behnkeii*, Montgomery 1995); however, this author used unconventional methods relative to modern protocol. Considerable debate surrounds this designation and finespotted cutthroat are not generally recognized as a separate subspecies due to a lack of genetic and meristic differentiation and ecological separation from cutthroat trout indigenous to the Yellowstone River drainage (Loudenslager and Kitchen 1979; Loudenslager and Gall 1980; Leary et al. 1987; Behnke 1992). The finespotted cutthroat trout and large-spotted YSC occur sympatrically in the Snake River drainage; the only two cutthroat trout forms not geographically isolated. Additionally, the Snake and Yellowstone river drainages are connected via Pacific and Atlantic Creek drainages. Regardless of the lack of genetic differentiation, Behnke (1992) argues that the finespotted cutthroat trout represents a unique evolutionary unit (i.e. large river form) in the cutthroat trout lineage and should be considered a separate subspecies. With electrophoresis, Robb Leary (WTSGL, personal communication) suggests the presence of finespotted hybridization with YSC outside the Snake River drainage can be detected by the presence of one allele (AK-1*333) that is common to finespotted cutthroat trout populations, but rare in YSC outside the Snake River drainage. Because of this confusion, many biologists are hesitant to split the two trout forms into distinct subspecies; however, the classification of finespotted cutthroat trout has major implications regarding the remaining distribution of YSC.

The finespotted cutthroat trout is found throughout most of its historic range (Behnke 1992) of 2,820 km of perennial streams in the Snake River watershed (May 1996). If considered a form of YSC, the addition of the present day finespotted cutthroat trout range results in a much less exceptional decline of the YSC subspecies. Finespotted cutthroat trout are currently propagated in Wyoming and from 1972 to 1975 they were extensively stocked outside the Snake River drainage into the study watersheds. Prior unidentified cutthroat trout introductions may also have included the finespotted form (WGFD records). My genetic analysis detected the AK-1*333 allele throughout the Greybull River drainage and Marquette Creek in the SF Shoshone River drainage. If finespotted cutthroat trout are a unique subspecies, then their genetic presence (and past stocking history) eliminates the Greybull River drainage as genetically pure, native YSC, leaving only four tributaries in the SF Shoshone River drainage as pure YSC within the study area.

Individual, genetically pure YSC were found amongst rainbow trout and cutthroat trout x rainbow trout hybrids in some tributaries in the NF and SF Shoshone River drainages, however, these individuals were not considered to represent viable YSC populations. While it could be argued that inclusion of these fish in my status assessment would moderate the outcome, I consider them insignificant for two reasons: (1) most genetically pure individuals were adult fish, indicating that very few genetically pure progeny have been produced in recent years, suggesting that hybrids are overwhelming the gene pool, and (2) management of genetically pure fish as individuals, among a population of exotic trout, would have no conservation benefits. Without a definable conservation unit (e.g., population) and the necessary assumption of possible hybridization in every individual, management focused on a few, possibly genetically pure individuals within populations of hybrids and rainbow trout would be senseless.

The declines of interior cutthroat trout and other salmonids within their native ranges has fragmented populations into smaller units and focused research on the viability or long-term persistence of isolated populations (Boyce 1992; Emlen 1995; Young 1995; Guffey et al. 1998). Extinction probabilities for cutthroat trout increase as population connectivity and size decreases and stocks are exposed to deterministic, stochasitic, and genetic risks with little opportunity for "rescue" (Brown and Kodric-Brown 1977) by neighboring populations (see Harrison 1991; Rieman and McIntyre 1993 for a thorough discussion of extinction risks). Isolated populations are more likely to go extinct from environmental and demographic stochasticity than from loss of genetic variation or inbreeding (Shaffer 1987; Lande 1988; Stacey and Taper 1992; Rieman and McIntyre 1993). Thus, it is reasonable to expect conservation protocols which "minimize the effects of environmental and demographic stochasticity to minimize genetic risks at the same time (Rieman and McIntyre 1993)."

Environmental stochasticity may be the most important cause of local extinction in isolated populations because of its ability to decimate populations regardless of population size (Harrison 1991). However, while environmental events are known to disrupt or decimate aquatic communities (Siegfried and Knight 1977; Reice et al. 1990; Lamberti et al. 1991; Bozek and Young 1994), their unpredictability (timing and level of effect) precludes the establishment of minimum population levels needed to survive, as well as management prescriptions which directly alleviate, the effects of environmental stochasticity. Flood flows, severe droughts (30 - 100 year cycles in the Bighorn River basin, Martner 1982), and debris torrents (50 - 200 year intervals, Swanson et al. 1987) can locally extirpate cutthroat trout populations and due to the geologic instability and climate of the Absaroka Mountains are less than rare events in the study area. This is evidenced by cutthroat trout population loss and decline caused by the 1988 Yellowstone fires and recent, abnormally high spring flows. Despite the random nature of environmental stochasticity, managers need to consider the ramifications of catastrophic events and insure against population extinction by providing for instream refugia (Hawkins and Sedell 1990; Sedell et al. 1990) and population connectivity (Wilcox and Murphy 1985; Taylor et al. 1993) in conservation strategies. Although YSC population loss has been extensive throughout the study area, most tributaries still containing YSC (with the exception of Marquette Creek) are connected to a minimum of three other tributaries. This connection provides habitat refugia and recolonization propagules during localized events and may allow current populations to survive through all but extreme environmental events. This connected population structure is very important in overall YSC in the study area. Demographic stochasticity, or changes in population size due to random fluctuations in birth and death rates, is considered inconsequential unless populations fall below a small threshold size (Shaffer 1987; Harrison 1991; Boyce 1992. Demographic stochasticity may play a large role in driving already declining populations to extinction or preventing colonizing propagules from establishing viable populations in barren habitats (Harrison 1991). Demographic fluctuations may be an important extinction factor for small populations of YSC if random declines in productivity push populations below threshold values. Rieman and McIntyre (1993) suggest that demographic concerns are unfounded until effective populations are reduced to about 20 individuals (bull trout), whereas Young (1995) suggested 30 - 50 individuals. All four populations in the study area exceed (in EPS) these suggested size levels, indicating that demographic constraints are probably not limiting their viability or long-term persistence. Because of limited anthropogenic habitat manipulation in areas which still contain YSC, these populations have probably persisted at similar densities since prior to settlement by European man.

The minimum number of individuals needed to mitigate genetic loss is difficult to ascertain (Rieman and McIntyre 1993; Rieman et al. 1993), but Soule (1987) proposed the "50/500" rule, arguing that the public needs scientific input to guide conservation programs. Under this rule, EPS's of 50 are needed to circumvent excessive inbreeding in isolated populations, while 500 individuals can maintain genetic variation in the long-term, preserving the organism's adaptive ability. Genetically based with little definitive evidence, this "rule of thumb" approximates population sizes needed for persistence, but similar to demographic guidelines, appropriate sizes can be expected to change from species to species or among groups of species (Boyce 1992). The four remaining YSC populations in the study area far exceed the lower minimum of 50 individuals and the connectedness among individual tributaries increases the EPS's to levels above 500 in all cases, allowing genetic exchange and enhancing population survival and adaptability. The smallest and most isolated population in the study area (Marquette Creek) exceeded 500 (i.e.,1500 individuals) making it large enough to have minimal risk of genetic extinction. Similar to demographic risks, genetic processes do not appear to be an immediate conservation concern for the YSC populations remaining in the study area.

Rieman and McIntyre (1993) suggest that stochastic processes are important for salmonids and are exacerbated by habitat loss or poor habitat. They suggest that habitat loss or the incapability of habitat to support more than 2,000 effective individuals enhances the probability of extinction, not withstanding the previous guideline for demographic and genetic viability. Given the poor habitat in the study area (see Chapter III) there should be concern regarding the Marquette Creek and South Fork Shoshone River populations, especially if the tributaries require connectedness for survival (e.g., operating with a metapopulation-like structure). Yellowstone cutthroat trout have persisted for centuries in poor habitat and harsh conditions in the study area and appear resilient to demographic, genetic, and environmental influences when main channel and lower elevation refugia are available. Current populations should maintain themselves if unmolested by external factors. However, the ability of non-indigenous trout to fragment YSC populations indicates that only those watersheds not containing exotic trout (Greybull and Yellowstone River drainages) may persist.

For conservation purposes, I evaluated the risks threatening each remaining population. One ominous omission from this categorization was the frequency or probability of environmental events whose random nature makes it difficult to include in such a scoring system. Two of the four populations were vulnerable to threats from of non-native species, otherwise the populations appear viable in the short-term. However, managers should not interpret this to mean the status quo is adequate for continued YSC persistence in the study area. The value of this evaluation is not to provide an absolute measure of viability, but rather to provide direction for conservation action. I suggest management prescriptions be focused on improving the security of populations that received moderate or high rankings in any risk category.

Remaining populations of YSC and other declining subspecies of cutthroat trout are commonly found at the highest elevational extent of present day trout distributions (Hanzel 1959; Varley and Gresswell 1988; Behnke 1992;Young 1995). Empirical evidence suggests that headwater populations of cutthroat trout might enjoy a segregating mechanism which prevents invasion by other non-native salmonids present in the watershed. While several papers have discussed general patterns in trout distribution and possible exclusion mechanisms (Hearn 1987; Fausch 1988; Fausch 1989), no research identified habitat preferences or habitat conditions conducive for cutthroat trout to dominate or isolate themselves from other salmonids. My results provide no evidence of physiological or behavioral isolation of YSC in the study systems. Rainbow trout alleles were found at all sites along the elevational profile in three of the four study streams and pure rainbow trout were found at the highest elevational extent of trout in two of the four streams. The only stream that did not have rainbow trout alleles at the highest site was the SF Shoshone River which had a large, lower mainstem population of brown trout, possibly inhibiting the movement of rainbow trout to higher elevations. Additionally, all streams containing *Oncorhynchus* trout in the lower SF Shoshone and entire NF Shoshone river had morphologically identifiable rainbow trout or rainbow trout x cutthroat trout hybrids at the highest sites sampled, further evidence that rainbow trout can persist at high elevations. The proportion of rainbow trout alleles decreased from low- to high-elevation sites indicating that rainbow trout and hybrid offspring were more common in the low-gradient, wider stream reaches (as suggested by Fausch 1989; Bozek and Hubert 1992) typical of downstream sites, but their presence upstream suggests they can use smaller, steeper stream habitats throughout the study area (similar to what was shown with habitat data in Chapter III). Based on these results, perpetual isolation of genetically pure, headwater populations of YSC from rainbow trout is not assured unless YSC populations are guarded by fish migration barriers, whose isolating effects present another suite of problems to the persistence of populations.

One caveat to this conservation assessment is the assumption that YSC were always present in headwater habitats. Although metapopulation theory may or may not accurately describe past or present

YSC population structure, movement or dispersal of individuals is a proven characteristic of inland trout populations (highlighted in recent works by Brown and MacKay 1995; Young 1996; Jakober et al. 1998). Historically, poor habitat and environmental variability may have necessitated frequent, large-scale movements of YSC from headwater areas into mainstem and lower tributary refugia; thus, headwater habitats may not have supported permanent YSC populations, but rather served as sink areas for dispersal from lower elevation habitats during favorable years. This plausible scenario suggests that conservationists may be preserving YSC in areas that did not support permanent populations of YSC, but are assumed to have done so because that is where remaining populations are found. If the mainstem rivers are considered refugia (source areas) for headwater populations during vulnerable periods (e.g., flood, drought, debris flows), over 68% (164 of 242 km) of this critical habitat has been lost within the Greybull and Shoshone river watersheds.

A foremost priority in YSC conservation in the study area is the protection of the one population that is not threatened by exotic trout (Greybull River). Elimination of non-native introductions, measures to prevent them from infiltrating the current YSC population, regulations concerning take, and public awareness will help insure the preservation of these remaining population. However, YSC conservation should not only protect current populations but also use an ecosystem approach to expand present ranges in impacted drainages and insure viability by reestablishing metapopulations with refugia, movement corridors, and essential habitats.

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Chapter V

The Potential for Preserving Yellowstone Cutthroat Trout in Northwestern Wyoming by Isolating Populations in Headwater Streams

Abstract. – Isolation of native cutthroat trout *Oncorhynchus clarki* with man-made or natural barriers is a proactive approach to preserving extant populations. I evaluated the viability of isolating populations in 24 individual tributaries which compose the three Yellowstone cutthroat trout *O. c. bouvieri* populations remaining in the Bighorn River drainage in the Absaroka Mountains of northwestern Wyoming. Only two of the 24 populations in evaluated streams would have a demographic risk if isolated, but 16 would be at risk of extinction due to either short- or long-term genetic deficiencies. Nine of the populations in isolated tributaries would exceed the minimum 500 effective individuals needed to maintain long-term genetic variation. Most of the tributaries in the Wood River and South Fork Shoshone River would be threatened by the presence of brook trout. No native, wild populations of YSC were found above the 33 natural fish migration barriers identified in the study area. Logistic analysis indicated that habitat above six of the 33 barriers would have a high probability of supporting a YSC populations based on watershed and stream characteristics. Four of the possible introduction sites were in the Greybull River drainage and two were in the South Fork Shoshone River drainage. Due to the remoteness and instability of the habitat in individual tributary streams, man-made barriers would have the highest probability of preserving sustainable populations of genetically pure YSC if multiple, connected streams were protected as a unit.

Historically, Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*, YSC) were distributed throughout all but the most downstream reaches of lotic habitat in northwestern Wyoming (Behnke 1992); however, most remaining enclaves of YSC are confined to high-elevation, headwater streams. Although relatively pristine and protected from anthropogenic influences by public ownership (e.g., U.S. Forest Service), these streams are typically suboptimal habitat with substantial temporal stochasticity and individual tributary streams do not support large populations of trout. Most extant YSC populations are disjunct and fragmented as a result of interactions with non-native trout species, habitat deficiences, and man-made barriers to migration (see Chapters III and IV). As populations continue to decline into smaller and more discontinuous groups, isolation increases, and natural processes supported by movement among populations (or portions thereof), such as genetic exchange (Allendorf and Leary 1988), rescue (Brown and Kodric-Brown 1977), dispersal, resource selection (Fausch and Young 1995), and colonization (Hanski 1991; Hanski and Gilpin 1997), are disrupted. Continual erosion of populations by interactions with non-native salmonids and poor connectivity among remaining enclaves increases the probability of extinction through genetic, stochastic (environmental and demographic), or deterministic processes (Harrison 1991; Reiman and McIntyre 1993; Fausch and Young 1995).

Watersheds in northwestern Wyoming have been fragmented with similar patterns. Mid-century introductions of rainbow trout and brook trout, usually at accessible, low-elevation locations (WGFD records), proliferated in the mainstem rivers and lower reaches of major tributaries effectively fragmenting YSC among headwater streams. Gradual expansion of non-native trout populations has exposed many of the fragmented YSC populations remaining in individual tributaries to environmental stochasticity (see Fausch and Young 1995) and the liabilities of small population size (Shaffer 1987; Rieman and McIntyre 1993). Within that portion of the Absaroka Mountains drained by the Bighorn River (the majority of present day YSC range in Wyoming), viable YSC populations are currently found only in networks of connected tributaries, no single tributary supports a viable YSC population unless protected by a barrier (Chapter IV).

Despite the mounting body of literature suggesting lower survival probabilities for isolated populations (e.g., Wilcox and Murphy 1985; Allendorf and Leary 1988; Dodd 1990), many conservation assessments discuss isolation of small populations in high-elevation tributaries as a key strategy in the preservation of cutthroat trout (see Behnke 1992; Young 1995; Young et al. 1996; May 1996; Lentsch et al. 1997). Reacting to the proliferation of non-native salmonids, managers have commonly isolated extant or reintroduced populations of cutthroat trout in headwater areas with natural or man-made structures. Critical to this strategy is that physical fragmentation will not preclude survival while long-term solutions are initiated. While the conservation motive for use of physical barriers is straightforward (Fausch and Young 1995; Young et al. 1996), the argument supporting biological segregation is not based on scientific evidence.

