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Distribution, Status, and Likely Future Trends of Bull Trout within the Columbia River and Klamath River Basins

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Abstract.—We summarized existing knowledge regarding the distribution and status of bull trout *Salvelinus confluentus* across 4,462 subwatersheds of the interior Columbia River basin in Oregon, Washington, Idaho, Montana, and Nevada and of the Klamath River basin in Oregon, a region that represents about 20% of the species' global range. We used classification trees and the patterns of association between known distributions and landscape characteristics to predict the likely distribution of bull trout in unsampled subwatersheds. Bull trout are more likely to occur and the populations are more likely to be strong in colder, higher-elevation, low- to mid-order watersheds with lower road densities. Our results show that bull trout remain widely distributed and occur in most of the subbasins representing the potential range. Some strong and relatively secure populations exist. In general, bull trout are better represented in the region as a whole than many other native species. Important declines in distribution and status are evident, although the extent of change is clouded by uncertainties in the historical distribution. Despite the broad distribution, much of the current range is poorly represented by strong or protected populations. The southern margins of the range are a particular concern and could be an important priority for conservation management. Continued habitat loss associated with disruptive land use practices threatens remaining bull trout populations. Even with no further habitat loss, existing fragmentation could contribute to continuing local extinctions aggravated by the expansion of introduced species and the effects of climate change.

Many biologists have expressed concern that bull trout *Salvelinus confluentus* are in trouble. Declining populations may be threatened with extinction through habitat loss and fragmentation, introduced species, and overfishing (e.g., Mongillo 1992; Ratliff and Howell 1992; Thomas 1992; Rieman and McIntyre 1993; Henjum et al. 1994; Jakober 1995). Petitions for listing under the U.S. Endangered Species Act culminated in a 1994 decision by the U.S. Fish and Wildlife Service that listing was warranted but precluded because of other priorities (U.S. Office of the Federal Register [June 10, 1994]:30254). That decision was continued in 1995 (U.S. Office of the Federal Register [June 12, 1995]:30825). Despite the attention, uncertainty and debate regarding the status of bull trout remain.

A growing body of work suggests many bull trout populations are at risk. Migratory life histories have been restricted or lost entirely (Ratliff and Howell 1992; Rieman and McIntyre 1993; Goetz 1994; Jakober 1995). There is evidence of declining trend in some populations (Mauser et. al. 1988; Weaver 1992; Rieman and McIntyre 1996; Rieman and Myers 1997) and local extinctions have been reported across the species' range (Mongillo 1992; Ratliff and Howell 1992; Thomas 1992; Goetz 1994). Population declines are attributed largely to the effects of land management and development (Ratliff and Howell 1992; Rieman and McIntyre 1993; Henjum et al. 1994), but the expansion of exotic species (Donald and Alger 1992; Markel 1992; Ziller 1992; Leary et al. 1993) and the isolation of habitats by dams, diversions, or other barriers (Ratliff and Howell 1992; Jakober 1995) also appear important.

The present distribution and status of bull trout are poorly defined in many areas. Attempts to quantify extinctions are limited by a lack of historical information. Status reviews have been completed by each of the states with populations, but a comprehensive and consistent picture across the species' range has yet to emerge. In their review for the proposed endangered species listing, the U.S. Fish and Wildlife Service was limited predominantly to gray and anecdotal literature. A useful "meta-analysis" has been limited by an inconsistent methodology, scale, and updating of available information. A comprehensive picture is limited by the lack of sampling across a substantial portion of the species' potential distribution.