Regardless, the threat of invasion of non-native trout into many of the remaining populations of YSC has triggered managers to consider the conservation value of isolating individual (or groups of) streams in order to decrease hybridization and competition risks. However, both exotic invasion and artifical isolation can affect a population in similar ways. Typically, non-native trout will initially colonize the mainstem and lower reaches of larger tributaries cutting off dispersal of YSC among tributaries and ultimately resulting in a pattern of fragmentation similar to artificial barriers. While these two scenarios may or may not have different long-term impacts on a YSC population, both are possible endpoints in conservation planning.

My goal was to evaluate the potential short-term consequences of purposeful fragmentation on remaining YSC populations in the headwaters to the Bighorn River within the Absaroka Mountains and to assess the increase in extinction risk that results. I estimated effective population size's (EPS) for each individual stream inhabited by YSC under the assumption that each stream could be isolated from the network of streams that currently support YSC. I evaluated demographic and genetic viability for each stream based on the estimated EPS. Given the results of viability analysis, I focused on the role of stream isolation as an acceptable conservation strategy in northwestern Wyoming, including the role of natural geologic barriers in the possible conservation of genetically pure YSC. Based on current distribution patterns of YSC, I hypothesized that few of the individual tributaries could support viable populations of YSC if isolated from the main population.

Methods

Three large populations (designated as Greybull, Wood, and South Fork Shoshone) of YSC were identified in an intensive survey (172 tributary streams) of the Bighorn River headwaters (Greybull, North Fork and South Fork Shoshone River watersheds) in the Absaroka Mountains of northwestern Wyoming (see study area and Figure 1 in Chapter IV). Perenniel tributaries known to contain genetically pure YSC in these populations were sampled during low-flow months from 1994 to 1997 with Smith-Root model 12-B electroshockers. A 100-m stream reach was electrofished (single-pass) every 1.5 km, or where access allowed, until fish were absent from two consecutive reaches. Additional habitat units were selectively sampled after each barren reach to assure fish absence. Fish migration barriers were defined as geologic structures at least 1.5 m in height or reaches of very high channel slope or water velocity (Stuber et al. 1988; Rieman and McIntyre 1993). Reaches were sampled immediately above and below barriers. Barrier locations were identified with global positioning units and U.S. Geological Survey (USGS) 1:24,000 scale topographic maps.

Wetted stream width was measured at each reach with a tape perpendicular to stream flow at five transects equally spaced through the 100-m reach. Stream length was measured with an electronic map wheel from USGS topographic maps. Because my estimate of the location where YSC occupancy in the stream ended was not exact, distributions of YSC in each tributary were calculated based on the length of stream from the tributary outlet to a point halfway between the last occupied site and first barren site, assuming that trout presence was limited somewhere between these two reaches.

After electrofishing each reach, captured YSC were enumerated, measured (total length, TL, cm) and returned to the study reach. Eye, muscle, and liver tissue was removed from a subset of captured trout, frozen in liquid nitrogen, and electrophoretically analyzed to corraborate the genetic purity of the cutthroat trout in the tributary. Genetic analysis was performed by the Wild Trout and Salmon Genetics Laboratory in Missoula, Montana.

I defined each tributary as a separate population to test the viability of the YSC population assuming that each tributary could be isolated near the mouth with a man-made barrier. If the mainstem river or large tributaries currently supporting YSC populations were colonized by exotic trout species, each tributary could be viewed as a unique biological population upon which such management efforts might focus.

Population size within each tributary having a genetically pure population was calculated (see Chapter I). For each 100-m sample, the one-pass electrofishing abundance was converted to an overall population estimate using the equation TA = -1.863 + 1.181 ONE + 0.797 W; where TA is the estimate of total abundance in the 100-m reach, ONE is the number of fish captured with one electrofishing pass, and W is the wetted stream width. Corrected abundance estimates for 100-m reach were averaged across all sample reaches containing pure YSC and multiplied by the total occupied stream length to provide an estimate of total population size in each tributary.

The total estimated population size within each tributary was converted to an effective population size (EPS) by multiplying the estimate by the proportion of individuals greater than 200 mm in length (TL) in the samples from each drainage. Although most fluvial YSC spawners exceed 275 mm (Thurow et al 1988), reproduction is common in fish of 200-275 mm; thus all fish greater than 200 mm were considered as part of the effective breeding population. Length structure of *Oncorhynchus* trout within each drainage was pooled across tributaries to give an overall proportion of spawning fish by drainage (Greybull = 0.527, SF Shoshone = 0.568).

Viability was assessed by comparing EPS's to minimum values in the literature considered necessary to prevent population extinction due to demographic stochasticity or loss of genetic variation. Effective population sizes were defined as the number of sexually mature, spawning adults in the population and compared to minimum values suggested to prevent demographic stochasticity (20 to 30, Rieman and McIntyre 1993, Young 1995) and excessive inbreeding (50), and to maintain long-term genetic variation (500, 50/500 rule, Soule 1987). Conversion of total population size to effective population size, or the level of genetic variability in the breeding population, is difficult, but estimates of EFP's for populations have ranged from 10 to 75% of the total population size (Reiman and McIntyre 1993). I feel my method of approximating EPS's for YSC is appropriate for the intended purpose.

Threats to population persistence were evaluated for each population in a tributary that might result from fragmentation of the watershed. Population size (demographic and genetic), isolation, and the presence of non-native salmonids were considered the most prodigous risks to population survival and risk levels (high, moderate, low, or non-existent; Table 1) were assigned to each population to indicate the extinction vulnerability (conservation priority) of each population based on EPS. Populations with fewer than 20 individuals were considered at high risk (eminently threatened) from demographic and genetic extinction because the population was below excepted minimums for these categories. Demographic and genetic risks decreased as EPS increased (four levels, Table 2) and population size exceeded the levels required to sustain a population. Remaining YSC populations were not considered secure, or having a high probability of long-term persistence, unless risks were either low or non-existence for all categories in Table 2.

Demographic and short-term genetic risks were considered low (a potential risk, but of limited concern) when EPS exceeded 50. Maintenance of long-term genetic variability was no longer a risk when estimated population size surpassed 500 individuals.

The threat of brook trout was evaluated at two levels: present in the watershed and present in the population. Because of their ability to outcompete YSC, brook trout within the geographical limits of a current YSC population were considered a high risk to all but the largest populations. Large populations have a higher likelihood of sustaining themselves if brook trout are present, however, brook trout are still a moderate risk (threatening long-term survival) and any adverse effects (e.g., decrease in YSC population size) would shift the risk rating from moderate to high. The presence of brook trout in the watershed outside the geographical extent of the YSC population is less threatening to larger populations which have the potential to withstand or overwhelm a brook trout invasion, but is still a high risk for small populations. If brook trout did invade a small YSC population, their prolific nature may overwhelm the YSC in only a few generations.

The presence of rainbow trout was considered an eminent threat to all population sizes because of the detrimental and additive effects of both hybridizing and competitive interactions with YSC. Because YSC populations which contained rainbow trout in them were not considered viable risks were only assigned if rainbow trout were present in the watershed, not in the population.

Isolation was considered highly risky for population survival unless population size was large. Isolation not only amplifies demographic and genetic risks, but also exposes a population to environmental catastrophes with no chance of recolonization. Larger populations, with more individuals and habitat, have a higher probability of surviving environmental catastrophe and are less at risk from isolation. Additionally, isolation of large populations, which are less susceptible to genetic and demographic risks, can protect the population from invasions of exotic salmonids. Thus, large populations which are isolated from exotic immigration receive lower risk rankings than those open to rainbow trout colonization.

The adequacy of habitat to support YSC above identified fish migration barriers within the three drainages was assessed to evaluate the feasibility of YSC reintroduction upstream of the barriers. The stream segment above each barrier was treated as a unique watershed and the probability of trout surviving in the watershed was predicted using a logistic model (Model 12 from Chapter III, see Table 2 for model equation and parameters) which included the length of perennial stream (km) above the barrier and the highest basin elevation (m). If the predicted probability for a watershed to support a trout population was 50% or more, a site-scale model (Model 1) was applied to evaluate the instream habitat. Model 1 (Chapter III) used channel slope (%) and width (m) to assess whether the instream habitat would likely support trout. Because of prediction error in both models and the necessity to recommend sites with a high probability of reintroduction success, only those sites with an overall probability (probability from watershed analysis times the probability from site-scale analysis) of 80% or better were considered viable reintroduction sites.

Results

Man-made barriers

The three remaining YSC populations had 27 tributaries or headwaters that could potentially be isolated by a fish migration barrier. The Greybull River population included 14 tributaries and the headwater, the Wood River contained six tributaries and the headwater, and the South Fork (SF) Shoshone population had four tributaries and the headwater. Viability analysis was performed on 24 of the 27 streams. Because only two adult fish were captured in the entire 1.5-km length of Mable Creek in the Greybull River drainage, the stream was not considered to represent a viable cutthroat trout population. Additionally, discharge on the mainstem SF Shoshone River was too high to efficiently sample with electrofishing, precluding an accurate estimate of fish densities and subsequent viability analysis. Marquette Creek, one of five segments in the SF Shoshone drainage, was analyzed in Chapter IV as a separate biological population.

Only one population (Dundee Creek) had an estimated EPS less than the suggested minimum for demographic stability (< 20), while a second (SF Anderson Creek) was only slightly larger (32). Most populations would exceed 50 effective individuals if isolated, indicating demographic and short-term genetic stability. The minimum of 500 individuals required to preserve long-term genetic variation and adaptability was exceeded in nine of 24 populations (Table 3). Because all three current YSC populations contain rainbow trout in the watershed, all tributaries would have a moderate risk from rainbow trout when isolated with man-made barriers. Two populations have demographic risks, while 16 have either short- or long-term genetic risks. The presence of brook trout are a risk for almost all the streams in the Wood River and SF Shoshone populations. Because of low or non-existent risks for all the categories, streams in the Greybull River population had the highest likelihood of supporting populations if fragmented (Table 4).

Natural Barriers

Barriers to upstream migration of YSC were found on 33 of the 172 streams in the overall survey of the three drainages. No wild cutthroat trout were found above fish migration barriers. Trout (of any species) were present in 30 of 33 streams and in 27, fish were congregated at the base of the barrier, but absent upstream. The other three streams had YSC that had been recently stocked above the barriers by the WGFD. Watershed analysis indicated that 15 of the 33 streams upstream from fish migration barriers had a 50% or greater probability of supporting trout in the segment of stream above the barrier (Table 2). Twelve of the 15 appeared to have adequate ($\geq$ 50% chance of supporting trout) instream habitat; however, only six exceeded the minimum combined probability (of supporting trout) of 80% – four streams in the SF Shoshone River drainage (Boulder Creek, Deer Creek, Ishawooa Creek, and Needle Creek) and two in the Greybull River drainage (SF Wood River, Wood River).

TABLE 1. Risk factors associated with the vulnerability of remaining Yellowstone cutthroat trout (YSC) populations. A risk rated highly is of immediate concern for population persistence, moderate risks have potential to harm a population in the short-term, while low rated risks are of little concern in the short term, but may have long-term consequences on population persistence. Risk categories include all columns to the right of population size.

EPS	Demographic Risk	Short-term Genetic Risk	Long-term Genetic Risk	Brook trout presence - watershed [a]	Brook trout presence - population [b]	Rainbow trout presence - watershed [c]	Isolation
< 20	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH
21 - 50	MODERATE	HIGH	HIGH	HIGH	HIGH	HIGH	HIGH
51- 500	LOW	LOW	MODERATE	MODERATE	HIGH	HIGH *MODERATE when barrier present*	MODERATE effects on the population directly but protects populations from exotic species
> 500	NONE	NONE	NONE	LOW	MODERATE	HIGH *MODERATE when barrier present*	NO effects on population directly and protects population from exotic species

[a] Indicates that brook trout are present within the watershed where the YSC population is found, but not sympatrically.

[b] Indicates that brook trout are found sympatrically with YSC.

[c] Indicates that rainbow trout are present within the watershed where the YSC population is found, but not sympatrically. When rainbow trout were found in the population it was not considered pure YSC, thus there is no "within population" category.

TABLE 2. Streams containing natural fish migration barriers for which watershed analysis indicated a 50% or greater chance that fish would persist if reintroduced above the barrier. Logistic models were used to predict probabilities of trout presence at the watershed- and site-scale. The wateshed equation was $Y = -6.084 + 0.342$(stream length) $+ 0.001$(hi elevation) and the site-scale equation was $Y = 1.600 - 0.289$(channel slope) $+0.320$(channel width). The sixth streams with a good chance of supporting a reintroduced Yellowstone cutthroat trout population, based on the combined prediction probabilities, are indicated in bold. GRB = Greybull River drainage, NFS = NF Shoshone River drainage, and SFS = SF Shoshone River drainage.

Stream	Basin	Stream km above barrier	Highest basin elevation (m)	Probability of trout presence - watershed analysis	Channel slope (%)	Channel width (m)	Probability of trout presence - site analysis	Overall probability
Jack	GRB	11.3	4009	0.85	6.2	3.5	0.72	0.61
SF Wood	**GRB**	**13.9**	**3707**	**0.91**	**3.3**	**5.1**	**0.91**	**0.83**
Wood	**GRB**	**14.0**	**3765**	**0.92**	**3.0**	**7.7**	**0.96**	**0.89**
Avalanche	NFS	8.2	3463	0.54	4.0	3.8	0.84	0.46
Canyon	NFS	8.5	3414	0.56	9.0	3.0	0.49	0.27
Sheep	NFS	14.0	3684	0.92	10.0	6.7	0.70	0.64
Boulder	**SFS**	**14.6**	**3690**	**0.93**	**3.0**	**10.5**	**0.98**	**0.92**
Cabin	SFS	18.4	3446	0.97	9.2	6.2	0.72	0.70
Castle	SFS	10.0	3516	0.70	12.0	5.1	0.44	0.31
Deer	**SFS**	**15.8**	**3512**	**0.94**	**5.9**	**6.8**	**0.89**	**0.84**
Hardpan	SFS	12.7	3701	0.88	10.0	4.5	0.54	0.47
Ishawooa	**SFS**	**14.9**	**3613**	**0.93**	**3.5**	**11.6**	**0.99**	**0.92**
Needle	**SFS**	**13.6**	**3806**	**0.92**	**5.0**	**11.6**	**0.98**	**0.90**
Yellow	SFS	8.3	3642	0.60	17.1	3.5	0.10	0.06
Younts	SFS	15.2	3492	0.93	8.5	3.5	0.57	0.53

TABLE 3. Estimated effective population sizes (EPS) for 24 of the 27 streams containing genetically pure Yellowstone cutthroat trout. EPS is based on the number of trout per 100-m sample reach, averaged across sampled reaches, and extrapolated to the entire occupied portion of the stream. Stream numbers correspond to those areas shown in Figures 2 - 4 in Chapter IV. For example G11 is the stream numbered 11 in the Greybull River drainage. W = Wood River drainage and SF = SF Shoshone River drainage.

Stream	Mean number of cutthroat trout per 100-m reach	Total stream km containing cutthroat trout	Estimated population size	Estimated EPS
Anderson (G14)	12.79	9.35	1196	630
Cow (G18)	13.95	4.65	649	342
Eleanor (G13)	8.39	5.61	471	248
Francs Fork (G26)	25.57	16.14	4127	2175
Greybull River (6)	21.90	47.71	10450	5507
Jack (G12)	18.15	3.86	700	369
NF Pickett (G9)	10.06	6.00	604	318
Pickett (G8)	8.48	19.52	1654	872
Piney (G10)	4.94	7.78	384	203
Red (G17)	10.85	1.16	125	66
SF Anderson (G15)	2.22	2.72	60	32
Venus (G16)	8.55	8.63	737	389
Warhouse (G11)	17.42	1.86	323	170
WF Timber (G25)	17.60	10.05	1768	932
Brown (W24)	22.71	2.53	575	303
Chimney (W23)	12.89	5.04	650	342
Deer (W19)	3.89	3.59	140	74
Dundee (W20)	3.42	0.82	28	15
Middle Wood (W21)	23.21	17.78	4128	2175
SF Wood (W22)	39.37	7.28	2865	1510
Wood River (7)	18.00	9.61	1731	912
East Fork (SF3)	6.78	7.00	475	270
Genetain (SF4)	8.95	1.61	145	82
Younts (SF2)	11.95	2.70	322	183

TABLE 4. Risks threatening the 24 streams containing Yellowstone cutthroat trout base on population size, isolation, and the presence of non-native salmonids in the watershed. Any population with at least one high risk ranking (see Table 1) can be considered unsecure (long-term persistence is threatened). Streams in the Greybull drainage indicated by G, W = Wood River, and SF = SF Shoshone River.

	Risk Assessed						
Stream	Demographic	Short - term Genetic	Long - term Genetic	Brook trout - watershed	Brook trout - tributary	Rainbow trout - watershed [a]	Isolation [a]
Anderson (G)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Cow (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
Francs Fork (G)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Greybull River	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Jack (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
NF Pickett (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
Pickett (G)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Piney (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
Red (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
SF Anderson (G)	MOD	HIGH	HIGH	NONE	NONE	MOD	HIGH
Venus (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
Warhouse (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
WF Timber (G)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Eleanor (G)	NONE	LOW	MOD	NONE	NONE	MOD	MOD
Genetain (SF)	NONE	LOW	MOD	MOD	HIGH	MOD	MOD
Younts (SF)	NONE	LOW	MOD	MOD	HIGH	MOD	MOD
Brown (W)	NONE	LOW	MOD	MOD	NONE	MOD	MOD
Chimney (W)	NONE	LOW	MOD	MOD	NONE	MOD	MOD
Deer (W)	NONE	LOW	MOD	MOD	HIGH	MOD	MOD
Dundee (W)	HIGH	HIGH	HIGH	HIGH	NONE	MOD	HIGH
East Fork (SF)	NONE	LOW	MOD	MOD	HIGH	MOD	MOD
Middle Wood (W)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
SF Wood (W)	NONE	NONE	NONE	NONE	NONE	MOD	NONE
Wood River	NONE	NONE	NONE	NONE	MOD	MOD	NONE

[a] - The ranking takes into account the assumed man-made barrier on each stream. A moderate ranking is abbreviated MOD.

Discussion

Declines in cutthroat trout distributions over the past half-century have promoted the conservation of YSC and other cutthroat trout subspecies to the forefront of native fish management in Wyoming. Of the six subspecies of cutthroat trout historically present in Wyoming, only the finespotted (Snake River) subspecies has escaped marked losses in distributions. Thus, managers have been galvenized to develop and implement conservation strategies that will preserve remaining stocks of YSC.

While considerable interest and debate has been focused on salmonid population structure (e.g., metapopulation dynamics, source-sink dynamics, movement, biological or geographical population units, evolutionarily signficant units; Pulliam 1988; Harrison 1991; Faush and Young 1995; Waples 1995; Hanski and Gilpin 1997; Jakobar et al. 1998), most researchers agree that disruption of population processes predicated on movement (e.g., dispersal, genetic exchange, resource selection) or reduction in population size through fragmentation will increase the risk of population extinction due to demographic problems, loss of genetic variation, or environmental stochasticty (Shaffer 1987). Along these lines, exotic trout introductions and anthropogenic influences have relegated most remaining populations of interior cutthroat trout to small, disjunct headwater locations and has focused attention on the their viability or long-term persistence (Ryman and Utter 1987; Boyce 1992; Rieman and McIntyre 1993; Guffey et al. 1998). For survival to occur these isolated habitats must provide the critical resources necessary to sustain a population, as well as the spatial diversity and areal extent necessary to withstand environmental stochasticity and change.

Isolation management - man-made barriers

Based on estimated population sizes and associated risks (Tables 3 and 4) it appears that isolation of tributaries and headwater streams containing YSC by artificial barriers could be considered as a potential conservation tool in the three drainages within the Bighorn River watershed of the Absaroka Mountains. However, I suggest that unless a potential population fragment is large and there is little or no risk to the long-term persistence, such a strategy would be questionable. Several possible isolated populations in tributaries to the Wood River and SF Shoshone River watersheds would have high risk factors and isolation management of these streams would be detrimental to their short-term persistence. Isolation management would be a more viable conservation alternative in the Greybull River watershed where several large populations could exist with low risk factors. However, none of these populations would be immune from the invasion of rainbow trout in the drainage which makes their long-term survival questionable without aggressive non-native trout control. An important omission from my risk assessment was the effects of environmental stochasticity. The isolation category attempts to include this variable, but its unpredictability makes it difficult to assess. Only the nine largest tributary populations were classified as having little or no risk from isolation resulting from the potential effects of environmental perturbations on isolated populations.

Environmental variability can decimate healthy populations and is likely to be leading cause of population loss in isolated streams (Shaffer 1987; Lande 1988; Rieman and McIntyre 1993; Dunham et al. 1997). The variation in timing, intensity and effect of catastrophic events limits our ability to directly alleviate the effects of environmental stochasticity (see Siegfried and Knight 1977; Lamberti et al. 1991; Rieman and McIntyre 1993). However, connectivity provides fish the opportunity to escape environmental events and obtain refuge elsewhere in the watershed providing recolonizing propagules for a decimated area following a stochastic event; isolation eliminates this flexibility in a population. Given the geologic instability and mountainous topography of the study area, catastrophic events such as floods, droughts, and debris torrents are relatively common events and managers need to consider their potential impacts if small populations (i.e., individual tributaries) are isolated in the future.

The declines in the subspecies of interior cutthroat trout are not a new phenomenon and management strategies have been discussed for some time (Behnke and Zarn 1976; Gresswell 1988; Young 1995). Several proactive options to protect, enhance, or increase cutthroat trout populations include: (1) restrictions on terminal fishing tackle, (2) habitat enhancement, (3) reclamation by poisoning, (4) stocking genetically pure hatchery fish, (5) intra- or inter-basin transfers of natural populations, and (6) protecting extant stocks with artificial barriers or stocking genetically pure fish in barren habitat above natural barriers (Varley and Gresswell 1988; Thurow et al. 1988; Young 1995; Dunham et al. 1997; Guffey et al. 1998). The conservation goal is to reestablish new and reconnect existing populations of cutthroat trout throughout their historic range and maintain viability by ensuring essential habitat, refugia, and movement corridors are protected (Young 1995). All of these proactive options can move conservation efforts towards the conservation goal, but reclamation, restocking with genetically pure hatchery fish, and protection by barriers have the greatest potential for immediate improvement in the status of cutthroat trout, and subsequently have received the most attention in conservation planning.

Isolation management is being used for Colorado River cutthroat trout in south-central Wyoming and north-central Colorado (Young 1995; Thompson and Rahel 1998). Short term conservation efforts have concentrated on removing non-native trout using electrofishing or ichthyocides and restocking with native fish upstream from barriers in hope of reconnecting the isolated fragments in the future (Young 1995; Young et al. 1996; Thompson and Rahel 1996, 1998). Similar strategies have been discussed for conservation of southern Appalachian brook trout (Gulley et al. 1998) and Bonneville cutthroat trout in Utah (Lentsch et al. 1997).

While barriers appear to be a viable option for short-term protection of cutthroat trout stocks, there are several limitations to their application. Most barriers isolate populations in a single or few tributaries at high elevations containing habitat incapable of supporting large, resilient populations. The isolated populations are at risk of demographic and genetic extinction processes and the limited habitat matrix provides little refugia and minimal recolonization or rescue after catastrophic environmental events. Relatively rapid genetic changes may occur under strong selection in isolated populations (Fausch and Young 1995) resulting in higher within population genetic differences than would naturally occur and possibly selecting against traits such as mobility and dispersal. Artificial barriers are expensive to install and maintain, and commonly fail, either through loss of physical integrity or unsuccessful inhibition of upstream movement by undesired fishes (Young et al. 1996; Thompson and Rahel 1998). Young et al. (1996) reported that 22% of barriers protecting populations of Colorado River cutthroat trout failed to prevent infiltration by non-native salmonids, while Thompson and Rahel (1998) indicated a 50% fail rate of barriers in their study.

Additionally, the ability of rainbow trout to persist in high-elevation environments (Chapter IV) indicates that their presence in an isolated YSC population will ultimately lead to the demise of extant or reintroduced YSC population. Thus, any conservation success with physical isolation in the study area, aside from protecting extant populations, will require elimination of hybridizing and competing non-native salmonids above any barrier, with subsequent reintroduction of native trout. Ubiquitous distributions of non-native trout, the need to preserve large amounts of habitat, and the likelihood of barrier failure make this option difficult to achieve.

Isolation management - natural barriers

Prior to initiating this study, I expected geologic barriers to be an integral component in YSC conservation by excluding non-native salmonids from genetically pure populations. The absence of YSC above fish migration barriers in the three watersheds, excluding those populations recently introduced by the WGFD, suggests that YSC were either not able to establish themselves in habitats above barriers or populations above barriers are extinction prone. Evidence suggests that the later scenario may be the case. In 1994, after 5 years of low flow and two separate stocking events (1988 and 1993), Eleanor Creek in the Greybull River drainage, one of three streams stocked above fish migration barriers, had average abundance estimates of greater than 8 fish/100-m reach (5 sampling stations, Table 3); in 1997, after three years of higher than average spring flows, a 400-m sample produced four fish (0.25 fish per 100-m). This suggests that relatively minor environmental perturbations may have substantial impacts on YSC populations above barriers when a short distance of naturally poor stream habitat is available.

Similarly, a population of rainbow trout x cutthroat trout hybrids above a barrier on Red Creek of the NF Shoshone River drainage disappeared following the 1988 Yellowstone fires. Fish were present at the base of the cascade in 1996, but had not recolonized above the barrier. With a few exceptions, barren areas of adequate habitat above barriers are only a few kilometers in length. These relatively short distances and the naturally pauperate and unstable nature of the habitat (Chapter III) provides little opportunity for small populations to resist extinction in the face of catastrophic environmental events such as those described by Lamberti et al. (1991). Similar environmental disturbances extirpated isolated headwater populations of Gila trout *O. gilae* in New Mexico (Fausch and Young 1995).

Although the role of natural barriers is less defined in cutthroat trout management, their importance in protecting native fishes has been shown for Colorado River cutthroat trout, as well for other species in the Appalachian Mountains (Larson and Moore 1985) and in Australia (Townsend and Crowl 1991). I expected natural barriers to play an important role in YSC conservation, but natural barriers did not protect any genetically pure, native populations of YSC. Aside from failure considerations, concerns regarding isolated populations above natural barriers are similar to those mentioned for artificial barriers.

Because of the perceived short-term benefits, stocking upstream from natural barriers might be considered as a conservation alternative for YSC. However, in light of the previous discussion and geologic conditions in the Absaroka Mountains, it is unlikely to be successful. The volcanic geology and montane climate, which result in unstable substrates, migrating channels, high spring and flashy summer flows, and copious erosion preclude the option of artificial barriers on individual tributaries. It is probable that artificial barriers would have very high failure rates in the Absaroka Mountains. Barrier installation requires accessibility to sites with stable stream banks (Novotny and Binns 1990), both of which are rare commodities in these shifting streams located predominately on national forest lands with a majority in federally designated wilderness areas. Most barren stream reaches above barriers have relatively short distances of habitat, preventing the establishment of large, viable YSC populations with enough refugia to escape environmental extinction.

Potential may exist for establishment of YSC populations in six relatively long reaches with suitable habitat above natural barriers (Table 2). Because of the isolation effects, genetically pure populations of YSC established above natural barriers should be carefully monitored to insure persistence. In the event native YSC are introduced above natural barriers, careful consideration must be given to the source of introduced fish. Allendorf and Leary (1988), Ferguson (1990), Krueger and May (1991), Hindar et al. (1991), and Hayes et al. (1996) provide good reviews on the genetic implications of introducing hatchery selected or out-of-basin stocks into a native drainage. Among other things, unique genetic characteristics, co-adapted gene complexes, genetic variation, and fitness (heterozygosity) can be compromised by indiscretionary introductions. While some introductions are necessary in restoration programs, especially in endangered and threatened species (Krueger and May 1991), within basin transfers of genetically pure fish is the best insurance against adverse genetic consequences.

Application

Given the numerous risks, isolation management on individual streams should be used as a conservation tool only to prevent complete extirpation of a YSC population in the short-term, with a goal of long-term stability through reconnection of isolated fragments. Because of its immediate, visible impact, small-scale isolation management is an attractive option, but care should be taken to consider all the risks before it is applied. The ideal application of isolation management is to isolate groups of streams together, providing a network of connected refugia and movement corridors. Downstream (off national forest lands) habitats are, for the most part, irreversibly impacted and conservation should not focus on reconnecting major watersheds (e.g., Greybull and Wood rivers), but rather on less impacted portions within watersheds. If several tributaries connected by a portion of the mainstem habitat can be protected (i.e., isolated) together, isolation management will have a higher probability of success. In this context, isolation could be used to manage the entire Wood River and Greybull River populations until long-term goals and non-native control are established.

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CHAPTER VI

Additional Observations on Genetically Pure Yellowstone Cutthroat Trout in Northwestern Wyoming

Abstract. – The presence of genetically pure Yellowstone cutthroat trout Oncorhynchus clarki bouvieri (YSC) was assessed in selected streams in the upper Yellowstone River and the Clark's Fork of the Yellowstone River, within the Absaroka Mountains and on the western slope of the Bighorn Mountains. Genetically pure populations of YSC were identified in the upper Yellowstone River drainage, one small stream in the Clark's Fork drainage, and three small streams in the Bighorn Mountains.

The upper Yellowstone River drainage upstream from Yellowstone Lake is known to have a large population of Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* (YSC). It is believed that a substantial portion of the population in this drainage migrate between Yellowstone Lake and the headwaters of the Yellowstone River and its larger tributaries.

The Clark's Fork of the Yellowstone River is believed to have supported a native population of YSC. However, fish were not present in the upper portions of the watershed due to a barriers falls (Jordan 1891, *in* May 1996). Extensive stocking of YSC and exotic salmonids has distributed trout throughout the drainage. The possibility exists that genetically pure YSC introduced upstream from the falls may persist in portions of the drainage.

In the Yellowstone River drainage on the western and northern sides of the Bighorn Mountains, YSC occurred naturally. Extensive introductions of exotic trout have eliminated YSC from most streams, but there is evidence that genetically pure YSC may persist in some headwater streams.

During 1997, I sampled several streams suggested by the Wyoming Game and Fish Department as having a highest likelihood of containing YSC based on previous surveys, in the upper Yellowstone River drainage (Pass, Open, Hidden, Thoroughfare, and Atlantic creeks, as well as the mainstem river), the upper Clark's Fork drainage (Corral, Elk, Gas, Little Sunlight, Lodgepole, Muddy, Sunlight, Sulphur, and Spring creeks), and the Bighorn River drainage on the western side of the Bighorn Mountains (Deer, Cedar, and South Fork of Paintrock creeks) to determine if genetically pure YSC might persist in them.