A recent assessment by the Forest Service and

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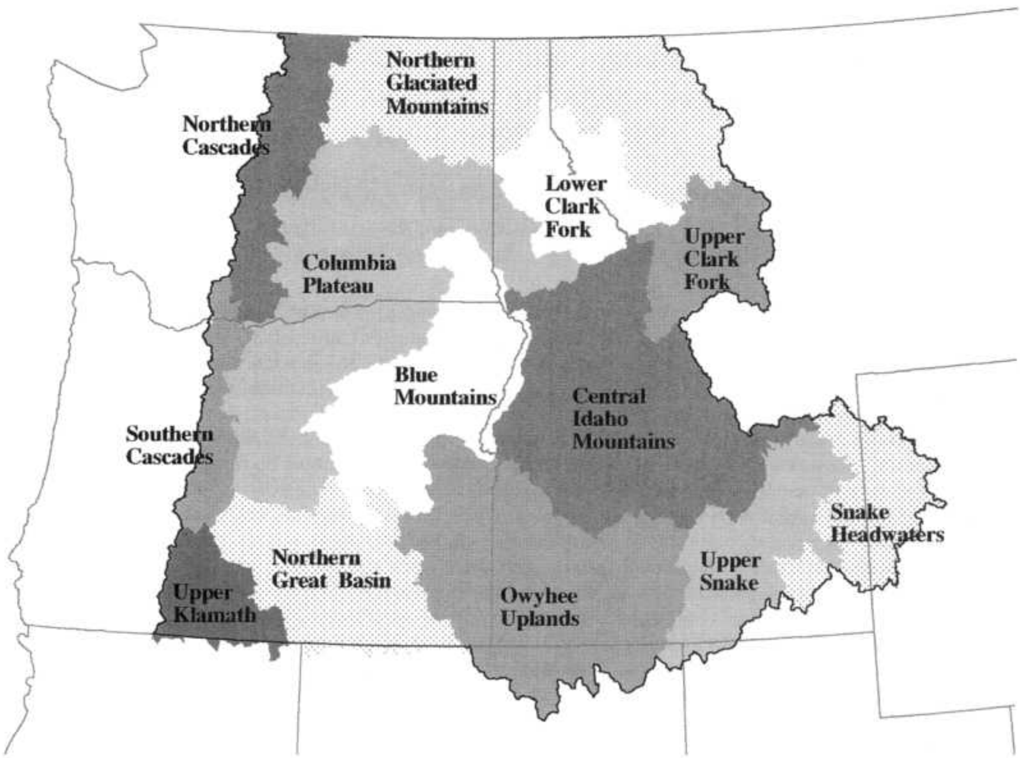

FIGURE 1.—Interior Columbia River basin within the United States and part of the Klamath River basin represented in this study. Ecological reporting units (ERU) used to summarize information across broad regions of similar biophysical characteristics are also shown.

Bureau of Land Management of ecological systems throughout the interior Columbia River basin within the United States and portions of the Klamath River and Great basins (Quigley and Arbelbide 1997) provided the opportunity for a more complete picture. The project was an attempt to characterize large regions from a number of perspectives, and thus it provided the opportunity to look at fishes in a broad landscape context. In this paper we focus on the results of our work with bull trout; a general look at other salmonids is provided by Thurow et al. (1997, this issue).

Our objective is to describe the distribution and status of bull trout across a major part of the species' range. Our approach was based on a summary of current knowledge provided by more than 150 biologists working throughout the study area. We extrapolated to unsampled areas with classification models based on associations of known occurrences with landscape characteristics. We use our results to describe current (or recent) conditions and to consider factors that are likely to influence the distribution of the species in the future.

Background and Study Area

The study area included all lands in the Columbia River basin east of the Cascade Mountain crest within the United States and those portions of the Klamath River basin and Great Basin in Oregon (Figure 1). The area includes over 58.3×10^6 ha in Idaho, Montana, Nevada, Oregon, Washington, and Wyoming. The Klamath basin within the study area comprises 1.5×10^6 ha. Bull trout do not occur in the Great Basin, so that area was excluded from analysis for this paper.

Topography was used to define a hierarchical system of subbasins, watersheds, and subwatersheds. Within the study area, 164 large subbasins were defined (Figure 2). The subbasins were further divided into watersheds, which average about 22,820 ha in surface area. The watersheds were divided into 7,498 subwatersheds averaging 7,800 ha each. The hydrologic divisions follow the hierarchical framework of aquatic ecological units described by Maxwell et al. (1995). The delineations and map coverages were provided for our use by the Columbia Basin Project (Quigley and

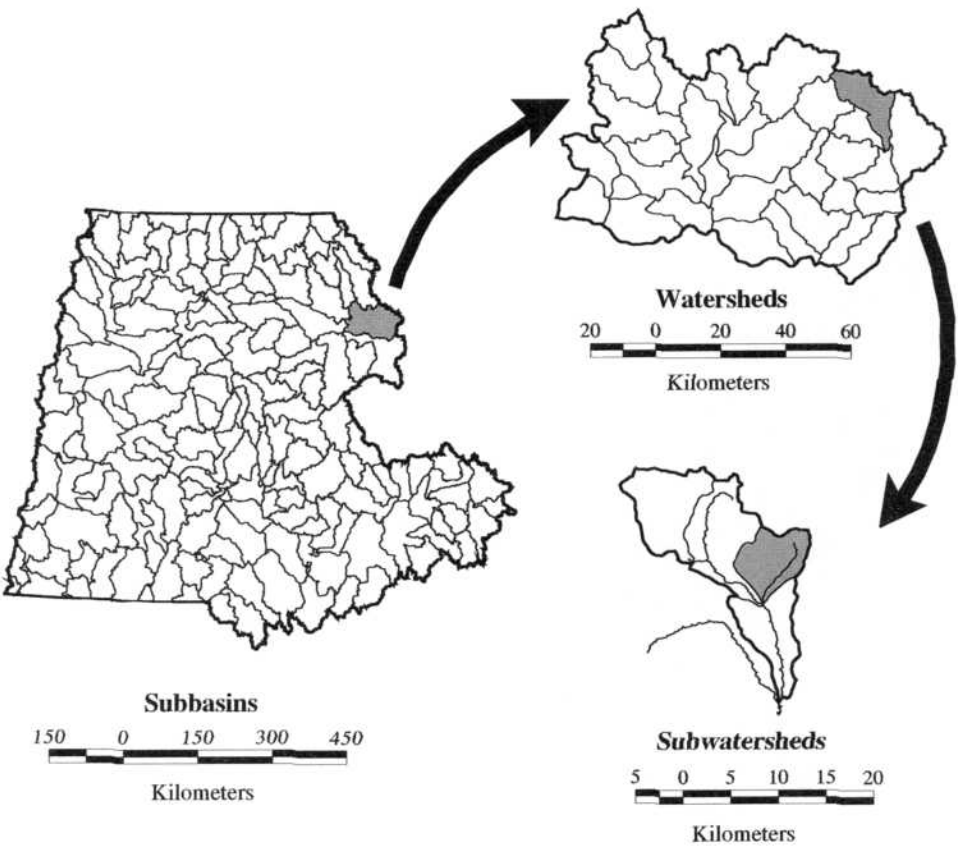

FIGURE 2.—Hydrologic divisions of subbasins, watersheds, and subwatersheds used to characterize landscape information and classify the status and distribution of bull trout across the interior Columbia River basin within the United States and part of the Klamath River basin. The hierarchical framework of drainage boundaries was defined from topography as described by Maxwell et al. 1995. Detailed descriptions and derivations are available in Quigley and Arbelbide (1997).

Arbelbide 1997). We used the subwatersheds as our basic unit of summary and prediction.

We also considered 13 larger landscape classifications, known as ecological reporting units (ERUs; Figure 1), representing distinct land areas of broadly homogeneous biophysical characteristics (Jensen et al. 1997). Species that are distributed over a broad geographic range likely have evolved under a similarly broad range of environmental conditions. If gene flow has been limited by either distinct barriers or distance, there is potential for local and unique adaptations to those environments (Lesica and Allendorf 1995). Because the ERUs may represent distinct environments for bull trout, there is the potential for significant evolutionary divergence across the species' range. Conservation of the full genetic diversity and evolutionary potential may imply conservation of populations representing that full range (Leary et al. 1993; Li et al. 1995; Allendorf et al. 1997). We summarized our results by ERU to consider potentially important gaps or differences in the representation of distinct populations and environments.