Methods

Trout were captured by electrofishing from each stream. Fish in the *Oncorhynchus* genus were visually classified as cutthroat trout, rainbow trout, or cutthroat trout x rainbow trout hybrids based on morphological features (see Chapter II). At sites where visual identification indicated that a genetically pure population of YSC may persist, tissue samples were taken for electrophoretic verification of genetic purity. Eye, muscle, and liver tissue was removed from 15-20 fish, individually coded to identify sampling location, and frozen within 1 hr in liquid nitrogen. Electrophoretic analysis were performed by the Wild Trout and Salmon Genetics Laboratory at the University of Montana, Missoula (for specific techniques see Chapter II, III, IV and V).

Results

No rainbow trout genes were detected by electrophoresis in any of the streams sampled in the upper Yellowstone River drainage. Additionally, there was no indication of Snake River cutthroat trout genes among these fish. Genetically pure YSC appear to persist throughout this drainage.

One small stream (Muddy Creek) was found to harbor a genetically pure YSC population in the upper Clark's Fork drainage. No evidence of Snake River cutthroat trout genes were detected in this population. However, rainbow trout are present downstream from a natural barrier that isolates this population.

Three genetically pure populations of YSC were found in three small streams on the western side of the Bighorn Mountains (Deer, Cedar, and South Fork Paintrock creeks). Again no indication of introgression with Snake River cutthroat trout was found in these three streams.

Discussion

The extensive survey techniques applied in my primary study area were not used in the streams sampled in the upper Yellowstone River, Clark's Fork, or Big Horn River (western side of the Bighorn Mountains) drainages. Consequently, estimates of the size of the populations, descriptions of other trout in the streams, and determination of the possible presence of barriers isolating these populations was not made in most cases.

The upper Yellowstone River drainage has about 250 km of perennial streams suitable as habitat for YSC. Consequently, a large population of genetically pure YSC occurs in the system. Given the presence of Snake River cutthroat trout genes in the Greybull River drainage, the upper Yellowstone

River is likely the largest population of genetically pure YSC remaining outside of Yellowstone National Park. This population appears to be relatively secure due to its large size and the absence of exotic trout in the drainage; however, the recent discoveries of lake trout *Salvelinus namaycush* and the organism *Myxobolus cerebralis* that causes whirling disease in Yellowstone Lake may pose threats to this population.

Only a single, introduced population of genetically pure YSC was found among the streams sampled in the Clark's Fork drainage. The population in Muddy Creek is isolated by a natural barrier and no other trout were found upstream from the barrier. The genetic source of the population is unknown. Because of the extensive introductions of exotic salmonids, it is unlikely that other populations of YSC persist in the 1,500 km of perennial streams in this drainage; however, the portion of the watershed above the barrier falls should not be considered historic YSC habitat.

The three widely separated streams in the Bighorn Mountains harbor genetically pure YSC and do not appear to contain or be threatened by Snake River cutthroat trout influences. However, YSC from other sources have been introduced into the native population in all three streams, compromising their wild, endemic classification. These streams comprise a very small portion of the total length of streams that currently support trout fisheries in that portion of the Bighorn Mountains where YSC occurred prior to European man. Kozel estimated that YSC populations remained in only 4% of available habitat within their native range in the Bighorn Mountains (Steve Kozel, USFS, personal communication). This estimate appears reasonable.

Additional study is needed to determine the size and spatial distributions describe here, and to determine the potential for their persistence over time. These populations are likely to be found with threats similar to the remaining populations in the Absaroka Mountains – invasion by hybridizing or competing exotic trout, catastrophic environmental events, or population failure due to demographic or genetic factors associated with small populations.

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CHAPTER VII

Management options for Yellowstone cutthroat trout in northwestern Wyoming

The preceding chapters have discussed the status of Yellowstone cutthroat trout (YSC, *Oncorhynchus clarki bouvieri*) in northwestern Wyoming leading to the ultimate question "Where do we go from here?" Several thoroughly written conservation assessments regarding the status of inland cutthroat trout (Gresswell 1988; Young 1995; Duff 1996; Young et al. 1996) have included possible conservation strategies which could be implemented to preserve declining inland cutthroat trout stocks. My intent is to briefly discuss options which may be considered in management of YSC with special attention to their viability as strategies within the study area. Ultimately the soundest conservation strategy is to return the impacted watersheds to a level resembling historic conditions, a difficult task to say the least. Survival of YSC will depend on protection from exotic trout species, reestablishment of unfragmented metapopulations, and protection of essential habitats, migratory corridors, and well distributed habitat refugia (Young 1995).

The myriad of impacts on YSC and their habitat, including the presence of non-native salmonids, habitat alterations, and agricultural impacts at lower elevations (e.g., privately deeded lands) makes conservation or restoration of YSC in these areas an impossible task. Conservation efforts should be focused on the relatively pristine environments found on national forests and within wilderness areas. Even though these higher-elevation sites provide less habitat, both in quantity and quality, than comparable unimpacted or reclaimed lower elevation sites, their near-natural state provides the best opportunity for conservation gains.

Current distributions of genetically pure YSC, excluding Yellowstone National Park and the Snake River drainage (i.e., finespotted cutthroat trout), appear limited to five large populations (groups of connected tributaries with contiguous occurrence of YSC): (1) in the Greybull River drainage, (2) the Wood River drainage, (3) the upper South Fork Shoshone River drainage, (4) the upper Yellowstone River drainage, and (5) Marquette Creek in the South Fork Shoshone River drainage. Additionally, there are three small populations on the west slope of the Bighorn Mountains (Cedar, South Fork Paintrock, and Deer Creeks). Based on the extensive surveys conducted in the Greybull, Yellowstone, and Shoshone River drainages, as well as other WGFD sampling, the potential for discovery of any additional, large, genetically pure populations in the Yellowstone River drainage of Wyoming appears limited. Other small, isolated populations may persist in the Bighorn Mountains, but their discovery are not to likely change the conservation outlook for YSC.

Only the Greybull River and upper Yellowstone River drainages are not immediately threatened by exotic trout. However, the Greybull River populatiom, as well as the Wood River and Marquette Creek populations, contain finespotted cutthroat trout genes. Additionally, evidence (WGFD files) suggests that all populations, except the upper Yellowstone River drainage, have had non-indigenous cutthroat trout (i.e. other cutthroat trout subspecies or cutthroat trout from other watersheds) introduced. Thus, only the upper Yellowstone River drainage may be considered native, genetically pure YSC in their truest form.

The upper Yellowstone River drainage, including the Thoroughfare and Atlantic Creek tributaries, is the most secure of the remaining YSC populations. The downstream presence of Yellowstone National Park substantially reduces the risk of exotic trout invasion and the entire drainage is within federally designated wilderness and protected by laws governing its management. However, the recent discovery of lake trout and the parasite that causes whirling disease downstream in Yellowstone Lake are potential threats to this populations. While the remoteness of the drainage buffers major anthropogenic influences, the upper Yellowstone River does experience considerable use for outdoor activities. Fishing pressure, while not excessive, is rather high due to the preponderance of outfitter activity. Cutthroat trout are notoriously easy to catch and regulations prohibiting harvest of YSC may help preserve this critical population. While public opinion may oppose any management change in the drainage, users should be made aware of the future consequences of over harvest, accidental or intentional exotic trout introductions, or other activities detrimental to YSC and their habitat. With careful management and public awareness, the outlook for long-term survival of YSC in the upper Yellowstone River drainage is encouraging.

The Greybull River upstream from Sunshine Reservoir diversion dam contains a large, contiguous population of YSC with no exotic trout present in the drainage. The Sunshine Reservoir diversion has been extremely important in preserving YSC by preventing upstream movement of exotic trout. The presence of exotic trout in Sunshine Reservoir and the lower Greybull River are of concern and every attempt should be made to maintain the irrigation diversion, as well as prevent movement (i.e. barrier screens, etc.) of fish from Sunshine Reservoir into the Greybull River upstream from the diversion dam Because a portion of the watershed lies on deeded land, introductions of non-native trout into private waters within the drainage should be prohibited and policed. Any current populations of exotic trout on private land with potential to invade the Greybull River above the diversion should be removed. Similar to the upper Yellowstone River, harvest of YSC should be restricted and public awareness increased. Provided non-native trout do not infiltrate the drainage, the future of YSC in the Greybull River drainage is promising.

The Wood River population is less secure. Brook trout are present within the drainage (mainstem and Horse Creek) and rainbow trout, while not sampled on national forest lands, have been angled downstream near the Wood River Lodge. While I did not advocate the use of artificial barriers (see Chapter V) for conservation of YSC, consideration should be given to a barrier on the mainstem of the Wood River in the vicinity of Brown Mountain Campground. A barrier this low in the watershed could block rainbow trout infiltration (which I feel is the most critical threat to YSC persistence) from several tributaries containing YSC and not increase population fragmentation. Barrier failure is a possibility, but adequate access to the site, protection of a large area with multiple streams, and the threat from rainbow trout argue for implementation of barrier protection. Harvest should be restricted on YSC and liberalized on non-native trout in the entire watershed downstream to the confluence with the Greybull River. Large reaches of barren stream found in the mainstem and South Fork Wood River are the best sites in the study area to attempt introduction of YSC above natural barriers (Chapter V) and establish genetically pure populations for short-term conservation benefits. However, care should be taken when choosing the genetic source of any introduced population (see Chapter V).

Long-term preservation of genetically pure YSC in the four connected tributaries in the upper South Fork Shoshone River drainage is unlikely. The YSC in these tributaries exist sympatrically with brook trout and brown trout, and have large populations of brook trout upstream in Bliss Creek Meadows, as well as a large mainstem population of rainbow trout downstream. The current distributions of exotic trout, as well as the remoteness and instability of the tributaries, prohibits any strategy to isolate the tributary populations using barriers. There does not appear to be any viable options to conserve this population.

Marquette Creek, isolated low in the South Fork Shoshone River drainage and draining primarily deeded land, contains a robust population of genetically pure YSC. The creek flows into the South Fork Dike Pond, which coupled with water removal in lower reaches for irrigation, decreases its vulnerability to invasion by exotic trout. If complete isolation is occurring, barrier structures should be identified and preserved. Similar to other populations, harvest of YSC should be prohibited. Non-native introductions on private land within the drainage should be prohibited. Habitat improvement, such as water return and riparian improvement, should be considered. Although non-native trout are absent from the drainage, Marquette Creek should be carefully monitored for impacts from isolation effects and anthropogenic activities.

The three populations in the Bighorn Mountains need to be investigated further. Although Cedar, South Fork Paintrock, and Deer creeks were genetically pure at the single site on each stream that I visited, non-native trout and anthropogenic threats were not evaluated. These populations should be revisited to determine population size, habitat conditions, and external threats to their persistence.

Physical isolation of individual streams containing YSC to preserve small populations was discussed in Chapter V. In my opinion, the instability of stream channels in the study area, coupled with their remoteness, precludes efficient installation and use of artificial barriers on individual streams. A few sites above natural barriers hold potential for re-introduction (Chapter V) with the most likely locations being the upper South Fork of the Wood River, upper Wood River, and Boulder Creek in the South Fork of the Shoshone River drainage. These sites should be evaluated for adequate habitat (Chapter III) to ensure introductions will succeed.

Sources of YSC for re-introduction or re-establishment of populations should be genetically tested for purity and derived from a compatible source. Stream stocks, adapted to similar habitats, should be used as source locales for any YSC stocked into the study area. Given the ambiguousness surrounding the classification of finespotted cutthroat trout, under no circumstances should cutthroat trout from the Wood River, Greybull River, and Shoshone (North and South Forks) River watersheds be used for translocations or establishment of a brood stock. Finespotted cutthroat trout genotypes are present in these drainages and could contaminate introduction sites. The upper Yellowstone River drainage or sites within Yellowstone National Park appear to be the only reliable sources of genetically pure YSC in Wyoming.

Watershed or tributary reclamation with poison or electrofishing is a potential tool for expanding and reconnecting YSC distributions. Reclamation of an entire watershed (e.g. the North Fork of the Shoshone) is impossible given the scale and gear inefficiencies. The inability to protect individual reclaimed tributaries from ubiquitously distributed non-native trout limits reclamation as a viable alternative - exotic trout would simply reestablish themselves in any reclaimed tributary. Additionally, many drainages support important sport fisheries and public opposition to this alternative may be substantial. If the Wood River population was isolated by a barrier, the potential exists to enhance the YSC population by removing brook trout with electrofishing. However, it is unlikely all the brook trout could be removed and any benefit to the YSC would require an intense, annual effort to control the brook trout.

The ability of non-native trout to invade all habitats and displace YSC within the study drainages may be the most perplexing obstacle to YSC conservation. No simple solution for eliminating current non-native populations is apparent; however, all future introductions of trout should be strictly controlled. Introductions on private land should be investigated, especially in the Wood and Greybull river drainages, where further infiltration by rainbow trout could prove catastrophic. The consequences of intentional translocations of exotic or native trout should be explained to the public recreating in areas containing native YSC populations (e.g., upper Yellowstone and Greybull watersheds). Similarly, educational materials should be readily available at all levels (e.g., elementary schools to conservation organizations) to enhance public awareness regarding YSC conservation.

A foremost priority in YSC conservation should be the continued preservation of the Greybull and upper Yellowstone watersheds. These drainages likely represent the last large, viable populations of YSC. Conservation should focus on preserving conservation populations, or genetically pure, viable populations, around which management strategies can be developed. Ultimately, to ensure long-term persistence of YSC, large, unfragmented areas, void of non-native trout need to be established.

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APPENDIX A. Summary of habitat variables and species presence data for each 100 m sample site. Sites are alphabetized by stream by drainage with the most downstream site listed first. Unit of measurement is listed below each metric. Location of the site (latitude/longitude) is listed as degree/minute/second. Substrate categories may not add up to 100% as two minimally represented categories (Bedrock and Sand/Silt) were omitted for space. Cover was measured in a random 50 m sub-reach (within each 100 m site) as the linear stream distance containing each cover category, including boulder dam (bdp)and plunge (bpp) pools, log dam (ldp) and plunge (lpp) pools, scourpools (scp), undercut banks (ucb), large woody debris (lwd), and overhanging vegetation (ohv). Cover is summarized as total cover (TotalCov), amount of pool cover (PoolCov), and dominate cover category (DomCov) and listed as a proportion (pr) of the 50-m sample. For example, 0.46 indicates that 46% of the stream length sampled contained cover. Cover was measured at one site on each stream in the Greybull River drainage (grb) and at all sites in the North Fork Shoshone (nfs) and South Fork Shoshone (sfs) River drainages. Species sampled are coded as 1 = Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), 2 = finespotted cutthroat trout, 3 = unidentified cutthroat trout, 4 = identified cutthroat trout x rainbow trout (*O. mykiss*) hybrids, 5 = rainbow trout, 6 = brown trout (*Salmo trutta*), 7 = brook trout (*Salvelinus fontinalis*), 8 = the presence of other fish such as mountain whitefish (*Prosopium williamsoni*) and longnose dace (*Rhinichthyes cataractae*), 10 indicates insufficient habitat at that site or if the site number is one it indicates insufficient habitat in the entire stream, and 0 = available habitat but no fish sampled. Insufficent habitat is also indicated by "none" in the slope column, while missing data is indicated by "nodata".