Bull trout are restricted to North America (Cavendar 1978; Haas and McPhail 1991). The recorded distribution ranges from the McCloud River in northern California and the Jarbidge River in Nevada to the headwaters of the Yukon River in Canada (Figure 3). The western limits are near the Pacific coast in tributaries of Puget Sound. Bull trout have been found eastward to the headwaters of the Saskatchewan and Athabasca rivers in Alberta and the headwaters of the Columbia and Flathead rivers in British Columbia and Montana. They have been recorded throughout the Columbia River basin except for the contiguous waters of the Snake River above Shoshone Falls. The potential range of bull trout within

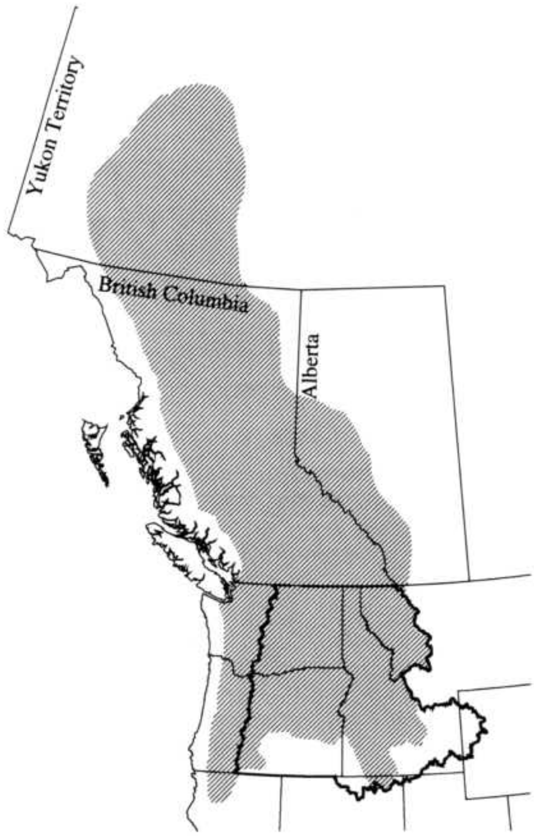

FIGURE 3.—Global range of bull trout and the area (within the heavy lines) of this study. Our representation of the complete distribution was adapted from Cavendar (1978) and Haas and McPhail (1991).

our study area represents about 20% of the species' global range (Figure 3).

Bull trout are believed to be a glacial relict (McPhail and Lindsey 1986), and the broad distribution probably has contracted and expanded periodically with natural climate changes (Williams et al. 1997). Patterns of genetic variation suggest an extended and evolutionarily important isolation between populations in the Klamath and Malheur river basins of Oregon and those in the Columbia River basin (Leary et al. 1993). Current work may extend the inference of that isolation to other basins in Oregon as well (P. Spruell, University of Montana, personal communication). Populations throughout the Columbia River basin appear more closely allied and may have expanded from common glacial refugia or maintained high levels of gene flow among populations in recent evolutionary time (Williams et al. 1997).

Bull trout primarily inhabit colder streams (Pratt 1984, 1992; Henjum et al. 1994; Rieman and McIntyre 1995), although individuals have been observed in larger rivers throughout the Columbia River Basin (anecdotal accounts include the main stems of the Columbia and Snake rivers near their confluence and upstream). Juveniles inhabit natal streams for one to three years (Shepard et al. 1984; Pratt 1992); older fish may remain in those streams for life, or they may range over entire river basins (Pratt 1992; Jakober 1995; Swanberg 1996).

Methods

Known status and distribution.—Through a series of workshops in early 1995, we asked state, federal, tribal, and privately employed biologists to characterize the status of bull trout in all of the subwatersheds of the study area. More than 150 biologists from across the region participated in the project by summarizing available information. At a first level of resolution, bull trout occurrence in each subwatershed was characterized as present, absent, or unknown. When bull trout were present, additional information (when available) was used to characterize a subwatershed as predominantly spawning and rearing habitat, or as supporting habitat used only seasonally (i.e., as migratory corridors, wintering, or staging areas). Populations in spawning and rearing areas were further classified as strong or depressed depending on abundance, current trends in abundance, and the full expression of potential life histories (Table 1). Biologists were asked to rely on biological information and not to make judgements regarding status from habitat or environmental conditions.

We submitted the original classifications to review by others familiar with the area in question whenever possible and attempted to use only the most current information. We summarized bull trout distribution information from existing state databases to validate and augment presence or absence classifications. We restricted our use to databases that had been created or updated after 1993. In general, biologists provided information in addition to and directly supporting that already available from the databases. Whenever a conflict occurred between any two sources that could not be resolved with current information, the subwatershed population was classified as "unknown."