Stream	Site	Drainage	Date	Latitude	Longitude	Elevation	Slope	Width	Boulder	Rubble	Gravel	Run	Riffle	TotalCov	PoolCov	DomCov	Species
			y/m/d	d/m/s	d/m/s	m	%	m	%	%	%	m	m	pr	pr		
anderson	9	grb	940801	44.05.18	109.24.44	2414		8.7	70	25	5						1,3,8
anderson	1	grb	940729	44.04.58	109.25.27	2505	7.5	6.6	60	35	5						1
anderson	2	grb	940730	44.04.49	109.26.15	2569	2.0	5.8	10	60	15						1
anderson	3	grb	940730	44.04.08	109.27.14	2652	3.0	7.4	20	70	10						1
anderson	8	grb	940801	44.03.56	109.27.48	2678	2.0	5.2	25	55	15	21	6	0.46	0.07	ucb	1
anderson	4	grb	940730	44.03.41	109.29.17	2765	5.0	5.3	60	30	10						1
anderson	5	grb	940731	44.03.07	109.29.23	2789	6.0	3.9	10	60	25						1
anderson	7	grb	940731			2816	5.0	3.2	5	50	40						0
anderson	6	grb	940731	44.02.18	109.30.57	2998	10.7	3.6	40	10	10						0
andersonnf	1	grb	940731	44.03.04	109.29.37	2816	9.0	3.5	70	20	10						0
andersonnf	2	grb	940731	44.03.13	109.30.44	2938	10.5	2.6	70	25	5						0
andersonsf	1	grb	940731	44.03.02	109.29.27	2801	6.3	4.9	10	50	30						1
andersonsf	2	grb	940731	44.02.41	109.29.41	2853	5.0	2.4	5	60	15						1
andersonsf	3	grb	940731	44.02.08	109.29.52	2897	6.0	4.0	25	40	30						0
andersonsf	4	grb	940731	44.01.44	109.30.04	3036	10.7	2.7	30	50	10						0
avalanche	1	grb	940711	43.57.47	109.22.30	2781	16.1	1.5	70	25	5						0
beaver	1	grb	940624				none										10
blanchette	1	grb	940809				none										10
bonnie	1	grb	940715	43.58.42	109.24.19	2646	10.2	2.7	40	40	10						0
bonnie	2	grb	940715	43.58.27	109.24.46	2816	7.0	2.5	40	35	20						0
brown	1	grb	940621	43.55.47	109.06.02	2200	2.0	1.9	15	60	5						1,2
brown	5	grb	940622	43.55.30	109.06.04	2231	3.5	2.5	40	40	10	23.5	19	0.15	0.07	bpp	1,2

brown	2	grb	940621	43.55.26	109.05.58	2243	3.0	2.3	0	75	20						1,2
brown	3	grb	940621	43.54.42	109.05.51	2278	4.9	2.6	10	55	30						1,2
brown	4	grb	940621	43.54.37	109.05.47	2356	9.3	1.7	40	40	15						0
brownbasin	1	grb	940618	43.52.37	109.17.48	2816	13.5	1.4	20	20	50						0
buckle	1	grb	940810	43.49.40	109.09.41	2565	4.2	1.6	10	30	50						0
bullelkdraw	1	grb	940816				none										10
calf	1	grb	940711	43.54.52	109.21.47	2963	10.0	1.8	65	30	0						0
canyon	1	grb	940618	43.53.46	109.16.35	2691	25.0	2.1	80	10	10						0
cascade	1	grb	940618	43.52.23	109.18.02	2806	19.5	3.2	80	20	0						0
cascade	2	grb	940618	43.52.20	109.17.47	2880	19.5	2.6	70	20	10						0
chimney	1	grb	940809			2355	2.3	2.9	5	60	15						1,3
chimney	2	grb	940810	43.51.52	109.06.47	2451	3.0	4.1	30	50	20						1,3
chimney	3	grb	940810	43.50.56	109.06.38	2498	3.0	2.1	10	50	20						1,3
chimney	4	grb	940810	43.50.32	109.06.04	2562	5.0	2.1	40	30	20						0
chimney	5	grb	940811	43.52.01	109.06.51		4.0	3.2	10	60	15	42.5	4	0.07	0.07	bpp	1,3
cow	1	grb	940716	43.57.12	109.22.42	2816	4.7	2.3	40	25	5						1
cow	5	grb	940718	43.57.29	109.23.16	2836	3.0	4.1	10	50	30	42	5	0.06	0.03	bpp	1
cow	2	grb	940716	43.57.15	109.23.34	2853	2.2	3.4	20	50	20						1
cow	3	grb	940716	43.56.40	109.23.49	2902	5.4	3.2	40	35	20						1
cow	4	grb	940718	43.56.00	109.24.10	2996	7.1	2.9	65	30	5						1
cownf	1	grb	940718	43.57.13	109.23.46	2877	6.3	3.2	20	20	40						0
deadman	1	grb	940810	43.49.37	109.09.37	2573	10.2	1.5	50	25	25						0
deer	1	grb	940621	43.56.02	109.08.31	2252	4.5	1.7	0	80	20						1,3
deer	5	grb	940622	43.56.26	109.08.58	2288	4.0	2.6	5	75	20						1,3,7
deer	6	grb	940623	43.56.36	109.09.01	2303	4.0	2.1	0	60	35	4.5	41	0.09	0.07	bpp	1,2,7
deer	2	grb	940621	43.56.37	109.09.02	2310	6.0	2.9	0	60	40						1
deer	4	grb	940622	43.57.18	109.09.24	2368	7.9	2.5	0	85	15						1
deer	3	grb	940622	43.57.29	109.09.44	2387	6.0	1.7	0	90	10						0
dick	1	grb	940902	43.59.23	109.07.01		3.9	2.9	1	10	75	11	13.5	0.51	0.21	ucb	1,2,7
dundee	1	grb	940625	43.52.14	109.10.43	2382	5.2	3.7	10	50	40						1
dundee	2	grb	940625	43.52.32	109.11.15	2444	9.7	2.9	40	40	20						1
dundee	3	grb	940625	43.52.26	109.11.30	2513	10.1	2.9	20	60	20	25	4.5	0.41	0.21	bpp	1
dundee	4	grb	940625				nodata										0
eleanor	4	grb	940729	44.04.08	109.26.22	2518	7.1	2.5	50	25	20						1
eleanor	3	grb	940721	44.05.20	109.26.49	2634	2.4	3.4	15	30	40	38.5	7.5	0.08	0.06	bpp	1
eleanor	1	grb	940729	44.05.29	109.28.19	2704	3.5	3.0	10	60	25						1
eleanor	2	grb	940729	44.05.08	109.28.49	2792	6.2	2.6	50	30	20						1

eleanor	5	grb	940729	44.04.52	109.30.21	2938	8.8	2.5	40	50	10					0
francsfork	1	grb	940829	44.06.03	109.11.29	2097	1.5	7.0	10	45	45					1
francsfork	2	grb	940829	44.04.51	109.13.04	2172	1.4	5.9	5	50	45					1
francsfork	5	grb	940829	44.03.37	109.14.16	2234	3.4	5.2	10	55	35	37	6	0.14	0.11	bpp	1,3
francsfork	3	grb	940829	44.02.57	109.14.54	2294	3.0	5.1	35	50	10					1
francsfork	4	grb	940829	44.01.42	109.15.27	2391	3.0	4.4	25	40	30					1
galena	1	grb	940619				none									10
greybull	8	grb	940816	44.04.00	109.25.01	2443	2.0	10.2	5	30	60					1,3,8
greybull	7	grb	940814	44.02.31	109.25.15	2484	1.0	15.8	5	50	40					1,3,8
greybull	5	grb	940720	44.01.51	109.25.37	2511	1.0	7.7	0	50	50					1,8
greybull	6	grb	940814	43.59.59	109.24.43	2573	2.5	9.9	5	80	5					1,8
greybull	3	grb	940716	43.57.43	109.22.55	2812	4.0	4.9	30	40	15					1
greybull	4	grb	940711	43.57.40	109.22.48	2812	3.5	5.1	50	30	0					1
greybull	2	grb	940711	43.55.29	109.21.10	2908	2.5	3.9	10	80	10					0
greybull	1	grb	940710	43.54.08	109.19.32	3117	8.1	3.6	60	30	5					0
haymaker	1	grb	940715	44.02.49	109.25.18	2487	10.7	1.6	55	15	20					0
haymaker	2	grb	940715	44.02.48	109.24.53	2598	4.0	1.7	40	20	20					0
horse	1	grb	940618	43.51.39	109.19.27	2958	7.5	5.4	20	65	15					0
horse	2	grb	940618	43.51.41	109.19.41	2993	12.5	2.6	50	45	5					0
jack	1	grb	940803	44.06.42	109.21.05	2320	3.0	4.0	20	20	50					1,2
jack	4	grb	940803	44.06.24	109.21.07	2327	7.8	4.3	50	25	20	19	6.5	0.49	0.26	bpp	1,2
jack	2	grb	940803	44.05.25	109.20.56	2463	6.8	3.3	50	30	20					1,2
jack	3	grb	940803	44.04.28	109.20.51	2623	3.0	4.4	5	30	60					0
jojo	1	grb	940619	43.56.11	109.12.45	2478	7.0	3.6	30	30	35					0
jojo	2	grb	940619	43.56.32	109.13.20	2566	none									0
jojo	3	grb	940619	43.56.49	109.13.25	2633	6.0	3.5	70	0	25					0
kay	1	grb	940829				none									10
last	1	grb	940715	43.58.33	109.23.18	2743	12.3	1.8	5	20	70					0
last	2	grb	940715	43.58.29	109.23.15	2890	15.3	1.7	25	25	10					0
mabel	1	grb	940711	43.59.52	109.24.48	2585	10.0	1.9	10	30	50					1
mabel	3	grb	940712	44.00.05	109.25.02	2597	7.0	1.4	10	50	20	6.5	42	0.03	0.03	bpp	1
mabel	2	grb	940711	43.59.42	109.24.55	2792	17.0	2.0	30	0	10					1
meadow	1	grb	940623	43.55.17	109.14.37	2536	2.0	3.0	0	15	80					0
meadow	2	grb	940623	43.55.15	109.15.06	2579	11.1	4.0	40	60	0					0
noname	1	grb	940625	43.49.49	109.16.03	2801	5.0	1.9	30	30	30					0
pearce	1	grb	940711				none									10
pickett	5	grb	940628	44.06.20	109.12.22	2121	1.5	4.7	40	50	5	10	39	0.02	0	veg	1

pickett	1	grb	940627	44.06.52	109.13.05	2124	2.0	4.8	0	95	5						3
pickett	2	grb	940627	44.08.35	109.14.45	2243	3.8	5.9	5	85	10						1,3
pickett	3	grb	940627	44.10.41	109.20.10	2707	5.0	4.0	40	50	10						1
pickett	4	grb	940627	44.11.12	109.20.48	2893	6.0	3.4	60	35	5						1
pickett	6	grb	940629	44.11.35	109.21.13	3121	6.5	3.2	55	30	10						1
pickett	7	grb	940629	44.11.38	109.21.16	3146	6.7	2.3	5	0	5						0
pickettnf	1	grb	940629	44.11.01	109.18.25	2626	4.0	3.4	30	50	15						1,2
pickettnf	2	grb	940629	44.11.59	109.18.30	2780	9.0	2.9	40	40	10						1
piney	1	grb	940817	44.08.12	109.21.22	2481	5.0	4.5	30	50	10						1
piney	3	grb	940817	44.08.34	109.22.29	2608	5.4	3.4	10	50	25	39	6.5	0.09	0.06	bpp	1
piney	2	grb	940817	44.09.02	109.22.56	2676	6.0	4.5	20	60	15						1,3
pyramid	1	grb	940711				none										10
red	1	grb	940710	44.00.06	109.24.35	2606	9.0	1.6	15	20	55						1
red	3	grb	940712	44.00.14	109.24.47	2615	11.0	1.4	30	40	20	20	30	0	0	bdp	0
red	2	grb	940712	44.00.14	109.24.18	2743	10.0	1.6	10	60	10						0
slaughter	1	grb	940810	43.48.43	109.09.12	2682	10.0	2.3	40	40	15						0
smugglergulch	1	grb	940626	43.50.33	109.14.46	2681	17.7	2.4	60	20	20						0
spar	1	grb	940626				none										10
steer	1	grb	940711	43.55.21	109.21.19	2912	5.0	4.1	25	60	10						0
steer	2	grb	940711	43.54.44	109.22.15	2987	8.0	3.1	25	25	25						0
stuart	1	grb	940000				none										10
timberw	1	grb	940829	44.04.07	109.09.29	2134	1.0	4.2	5	70	20						1,2
timberw	2	grb	940829	44.03.27	109.10.23	2195	2.5	3.9	0	75	10						1,2
timberw	5	grb	940829	44.03.41	109.10.58	2242	2.3	2.9	5	15	80	27	18	0.1	0.05	bpp	1,2
timberw	3	grb	940829	44.02.12	109.11.07	2320	6.2	1.7	30	40	30						0
timberw	4	grb	940829	44.01.09	109.11.07	2390	4.5	2.1	10	60	30						0
venus	5	grb	940719	44.01.32	109.25.52	2530	2.3	6.4	30	50	15						1,8
venus	6	grb	940719	44.01.11	109.26.15	2551	3.7	7.6	50	25	15						1,3
venus	1	grb	940712	44.00.17	109.27.53	2633	5.1	5.0	55	30	0						1
venus	7	grb	940815	44.00.13	109.27.59	2694	4.0	4.1	20	35	35	40	10	0	0	bdp	1
venus	2	grb	940712	43.59.39	109.28.50	2754	5.0	6.8	50	35	10						1,3
venus	3	grb	940712	43.59.05	109.29.32	2815	3.4	5.9	50	30	10						1
venus	4	grb	940713	43.57.57	109.30.25	2932	7.5	3.2	50	40	5						0
venusnf	1	grb	940713	43.58.59	109.29.39	2829	9.0	4.3	50	25	20						0
vick	1	grb	940801	44.05.36	109.25.28	2560	21.4	1.3	75	25	0						0
warhouse	1	grb	940803	44.05.48	109.23.28	2371	7.6	3.1	35	50	10						1,3
warhouse	3	grb	940817	44.06.05	109.24.00	2463	7.8	2.3	60	30	10	32	8	0.2	0.19	bpp	1,3