Despite the criteria provided for classification, an element of subjectivity remains in the data. Most of the information represented by the classifications is not published or peer reviewed. Inconsistencies probably occur in classifications, and the quality of available information may vary. It

TABLE 1.—Guidelines for biologists' classifications of the occurrence and status of bull trout in subwatersheds of the interior Columbia River basin and part of the Klamath basin.

Population status	Population characteristics in the subwatershed
Strong	A strong population meets all of the following criteria • Spawning and rearing occur within the subwatershed • All major life history forms that once occurred are still present in the subwatershed • Abundance is stable or increasing • The population, or metapopulation of which this subwatershed population is a part, supports an average of 5,000 individuals or 500 adults
Depressed	A depressed population meets at least one of the following criteria • A major life history component has been eliminated • Numbers within the subwatershed are declining, or bull trout occur in less than half of the historical habitat, or numbers are less than half of what the watershed supported historically • Total abundance for the population or metapopulation within the subwatershed, or the larger region of which this subwatershed is a part, is less than 5,000 individuals or 500 adults
Absent	A population is absent if both the following criteria are met • The species is either extinct or has never occupied the subwatershed • The subwatershed is within the natural range of the species and colonization of the subwatershed was historically possible
Transient	The subwatershed does not support spawning or extended rearing and functions only as a migrational corridor or as a seasonal staging and wintering area for migrating fish
Present	The species occurs in the subwatershed but not enough is known to classify type of use or status
Unknown	No information is available regarding the current presence or absence of the species in the subwatershed

is impossible, however, to generate a comprehensive and current view of any species distribution and status without relying on this kind of information. Recognizing the potential for errors, we believe these data represent as complete a summary of the current (or recent), collective knowledge of bull trout as is possible.

We also note that the resolution of our data may produce more optimistic estimates of current distributions than work based on length or area of streams. That is, if bull trout occurred anywhere in a subwatershed, they were considered present in the entire subwatershed. Analysis at the subwatershed level of resolution was necessary simply because of logistical and computational constraints imposed by the scale of our study. We believe, however, that because of the patchy nature of bull trout distributions, the potential for extended movement and dispersal, and the substructuring of regional populations apparent at roughly this scale (sensu Rieman and McIntyre 1995), subwatersheds actually are the most appropriate level for our analysis. In essence we, believe that subwatersheds best approximate the distributions of potentially discrete groups or local populations, and thus represent a better summary unit than stream reaches. To minimize any potential bias, all estimates of the distributions were based on the number of subwatersheds and not area.

Potential historical range.—We defined the potential historical range for bull trout as those waters either at least temporarily occupied by, or directly accessible to, the species within the study area prior to European settlement. Our estimate of that range was inferred from the historical distributions summarized for Washington (Mongillo 1992), Montana (Thomas 1992), Idaho (Idaho Department of Fish and Game, unpublished bull trout management plan) and Oregon (Ratliff and Howell 1992), the current distribution, and any additional historical accounts (e.g., Hubbs and Miller 1948). Sampling reports and anecdotal accounts indicate that bull trout still occur, at least occasionally, in the main-stem Columbia and Snake rivers. Bull trout often move throughout the river systems connecting subbasins and more localized spawning and rearing habitats (Bjornn and Mallet 1964; Jakober 1995; Swanberg 1996). Genetic work indicates substantial gene flow has occurred among subbasins in recent evolutionary time (Leary et al. 1993; Williams et al. 1997). For these reasons, we included all subwatersheds that were directly accessible according to the known current and historical occurrences as part of the potential historical range (hereafter referred to as potential range). Even in pristine environments, the distribution of bull trout is patchy (Rieman and McIntyre 1993, 1995), and it seems unlikely that bull trout occupied all of the waters of the potential range at any one time. However, because this species has ranged widely and still does so, we believe it likely that bull trout have occurred throughout the area.