warhouse	2	grb	940817	44.06.42	109.25.22	2670	8.3	2.0	60	30	10						0
wood	2	grb	940826	43.55.29	109.07.10	2188	1.1	8.4	10	80	10						1,7
wood	3	grb	940826	43.55.14	109.08.08	2213	2.5	10.3	10	60	30						1,2,7
wood	8	grb	940826	43.55.53	109.09.07	2246	2.0	11.5	20	40	10	5	44.5	0.01	0.01	bpp	1,2,7
wood	4	grb	940826	43.56.01	109.10.28	2286	2.5	7.9	30	50	15						7
wood	5	grb	940826	43.56.07	109.11.47	2353	4.0	6.5	60	20	20						1,7
wood	6	grb	940826	43.56.08	109.12.46	2475	10.1	4.4	70	10	15						0
wood	7	grb	940826	43.55.32	109.14.22	2519	0.5	7.7	0	50	45						0
wood	1	grb	940618	43.51.32	109.19.46	2941	4.5	3.4	40	50	10						0
woodef	1	grb	940810	43.50.17	109.10.16	2444	4.5	4.3	30	45	20						0
woodef	2	grb	940810	43.49.35	109.09.43	2571	5.5	3.5	40	30	20						0
woodef	3	grb	940810	43.48.43	109.09.12	2683	8.0	2.6	40	20	30						0
woodmdf	1	grb	940624	43.55.17	109.08.49	2244	1.5	6.3	0	60	40						1,2
woodmdf	4	grb	940626	43.51.42	109.11.16	2286	1.5	6.2	0	45	45						1,2
woodmdf	2	grb	940624	43.54.35	109.09.43	2289	1.0	9.0	0	50	50						1,2
woodmdf	7	grb	940628	43.52.53	109.10.28	2391	2.0	4.0	5	70	25	12	23	0.3	0.21	bpp	1,2
woodmdf	3	grb	940625	43.52.39	109.10.41	2403	2.3	12.8	2	50	48						1,2
woodmdf	5	grb	940626	43.50.31	109.14.48	2670	6.0	4.6	60	35	5						1
woodmdf	6	grb	940625	43.49.51	109.15.59	2850	5.4	3.1	20	40	40						1
woodsf	6	grb	940827	43.55.24	109.06.01	2205	2.0	6.7	0	70	20						1,2
woodsf	8	grb	940827	43.54.31	109.07.18	2237	1.0	6.4	25	50	20	40	3	0.14	0.09	bpp	1,2
woodsf	7	grb	940827	43.53.49	109.07.41	2265	3.0	6.7	25	45	30						1,2
woodsf	5	grb	940811	43.54.13	109.08.20	2316	3.4	6.4	25	50	20						1,2
woodsf	4	grb	940811	43.52.17	109.08.16	2365	5.0	5.2	15	40	40						0
woodsf	1	grb	940809	43.51.44	109.08.28	2403	2.0	5.1	15	60	20						0
woodsf	3	grb	940811	43.50.38	109.10.05	2464	3.5	6.8	5	40	45						0
woodsf	2	grb	940811	43.49.42	109.11.55	2565	3.9	4.6	10	45	40						0
yellow	1	grb	940710	43.54.09	109.19.51	3039	6.4	3.3	60	35	0						0
yellow	2	grb	940710	43.53.40	109.20.47	3146	4.0	3.3	nodata	nodata	nodata						0
aspen	1	nfs	960711	44.28.07	109.42.02	1856	8.0	0.9	20	26	37	29	13	0.16	0.16	bpp	0
avalanche	1	nfs	960906	44.19.34	109.53.08	2390	4.0	3.8	10	50	23	38.5	0	0.23	0.23	bpp	0
bear	1	nfs	960826	44.33.50	109.58.41	2097	4.0	5.3	16	44	29	39.5	5	0.11	0.08	bpp	3,4,7
bear	2	nfs	960828	44.34.36	109.59.06	2228	10.0	4.3	38	35	18	28.5	0	0.43	0.41	bpp	1,4
bear	3	nfs	960828	44.35.43	110.01.28	2528	3.0	3.1	7	4	73	15.5	11	0.47	0	scp	1
beargulch	1	nfs	960912	44.22.05	109.41.44	2123	6.8	1.6	17	33	43	47	0	0.06	0.06	bpp	3,4
beargulch	2	nfs	960912	44.22.14	109.42.23	2269	10.2	2.0	17	17	38	37.5	10	0.05	0.05	bpp	0
big	1	nfs	970904	44.31.31	109.31.49	2134	7.4	5.7	37	23	32	42	0	0.16	0.14	bpp	3,4

big	2	nfs	970904	44.32.03	109.32.36	2274	6.7	5.1	25	31	37	32	8	0.2	0.2	bpp	1,4
big	3	nfs	970904	44.33.13	109.33.47	2438	8.1	5.2	26	37	32	29	9	0.24	0.24	bpp	4
big	4	nfs	970904	44.30.13	109.30.55	1814	7.3	5.5	29	40	26	43.5	0	0.13	0.13	bpp	4
blackwater	1	nfs	960728	44.27.31	109.44.33	1901	5.4	4.0	20	42	33	42	3	0.1	0.09	bpp	0
blackwater	2	nfs	960728	44.26.30	109.44.52	1975	6.4	4.5	5	48	42	35.5	10	0.09	0.04	bpp	4,5,7
blackwater	3	nfs	960801	44.25.53	109.45.16	2144	8.3	3.8	13	41	40	30.5	7	0.25	0.13	bpp	3,4,5,7
blackwater	4	nfs	960801	44.24.35	109.45.27	2309	10.9	2.9	28	34	37	31	9	0.2	0.12	bpp	0
blackwaterwf	1	nfs	960802	44.25.33	109.45.44	2158	7.5	3.1	13	39	39	40	0	0.2	0.16	bpp	2,4,5
blackwaterwf	2	nfs	960802	44.24.42	109.46.48	2389	15.0	2.8	42	25	30	44	2	0.08	0.05	bpp	0
blind	1	nfs	960916	44.23.03	109.41.02	2073	9.1	1.2	9	19	34	47.5	0	0.05	0.05	bpp	0
bloom	1	nfs	960913	44.20.33	109.42.14	2160	10.1	1.6	11	47	37	42.5	5	0.05	0.05	bpp	3,4
bloom	2	nfs	960913	44.20.22	109.42.47	2377	10.9	2.0	9	19	32	34.5	11	0.09	0.09	bpp	0
breteche	1	nfs	960719				none										10
burnttimber	1	nfs	960913	44.20.50	109.41.40	2152	10.6	1.1	9	32	32	46	0	0.08	0.07	bpp	1,3,4,7
burnttimber	2	nfs	960913			2216	10.6	1.2	4	34	55	48.5	0	0.03	0.03	bpp	0
cabineg	1	nfs	960816	44.22.57	109.58.27	2220	8.5	7.6	48	32	18	39.5	2	0.17	0.13	bpp	7
cabineg	2	nfs	960816	44.24.18	109.59.23	2316	7.8	7.1	27	38	26	27.5	0	0.45	0.17	bpp	7
cabinelk	1	nfs	960914	44.21.27	109.42.10	2162	8.5	4.6	15	50	33	46	0	0.08	0.04	bpp	1,4,7
cabinelk	2	nfs	960914	44.21.07	109.43.36	2400	9.0	3.7	31	35	28	45	2	0.06	0.06	bpp	1
canfield	1	nfs	960809	44.29.20	109.55.51	2012	9.1	5.0	56	29	16	36.5	10	0.07	0.04	bpp	4,5
canfield	2	nfs	960809	44.28.51	109.56.07	2158	12.1	12.3	22	44	27	39	0	0.22	0.1	bpp	4,5,7
canyon	1	nfs	960710	44.26.59	109.31.35	1887	7.6	2.9	20	35	33	35.5	2	0.25	0.2	bpp	4
canyon	2	nfs	960719	44.25.45	109.31.45	2073	9.0	3.3	30	27	29	34.5	9	0.13	0.12	bpp	0
canyon/rat	1	nfs	960710				none										10
clearwater	1	nfs	960727	44.27.51	109.40.14	1838	3.2	10.0	7	44	45	25	16	0.18	0.18	bpp	4,5
clearwater	2	nfs	960729	44.28.33	109.40.34	1910	2.9	7.3	11	46	38	48	0	0.04	0.02	bpp	3,4,5
clearwater	3	nfs	960729	44.29.32	109.41.22	1960	3.0	13.5	7	40	45	30.5	17	0.05	0.02	bpp	4,5,7
clearwater	4	nfs	960729	44.29.58	109.42.24	2042	5.0	7.1	45	35	18	39.5	4	0.13	0.13	bpp	4
clearwater	5	nfs	960730	44.30.26	109.43.26	2123	6.0	8.1	34	28	32	30	2	0.36	0.2	bpp	4,5
clearwater	6	nfs	960730	44.30.56	109.43.47	2196	5.5	12.1	23	24	45	35	10	0.1	0.1	bpp	4
clearwater	7	nfs	960730	44.31.44	109.44.02	2288	6.0	4.8	17	23	18	46	0	0.08	0.08	bpp	0
clocktower	1	nfs	960710	44.27.38	109.34.30	1801	7.9	5.4	26	39	32	42.5	0	0.15	0.15	bpp	1,2,4,5
clocktower	2	nfs	960710	44.26.48	109.34.35	1913	7.7	5.2	19	42	36	45.5	2	0.05	0.05	bpp	1,4
clocktower	3	nfs	960710	44.26.13	109.34.49	2012	8.0	5.5	17	45	30	38.5	3	0.17	0.17	bpp	4
clocktower	4	nfs	960710	44.25.40	109.34.51	2073	7.0	4.5	42	33	22	43.5	3	0.07	0.07	bpp	4
cloudburst	1	nfs	960815	44.23.17	109.58.05	2280	5.5	7.0	10	43	44	35.5	12.5	0.04	0.035	bpp	7
cloudburst	2	nfs	960815	44.22.50	109.57.45	2353	9.0	5.5	40	30	22	31.5	15	0.07	0.07	bpp	0

crouch	1	nfs	960816	44.24.16	109.58.59	2292	7.2	4.3	64	24	9	28	16	0.12	0.06	bpp	7
crow	1	nfs	960719	44.30.49	109.58.04	2045	4.7	7.9	9	38	50	35	0	0.3	0.22	bpp	4,5,7
crow	2	nfs	960807	44.30.50	109.59.24	2193	6.0	9.6	17	36	35	24.5	0	0.51	0.47	bpp	4,7
crow	3	nfs	960807	44.30.39	110.00.40	2268	5.4	7.4	27	36	31	32	2	0.32	0.28	bpp	4,7
crow	4	nfs	960807	44.29.48	110.02.46	2340	2.7	6.1	0	14	78	25	14	0.22	0.02	ldp	7
crow	5	nfs	960807	44.30.49	110.04.11	2377	3.5	6.6	23	40	36	30.5	15	0.09	0.09	bpp	0
dunn	1	nfs	960709				none										10
eagle	8	nfs	960819	44.28.07	109.53.18	1972	2.0	11.2	5	51	42	40.5	4	0.11	0	scp	4,7
eagle	9	nfs	960819	44.27.59	109.54.11	1985	2.0	10.4	7	44	41	24	16	0.2	0.06	scp	4,5,7,8
eagle	7	nfs	960817	44.26.51	109.55.16	2062	7.7	10.0	42	20	25	34	0	0.32	0.28	bpp	4,6,7,8
eagle	6	nfs	960817	44.25.44	109.56.26	2099	1.5	15.9	0	22	70	18	17	0.3	0	scp	7
eagle	5	nfs	960817	44.24.14	109.57.45	2184	3.5	14.3	16	53	26	19	21	0.2	0.06	scp	7
eagle	4	nfs	960816	44.23.39	109.58.09	2262	3.0	10.9	6	45	41	40.5	0	0.19	0	lwd	7
eagle	1	nfs	960814	44.23.01	109.58.54	2271	1.0	8.0	0	1	59	24	2	0.48	0	scp	7
eagle	2	nfs	960815	44.22.21	109.59.51	2286	2.6	5.7	0	5	85	24	5	0.42	0	scp	7
eagle	3	nfs	960815	44.21.25	109.59.49	2341	3.8	6.2	3	46	42	29.5	5	0.31	0.01	lpp	7
elizabeth	1	nfs	960915	44.18.36	109.43.03	2275	11.0	3.6	27	29	32	40.5	0	0.19	0.19	bpp	1
elizabeth	2	nfs	960915			2318	16.0	nodata	0	0	0						0
elkfork	1	nfs	960819	44.27.39	109.37.54	1815	1.5	11.1	22	58	19	48.5	0	0.03	0.03	bpp	1,4,5,6,7,8
elkfork	3	nfs	960916	44.23.07	109.40.38	2022	5.0	12.2	41	30	20	34.5	5	0.21	0.19	bpp	1,4,5
elkfork	2	nfs	960912	44.21.24	109.41.39	2109	1.0	9.3	26	31	38	34	5	0.22	0.02	ucb	1,4,7,8
elkfork	4	nfs	960915	44.18.47	109.43.07	2216	6.0	7.2	25	37	34	35.5	0	0.29	0.23	bpp	1,4,7,8
eyrie	1	nfs	960796	44.21.30	109.53.08	2348	5.2	6.6	11	39	33	40	0	0.2	0.06	scp	0
fishhawk	1	nfs	960819	44.27.03	109.50.01	1932	2.0	11.4	30	53	18	32.5	8	0.19	0.04	ucb	1,4,5,7,8
fishhawk	6	nfs	960908	44.23.32	109.51.47	2124	2.5	9.0	26	38	27	42	2	0.12	0.1	bpp	1,4,7,8
fishhawk	5	nfs	960907	44.21.46	109.52.11	2236	3.7	8.1	43	34	22	40	0	0.2	0.2	bpp	4,7
fishhawk	2	nfs	960904	44.20.25	109.52.28	2309	1.0	11.0	4	45	48	37.5	6	0.13	0.01	ucb	1,7
fishhawk	4	nfs	960906	44.19.50	109.52.43	2327	3.0	9.4	2	48	41	30	5	0.3	0	scp	1,4,7,8
fishhawk	3	nfs	960905	44.18.21	109.52.36	2403	4.0	4.1	7	36	44	21.5	20	0.17	0.04	scp	0
frost	1	nfs	960912				none										10
glacier	1	nfs	960905	44.18.03	109.52.26	2409	7.0	5.0	20	39	36	38	0	0.24	0.2	bpp	0
goff	1	nfs	960712	44.27.21	109.50.21	1969	8.1	2.6	6	31	28	37.5	3	0.19	0.15	bpp	4,7
goff	2	nfs	960712	44.28.08	109.50.09	2102	8.4	3.1	11	43	44	36	0	0.28	0.05	lwd	0
gothic	1	nfs	960711	44.27.35	109.46.23	1902	11.1	1.6	27	31	32	45.5	3	0.03	0.03	bpp	0
green	1	nfs	960709	44.26.29	109.30.06	1956	9.2	2.1	21	34	42	28.5	8	0.27	0.22	bpp	0
grinnell	1	nfs	960818	44.29.42	109.56.00	2023	6.2	13.2	33	48	18	39	0	0.22	0.22	bpp	4,7,8
grinnell	5	nfs	960821	44.30.56	109.54.52	2158	8.5	11.6	44	34	20	35	0	0.3	0.26	bpp	1,4

grinnell	2	nfs	960820	44.31.48	109.53.43	2271	6.5	7.1	42	32	24	30	8	0.24	0.24	bpp	1,4
grinnell	3	nfs	960820	44.32.55	109.51.57	2455	2.0	11.4	1	25	62	26	10	0.28	0	ucb	1
grinnell	4	nfs	960820	44.33.13	109.51.36	2476	4.5	8.7	11	32	48	15	16	0.38	0.14	bpp	1,4
grizzly	1	nfs	960810	44.27.54	109.34.40	1792	6.4	2.6	20	36	38	26.5	15	0.17	0.14	bpp	1,4,5
grizzly	2	nfs	960810	44.28.36	109.34.26	1890	6.6	3.5	27	33	33	35	5	0.2	0.17	bpp	4
grizzly	3	nfs	960810	44.29.20	109.34.00	2024	6.4	2.1	23	37	32	21	20	0.18	0.18	bpp	4,5
grizzly	4	nfs	960810	44.29.52	109.35.02	2092	9.3	2.5	51	29	16	24	19	0.14	0.14	bpp	4
gunbarrel	1	nfs	960718	44.28.15	109.47.32	1999	5.0	6.7	18	49	25	40.5	0	0.19	0.19	bpp	4,5,7
gunbarrel	2	nfs	960718	44.29.06	109.48.09	2105	4.5	9.2	33	39	24	31	10	0.18	0.14	bpp	4,5
gunbarrel	3	nfs	960718	44.29.51	109.48.37	2176	7.5	7.4	32	29	20	25	14	0.22	0.22	bpp	4,5
halfmile	1	nfs	960709				none										10
horse	1	nfs	960716	44.27.49	109.35.58	1803	3.3	3.3	16	33	39	28	19	0.06	0.06	bpp	1,4,5,8
horse	2	nfs	960716	44.28.36	109.37.00	1882	3.9	3.1	8	46	42	37	7	0.12	0.12	bpp	1,4,5
horse	3	nfs	960716	44.29.54	109.36.43	2025	5.7	3.5	29	37	33	23.5	11	0.31	0.24	bpp	4,5
horse	4	nfs	960716	44.30.31	109.36.49	2112	5.4	3.3	16	38	44	19.5	20	0.21	0.14	bpp	2,4,5
hughs	1	nfs	960827			2512	75.0	nodata	nodata	nodata	nodata						0
icy	1	nfs	960916	44.23.00	109.40.35	2073	11.3	1.5	5	13	53	47.5	0	0.05	0.03	bpp	0
iron	1	nfs	960710				none										10
jim	1	nfs	960709	44.29.34	109.26.01	2195	12.1	3.7	19	37	36	37.5	0	0.25	0.06	ldp	0
jones	1	nfs	960830	44.33.30	109.59.53	2132	6.6	7.7	66	23	10	37	3	0.2	0.2	bpp	4,5
jones	2	nfs	960830	44.33.14	110.01.58	2230	2.0	6.4	18	29	22	39.5	5	0.11	0	scp	1,3,4,7
june	1	nfs	960711	44.27.19	109.43.01	1875	9.5	1.5	14	24	45	42	4	0.08	0.06	bpp	4,5
june	2	nfs	960711	44.26.54	109.43.02	1963	7.5	1.1	23	28	37	39.5	4	0.13	0.09	bpp	4
kitty	1	nfs	960715	44.27.22	109.51.36	1974	8.3	5.1	35	38	23	30.5	6	0.27	0.27	bpp	4,5
kitty	2	nfs	960715	44.26.32	109.51.41	2152	9.8	4.7	33	31	29	28	0	0.44	0.36	bpp	4,5
kitty	3	nfs	960715	44.25.45	109.52.17	2260	11.5	4.6	25	41	23	35	6	0.18	0.18	bpp	0
lake	1	nfs	960913	44.20.16	109.42.00	2219	8.5	2.9	31	40	27	46.5	0	0.07	0.05	bpp	1,4,7
lake	2	nfs	960913	44.20.23	109.41.41	2377	8.4	3.2	13	41	28	39.5	0	0.21	0.21	bpp	1,4,7
libby	1	nfs	960711	44.27.38	109.51.49	1974	10.0	2.9	18	37	43	36	4	0.2	0.2	bpp	3,5
libby	2	nfs	960711	44.27.27	109.51.25	2079	10.5	2.4	21	33	40	28.5	4	0.35	0.29	bpp	4,5
lost	1	nfs	960709	44.27.30	109.32.37	1786	8.5	0.8	4	18	48	46	0	0.08	0	lpp	0
mesa	1	nfs	960718	44.27.09	109.47.40	1923	8.7	2.2	6	40	50	42.5	0	0.15	0.1	bpp	4
mesa	2	nfs	960718	44.26.43	109.48.08	2095	9.3	1.7	18	39	39	34	11	0.1	0.1	bpp	0
middle	1	nfs	960809	44.30.04	109.57.48	2028	1.0	15.9	5	34	51	22	14	0.28	0	lpp	1,4
middle	2	nfs	960809	44.29.40	109.59.15	2078	2.0	14.8	15	47	32	36	5	0.18	0.06	lwd	1,4,7,8
mormon	1	nfs	960727	44.28.41	109.53.46	2012	11.0	6.8	9	37	42	33	10	0.14	0.11	bpp	4,7
mormon	2	nfs	960727	44.29.35	109.53.00	2286	13.6	4.5	18	40	36	33	5	0.24	0.22	bpp	0

moss	1	nfs	960711	44.27.31	109.43.07	1871	5.3	3.5	11	39	40	27	0	0.46	0.3	bpp	1,4,5,8
moss	2	nfs	970711	44.28.06	109.43.18	1932	4.5	4.3	8	44	41	39.5	5	0.11	0.11	bpp	4,7,8
moss	3	nfs	960712	44.28.42	109.43.45	2019	6.1	4.1	14	29	42	33.5	3	0.27	0.27	bpp	1,4,5
nameit	1	nfs	960708	44.27.34	109.33..07	1779	7.1	1.3	20	37	37	33	0	0.34	0.09	ucb	3,4,5
nameit	2	nfs	960709	44.26.37	109.33.38	1894	7.5	1.7	15	33	38	41	5	0.08	0.02	lwd	0
neva	1	nfs	960816	44.23.35	109.58.07	2265	2.9	3.8	0	26	62	14.5	28	0.15	0.01	ldp	7
newton	1	nfs	960708	44.29.43	109.43.51	1902	5.5	1.8	10	29	47	34	10	0.12	0.06	bpp	4,5,7
newton	2	nfs	960708	44.27.58	109.45.28	2030	8.7	1.6	44	32	12	38	5.5	0.13	0.13	bpp	0
norris	1	nfs	960908	44.23.38	109.51.56	2158	15.0	3.1	35	20	12	42	0	0.16	0.16	bpp	0
pagoda	1	nfs	960708	44.27.40	109.34.50	1817	6.6	1.3	10	37	48	36	9.5	0.09	0.07	bpp	4,5
pagoda	2	nfs	960708	44.27.13	109.35.42	1919	5.8	2.5	3	16	58	41	6	0.06	0.04	bpp	4,5
pagoda	3	nfs	960708	44.26.15	109.36.00	2056	7.9	1.1	12	20	55	38.5	9	0.05	0.05	bpp	0
rattlesnake	1	nfs	960710	44.34.07	109.21.03	1963	2.8	1.3	0	6	30	19	1	0.6	0.03	ucb	7
red	1	nfs	960826	44.34.40	109.57.34	2170	12.5	7.1	67	22	8						1,4
red	2	nfs	960829	44.35.31	109.57.55	2499	15.5	5.3	36	33	25	37	0	0.26	0.23	bpp	0
red	3	nfs	960828	44.36.39	109.57.23	2707	10.0	3.1	34	26	37	30	12	0.16	0.14	bpp	0
ruth	1	nfs	960907			2313	9.8	3.8	38	32	24	36	0	0.28	0.28	bpp	4,7
seclusion	1	nfs	960915	44.18.49	109.43.36	2261	5.0	8.5	27	46	26	44.5	0	0.11	0.1	bpp	1,4,7
sheep	4	nfs	960803	44.28.58	109.46.42	1923	5.2	6.4	15	47	33	34.5	4	0.23	0.15	bpp	4,5
sheep	3	nfs	960803	44.26.13	109.46.59	2123	7.0	6.6	17	35	34	34	2	0.28	0.1	bpp	0
sheep	2	nfs	960803	44.25.10	109.47.29	2274	10.6	6.8	39	27	30	44	3	0.06	0.06	bpp	0
sheep	1	nfs	960802			2530	10.9	6.5	39	34	23	36	5	0.18	0.18	bpp	0
shoshonenf	3	nfs	960829	44.34.33	109.57.35	2144	3.0	10.4	29	40	21	47	0	0.06	0.06	bpp	1,4,7,8
shoshonenf	2	nfs	960827	44.36.01	109.54.41	2275	3.0	10.8	19	38	37	27.5	13	0.19	0.16	bpp	1,4
shoshonenf	1	nfs	960827	44.36.48	109.49.03	2493	8.5	4.6	24	16	9	37.5	0	0.25	0.25	bpp	0
slack	1	nfs	960719				none										10
swede	1	nfs	960914	44.21.38	109.41.04	2101	7.0	6.0	16	39	37	36	8	0.12	0.12	bpp	4,5,7
swede	2	nfs	960914	44.21.06	109.40.27	2243	8.5	4.6	29	45	24	41	0	0.18	0.18	bpp	1,4
sweetwater	1	nfs	960727	44.28.03	109.37.41	1814	2.0	18.6	1	32	60	20	10	0.4	0	veg	3,4,8
sweetwater	2	nfs	960806	44.28.45	109.38.13	1838	2.5	16.4	4	41	48	38.5	9	0.05	0.05	bpp	1,4
sweetwater	3	nfs	960806	44.29.27	109.38.52	1870	2.7	13.6	7	45	40	34	8	0.16	0.1	bpp	4
sweetwater	4	nfs	960806	44.30.10	109.38.59	1901	2.0	9.5	23	38	33	45.5	0	0.09	0.05	bpp	4,8
torrent	1	nfs	960827	44.36.36	109.52.23	2362	2.5	4.8	7	26	52	29	13	0.16	0.16	bpp	1,4
wall	1	nfs	960719				none										10
aldrich	1	sfs	970710	44.14.45	109.29.29	1949	7.5	3.4	22	42	37	32	8	0.2	0.16	bpp	0
aldrich	2	sfs	970710	44.13.43	109.28.08	2182	9.0	3.8	57	32	10	31	5	0.28	0.28	bpp	0
aspen	1	sfs	970715	44.06.14	109.38.01	2042	13.5	2.1	31	31	27	35	8	0.14	0.14	bpp	0

bear	1	sfs	970708				none										10
belknap	1	sfs	970709	44.20.44	109.21.30	1807	7.3	2.8	29	41	25	39	2	0.18	0.12	bpp	0
belknap	2	sfs	970709	44.19.48	109.20.56	1951	9.0	4.8	15	54	26	40.5	7	0.05	0.05	bpp	0
bliss	1	sfs	970830			2505	4.5	5.6	1	33	64	6.5	34	0.19	0	lpp	7
bliss	2	sfs	970830	43.53.09	109.47.11	2560	6.4	4.2	42	37	20	39	8	0.06	0.05	bpp	7
bobcat	1	sfs	970715	44.16.28	109.30.55	1934	6.9	5.0	25	39	36	37	0	0.26	0.24	bpp	1,2,4,6
bobcat	2	sfs	970804	44.17.42	109.32.12	2140	10.0	3.7	35	40	23	42	0	0.16	0.15	bpp	1,7
bobcat	3	sfs	970804	44.18.07	109.32.28	2245	13.3	3.2	21	35	14	39	0	0.22	0.22	bpp	0
boulder	2	sfs	970818	44.11.40	109.37.41	1961	7.0	7.8	38	36	21	39.5	0	0.21	0.19	bpp	1,6
boulder	3	sfs	970818	44.10.10	109.32.01	2172	11.1	6.8	26	33	39	37	4	0.18	0.18	bpp	6
boulder	1	sfs	970806	44.07.48	109.33.48	2638	3.0	10.5	10	44	45	30	19.5	0.01	0.01	bpp	0
bull	1	sfs	970708	44.22.43	109.18.39	1713	4.6	2.2	17	29	45	48.5	0	0.03	0.02	bpp	8
bull	2	sfs	970708	44.21.35	109.18.17	1849	7.5	2.2	14	24	52	34	8	0.16	0.16	bpp	0
cabin	1	sfs	970819	44.07.32	109.38.25	1995	4.0	9.9	22	37	33	27	10	0.26	0.02	scp	1,6,7
cabin	2	sfs	970819	44.07.22	109.39.27	2085	5.0	6.4	52	30	15	34	3	0.26	0.26	bpp	0
carter	1	sfs	970707	44.25.03	109.13.24		2.2	3.3	0	3	88	28	13	0.18	0.02	ucb	6
carter	2	sfs	970707	44.23.22	109.12.28		4.2	1.3	2	56	38	37	9.5	0.07	0.07	bpp	0
carter	3	sfs	970707	44.22.26	109.11.19		4.7	2.3	26	59	13	43.5	0	0.13	0.07	bpp	0
castle	1	sfs	970818	44.10.10	109.32.01	2172	12.0	5.5	29	40	30	23.5	15	0.23	0.13	bpp	6
castlerock	1	sfs	970709				none										10
clark	1	sfs	970831	43.52.31	109.45.39	2512	6.4	4.8	55	21	22	39.5	7	0.07	0.07	bpp	0
corral	1	sfs	970701				none										10
crane	1	sfs	970710				none										10
crescent	1	sfs	970830	43.49.42	109.46.47	2569	5.0	5.7	10	45	39	10	33	0.14	0	scp	7
crescent	2	sfs	970830	43.51.29	109.48.16	2669	8.5	3.8	32	45	20	37	5	0.16	0.16	bpp	0
cut coulee	1	sfs	970814				none										10
deer	1	sfs	970723	44.09.33	109.37.14	1965	4.5	7.2	36	39	25	37.5	0	0.25	0.25	bpp	6,7
deer	2	sfs	970723			2060	12.6	5.7	26	35	31	36	0	0.28	0.26	bpp	0
deer	3	sfs	970724	44.09.31	109.39.40	2304	5.9	6.8	24	47	28	36	0	0.28	0.28	bpp	0
deer(low)	1	sfs	970708				none										10
eastfork	1	sfs	970901	43.58.10	109.42.05	2266	3.0	9.4	29	43	30	39	8	0.06	0.06	bpp	1,7
eastfork	2	sfs	970901	43.57.21	109.41.07	2337	5.2	10.3	43	27	27	22	12	0.32	0.32	bpp	7
fall	1	sfs	970810				none										10
gentian	1	sfs	970901			2338	8.0	4.7	51	32	13	32	8	0.2	0.12	bpp	1,7
hardpan	1	sfs	970804	44.18.33	109.27.43	1866	5.5	4.4	47	30	18	46	0	0.08	0.08	bpp	0
hardpan	2	sfs	970806	44.19.07	109.28.02	1928	6.5	5.4	38	42	19	27	7	0.32	0.04	lpp	1,6
hardpan	3	sfs	970820	44.20.10	109.28.19	2094	7.7	4.8	37	38	20	43	0	0.14	0.14	bpp	0

hardpan	4	sfs	970820			2193	9.5	4.9	49	20	29	41	0	0.18	0.18	bpp	0
houlihan	1	sfs	970709				none										10
hunter	1	sfs	970710				none										10
ishawooa	1	sfs	970812	44.16.10	109.30.49	1866	2.5	13.1	16	63	19	29.5	11	0.19	0.06	bpp	1,2,3,5,6,7
ishawooa	2	sfs	970813	44.15.52	109.34.19	1973	4.0	9.5	55	25	16	36	0	0.28	0.28	bpp	1,2,3,6,7
ishawooa	3	sfs	970814	44.12.23	109.35.04	2102	3.5	11.6	29	47	23	30	8	0.24	0.14	bpp	1,2,3,4,6,7
ishawooa	4	sfs	970814	44.13.38	109.39.22	2225	6.0	8.0	41	29	23	32	0	0.36	0.36	bpp	0
ishawooa	5	sfs	970814	44.13.52	109.40.54	2298	7.0	7.0	27	52	13	38.5	4	0.15	0.09	bpp	0
jordan	1	sfs	970709				none										10
lapalli	1	sfs	970814				nodata										0
legg	1	sfs	970710	44.11.51	109.35.33	1939	6.9	1.8	14	40	40	36.5	8	0.11	0.09	bpp	7
littleboulder	1	sfs	970818			2073	11.0	2.0	18	20	53	27	16	0.14	0.1	bpp	2
marquette	1	sfs	970707	44.25.10	109.13.42		1.4	1.2	0	0	23	40	0	0.2	0	ucb	3
marquette	2	sfs	970707	44.23.40	109.14.15		3.2	2.2	8	24	40	23.5	17	0.19	0.13	bpp	1,2,3
marquette	3	sfs	970707	44.22.51	109.14.47		4.4	2.6	3	31	53	21	15	0.28	0.05	lpp	1,2,3
marquette	4	sfs	970708	44.22.11	109.14.10		3.0	1.6	0	26	66	21.5	20	0.17	0.1	bpp	1,2,3
marquette	5	sfs	970708	44.20.59	109.13.36		7.5	2.5	3	27	40	21	18	0.22	0.08	bpp	1,2,3
marquette	6	sfs	970711	44.20.11	109.13.31		8.5	2.5	17	35	42	35.5	8	0.13	0.11	bpp	1
marston	1	sfs	970831	43.54.37	109.46.34	2386	3.0	8.1	2	44	41	20	17	0.26	0	scp	7
marston	2	sfs	970831	43.56.37	109.48.15	2475	3.8	8.3	4	45	33	25.5	11	0.27	0	lwd	0
mower	1	sfs	970701				none										10
needle	1	sfs	970809	44.02.22	109.38.35	2124	6.0	12.2	67	23	10	49	0	0.02	0.02	bpp	0
needle	2	sfs	970809	44.02.02	109.35.12	2397	5.0	11.6	26	42	32	27	11.5	0.23	0.2	bpp	0
robinson	1	sfs	970902	43.58.39	109.42.25	2263	6.0	7.8	57	29	13	41	0	0.18	0.18	bpp	7
rock	1	sfs	970722	44.16.09	109.23.18	1861	5.1	5.8	24	41	27	32	8.5	0.19	0.19	bpp	6,8
rock	2	sfs	970722	44.18.20	109.22.36	1958	5.0	5.3	27	28	35	38	6	0.12	0.12	bpp	6
rock	3	sfs	970722	44.16.55	109.22.17	2134	7.9	4.7	23	46	27	31	2	0.34	0.3	bpp	6
saddle	1	sfs	970808			2195	12.0	7.8	52	30	17	42	0	0.16	0.12	bpp	1
schoolhouse	1	sfs	970710	44.12.22	109.33.40	1911	11.2	0.9	3	42	44	35	12.5	0.05	0.05	bpp	0
scoria	1	sfs	970814				none										10
sfshos	3	sfs	970831	43.55.21	109.45.19	2350	1.5	12.8	4	52	40	48.5	0	0.03	0.03	bpp	7
sfshos	2	sfs	970831	43.53.03	109.46.31	2487	1.5	11.4	0	3	89	4	18	0.56	0	scp	7
sfshos	1	sfs	970802				nodata										1,2,4,5,6,8
sheep	1	sfs	970707	44.24.18	109.16.08	1687	5.5	2.6	8	39	33	15.5	28	0.13	0.12	bpp	5,6,8
sheep	2	sfs	970708	44.23.02	109.15.48	1779	5.0	1.6	0	7	28	18	29	0.06	0	scp	0
sheepeater	1	sfs	970715	44.08.03	109.36.55	1961	8.0	1.4	1	21	55	35	11	0.08	0.08	bpp	0
silver	1	sfs	970810				none										10

timber	1	sfs	970709	44.22.05	109.20.19	1750	5.7	1.0	11	12	58	35.5	13	0.03	0.01	scp	0
twin	1	sfs	970709	44.19.40	109.24.34	1837	8.2	2.2	11	21	51	31.5	11	0.15	0.11	bpp	0
westrock	1	sfs	970722	44.16.11	109.22.12	2219	6.4	4.2	14	54	24	42	2	0.12	0.12	bpp	0
willow	1	sfs	970708				none										10
yellow	1	sfs	970815	44.15.28	109.34.26	2060	17.1	3.5	20	35	33	25.5	12	0.25	0.2	bpp	1,4,7
younts	1	sfs	970901	43.56.59	109.44.02	2329	3.5	9.9	16	40	41	32.5	15	0.05	0.05	bpp	1,7
younts	2	sfs	970901	43.57.06	109.44.45	2422	7.6	3.5	22	17	18	32.5	4	0.27	0.11	bpp	0

APPENDIX B. Allele frequencies for seven populations from Greybull River drainage. Frequencies are listed as a percentage of each allele present in the sample. Samples ranged from 15 - 20 individuals. Alleles specific to a species are indicated in the species column where ysc = Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*) and fsc = finespotted cutthroat trout.

			Stream						
Locus	Allele	Species	Anderson	Greybull	Jack	Pickett	Middle Wood	South Wood	Wood
AK-1*	100	ysc			0.816		0.967	0.867	0.950
	333	fsc			0.184		0.033	0.133	0.050
sAAT-3,4*	100	ysc	0.933	0.725	0.842	0.776	0.800	0.667	0.788
	110	ysc	0.050	0.050	0.013	0.053	0.017	0.100	0.025
	90	ysc	0.017	0.225	0.145	0.171	0.183	0.233	0.188
bGLUA*	100	ysc	0.867	0.850	0.895	0.921			0.925
	70	ysc	0.133	0.150	0.105	0.079			0.075
6PGDH*	100	ysc	0.933						
	90	ysc	0.067						
IDDH*	100	ysc				0.974			
	0	ysc				0.026			
CK-C2*	100	ysc		0.974				0.933	
	50	ysc		0.026				0.067	
sMEP-1*	90	ysc		0.925			0.900		0.975
	100	ysc		0.075			0.100		0.025

Only characteristic cutthroat trout alleles were found in the analyzed samples; however, as indicated several Yellowstone cutthroat trout populations appear to be hybridized with finespotted cutthroat trout.

APPENDIX C. Allele frequencies for eleven populations from the North Fork and South Fork Shoshone River drainages. Only diagnostic alleles are shown and frequencies are listed as a percentage of each allele present in the sample. Samples ranged from 14 - 26 individuals. Species specific alleles are indicated in the species column where ysc = Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), fsc = finespotted cutthroat trout, and rbt =rainbow trout (*O. mykiss*).

			Stream										
Locus	Allele	Species	Bear	ElkFork1	ElkFork2	ElkFork3	Fishhawk1	Fishhawk2	Fishhawk3	Grinnell	HiddenLake	Ishawooa1	Ishawooa2
AK-1*	100	ysc										1.000	0.906
	333	fsc										---	0.094
sAAT-1*	165	ysc	1.000	0.260	0.300	0.605	0.217	0.433	0.375	0.935	1.000	0.806	1.000
	100	rbt	---	0.740	0.700	0.395	0.783	0.567	0.625	0.065	---	0.194	---
CK-A2*	84	ysc		0.192	0.467	0.861	0.109	0.300	0.500	1.000		0.889	0.969
	100	rbt		0.808	0.533	0.139	0.891	0.700	0.500	---		0.111	0.031
CK-C1-*	38	ysc											
	100	rbt											
mIDHP-1*	-75	ysc								0.875		0.806	0.938
	100	rbt								0.125		0.194	0.063
sIDHP-1*	71	ysc								0.934		0.857	1.000
	100	rbt								0.022		0.071	---
	40	rbt								0.044		0.071	---
sMEP-1*	90	ysc	1.000	0.192	0.333	0.778	0.130	0.500	0.647	1.000	1.000	0.917	0.906
	100	rbt	---	0.808	0.667	0.222	0.870	0.500	0.353	---	---	0.083	0.094

sMEP-2*	110	ysc	1.000	0.200	0.333	0.868	0.130	0.367	0.417	0.935	1.000	0.861	0.969
	100	rbt	---	0.800	0.667	0.132	0.870	0.633	0.583	0.065	---	0.139	0.031
PEPA-1*	101	ysc	1.000	0.250	0.233	0.816	0.152	0.267	0.222	0.978	1.000	0.861	1.000
	100	rbt	---	0.750	0.767	0.184	0.848	0.733	0.778	0.022	---	0.139	---
PEPB*	135	ysc	1.000	0.192	0.300	0.789	0.130	0.367	0.444	1.000	1.000	0.806	1.000
	100	rbt	---	0.808	0.700	0.211	0.870	0.633	0.556	---	---	0.194	---
PGM-1*	null	ysc	1.000	0.555	0.447	0.827	0.209	0.577	0.707	1.000	1.000	0.882	0.968
	100	rbt	---	0.445	0.553	0.173	0.791	0.423	0.293	---	---	0.118	0.032
	Average	ysc	1.000	0.263	0.345	0.792	0.154	0.402	0.473	0.962	1.000	0.854	0.878
	Average	rbt	---	0.737	0.655	0.208	0.846	0.598	0.527	0.038	---	0.146	0.028
	Average	fsc	---	---	---	---	---	---	---	---	---	---	0.094

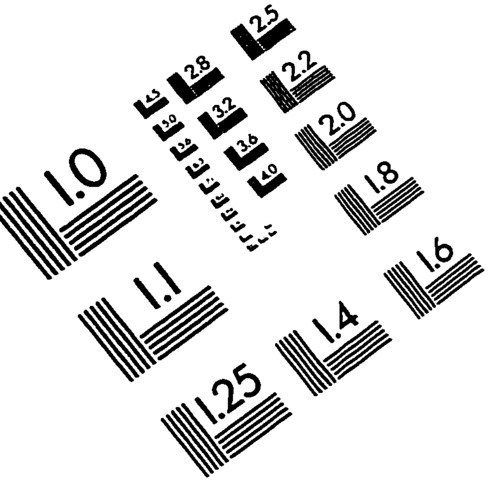
APPENDIX D. Allele frequencies for six populations from the North Fork and South Fork Shoshone and Yellowstone River drainages. Only diagnostic alleles are shown and frequencies are listed as a percentage of each allele present in the sample. Samples ranged from 14 - 26 individuals. Species specific alleles are indicated in the species column where ysc = Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*), fsc = finespotted cutthroat trout, and rbt =rainbow trout (*O. mykiss*).

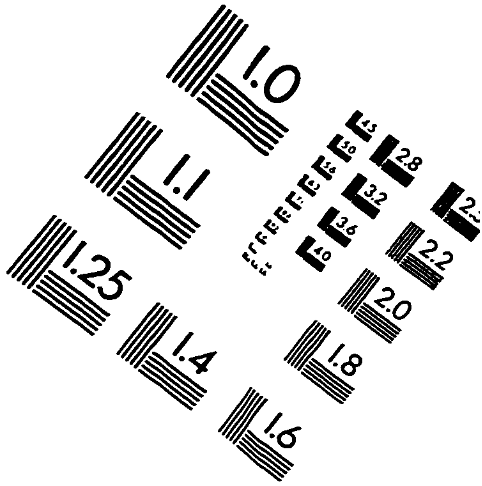
			Stream					
Locus	Allele	Species	Marquette	SFShoshone1	SFShoshone2	SFShoshone3	Thoroughfare	Yellowstone
AK-1*	100	ysc	0.950					
	333	fsc	0.050					
sAAT-1*	165	ysc	1.000	0.421	1.000	1.000	1.000	1.000
	100	rbt	---	0.579	---	---	---	---
CK-A2*	84	ysc		0.531	1.000	1.000		
	100	rbt		0.469	---	---		
CK-C1-*	38	ysc						
	100	rbt						
mIDHP-1*	-75	ysc		0.368	1.000	1.000		
	100	rbt		0.632	---	---		
sIDHP-1*	71	ysc						
	100	rbt						
	40	rbt						

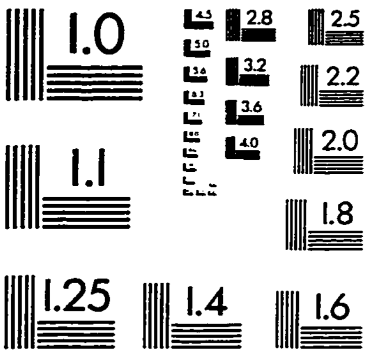
sMEP-1*	90	ysc	1.000	0.395	0.813	0.971	0.976	1.000
	100	rbt	---	0.605	0.188	0.029	0.024	---
sMEP-2*	110	ysc	1.000	0.342	1.000	1.000	1.000	1.000
	100	rbt	---	0.658	---	---	---	---
PEPA-1*	101	ysc	1.000	0.263	1.000	1.000	1.000	1.000
	100	rbt	---	0.737	---	---	---	---
PEPB*	135	ysc	1.000	0.368	1.000	1.000	1.000	1.000
	100	rbt	---	0.632	---	---	---	---
PGM-1*	null	ysc	1.000	0.459	1.000	1.000	1.000	1.000
	100	rbt	---	0.541	---	---	---	---
	Average	ysc	0.950	0.393	1.000	1.000	1.000	1.000
	Average	rbt	---	0.607	---	---	---	---
	Average	fsc	0.050	---	---	---	---	---

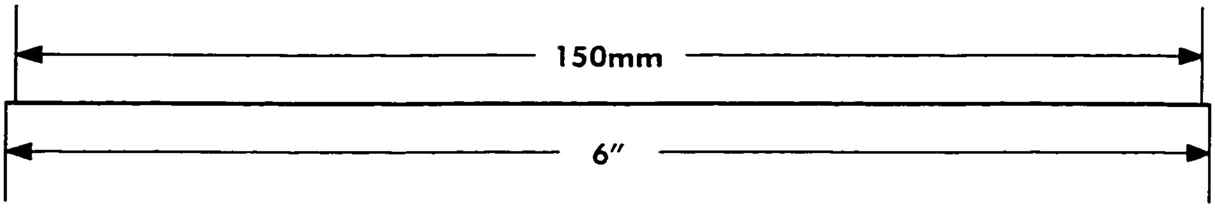
Elk Fork 1-3, Fishhawk 1-3, Grinnell, Ishawooa 1-2, and South Fork Shoshone 1 samples contain alleles characteristic of both Yellowstone cutthroat trout and rainbow trout at all or most of the diagnostic loci analyzed between these fishes. These samples undoubtedly came from hybridized populations of Yellowstone cutthroat trout and rainbow trout. The random distribution of alleles in Elk Fork 2, Fishhawk 2-3, and the South Fork Shoshone 1 indicates that all these fish are of hybrid origin. In contrast a significant number of fish contained only Yellowstone cutthroat trout alleles in Elk Fork 3, Grinnell, and Ishawooa samples, although these populations are hybridized, there are some genetically pure cutthroat trout remaining in the population. Finally, a significant number of fish in Elk Fork 1 and Fishhawk 1 contained only rainbow trout alleles indicating hybrid populations with genetically pure rainbow trout present. The AK-1*333 allele was found only in Marquette and Ishawooa samples, indicating that only these two are hybridized with finespotted cutthroat trout. Alleles characteristic of only Yellowstone cutthroat trout were detected at all loci analyzed in Bear, Hidden, South Fork Shoshone 2-3, Thoroughfare, and upper Yellowstone samples.

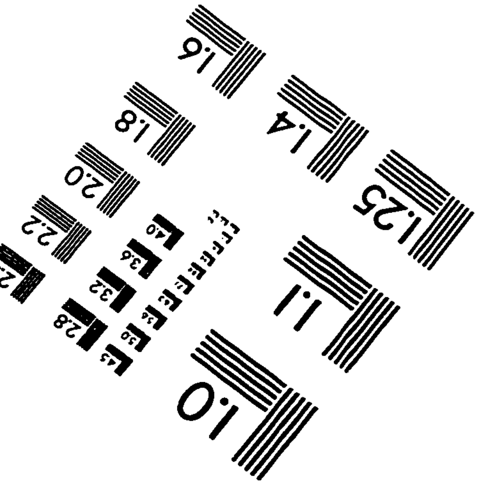
IMAGE EVALUATION
TEST TARGET (QA-3)

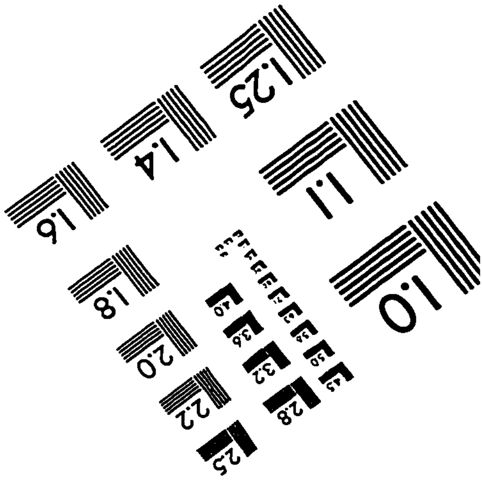












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