Predictive models.—The influence of the biophysical environment and land management on the status and distribution of bull trout was explored by means of statistical models known as classification trees (Breiman et al. 1984). Our primary objective in this analysis was to predict fish presence and status using landscape features and management history, and to identify the elements that are associated most prominently with bull trout distributions. Tree-based models represent a nonparametric alternative to conventional linear models that have more constraining assumptions about data structure (see Breiman et al. 1984; Clark and Pregibon 1992; Crawford and Fung 1992; Taylor and Silverman 1993). Tree-based models offer several advantages. First, where the set of predictor variables includes both continuous and discrete variables, tree-based models may be easier to interpret. Second, tree-based models are insensitive to monotonic transformations of the predictor variables, relying solely on the rank ordering of variables. Third, tree-based models are better at capturing nonadditive behavior. The disadvantage of tree-based models is that they are of limited utility for drawing statistical inferences. Thus, their primary uses are for building predictive models, data exploration, and hypothesis generation, rather than testing specific hypotheses.

For categorical response variables, such as species' presence or absence, tree-based models result in classification trees, so named because of the branching diagrams often used to display the models. Classification trees consist of a dichotomous rule set that is generated through a process of recursive partitioning. Recursive partitioning involves sequentially splitting the data set into more homogeneous units, relative to the response variable, until a predefined measure of homogeneity is reached, or until no further subdivision is desired or feasible. Data are split at each juncture based on a single predictor variable that produces the greatest differences between the two resultant groups of observations. Predictor variables can be reused at subsequent splits. The objective of the classification algorithm is to derive a terminal set of nodes, each containing a subset of the original data, where the distribution of the response variable is independent of the predictor variables to the greatest extent possible. Details of the algorithm used to build the classification trees can be found in Clark and Pregibon (1992) and Statistical Sciences (1993).

All analyses involving classification trees were performed with the Splus[2] programming language, following the procedures outlined in Clark and Pregibon (1992). We summarized 28 potential predictor variables (other than ERUs; Table 2) from more than 200 coverages representing landscape characteristics across the study area. We limited our variables to those with potential influence on aquatic ecosystems and generally eliminated many of those that were strongly correlated with or directly derived from others (Lee et al. 1997). The variables were both categorical and continuous and represented vegetative communities, climate, geology, landform and erosive potential, and past management or relative intensity of human disturbance (Table 2). Detailed descriptions of the complete landscape coverages, variables, and their derivations can be found in Quigley and Arbelbide (1997) and Lee et al. (1997). We developed two separate classification trees. In the first, known bull trout status was reduced to a binomial variable by combining present–strong, present–depressed, or migration corridor, into a single classification of present. A second tree was constructed with a trinomial response to distinguish spawning and rearing areas (present–strong or –depressed) from areas that are not used, or used only as migratory corridors or seasonal habitats. Present–strong and present–depressed were retained as separate responses, while migration corridor and absent were combined in the third permissible response. Both trees were optimized for fit using the cross validation and pruning routines described by Breiman et al. (1984) and Clark and Pregibon (1992). The final trees were used to estimate the probability of presence or absence of bull trout in subwatersheds classified as unknown and to predict status in subwatersheds classified as unknown or present unknown. All estimates and predictions were limited to the potential range.

Summary.—We summarized both the known and predicted information by ERU and across the study area. To estimate how much of the current distribution was protected by special land use designations, we also summarized the number of occupied subwatersheds within designated wilderness or National Park Service lands. Bull trout distributions were mapped using geographic information systems (GIS). The GIS coverages depicting the subwatersheds, land ownership, and management status were developed as part of the landscape information noted above (Quigley and Arbelbide 1997).

Results

The estimated potential range for bull trout, including main-stem corridors, represented about

[2] The use of trade or firm names in this paper is for reader information only and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

TABLE 2.—Descriptions of landscape variables used to build classification trees in the analysis of bull trout distribution and status in the Columbia River and Klamath basins. All values for physiographic, geophysical and vegetation variables were summarized for subwatersheds from complete coverages with a pixel resolution of 1 km^2. All values expressed as percentages refer to the percent area of the subwatershed. Detailed descriptions and derivations are described in Quigley and Arbelbide (1997).

Variable name	Description
ERU	Ecological reporting unit (see text and Figure 1)
	Physiographic and geophysical
slope	Area weighted average midslope based on 90-m digital elevation maps
slope2	Percent of area in slope class 2 (slopes >10%, <30%)
con1	Percent weakly consolidated lithologies
con2	Percent moderately consolidated lithologies
con3	Percent strongly consolidated lithologies
sdt1	Percent lithologies that produce coarse-textured sediments
sdt2	Percent lithologies that produce medium-textured sediments
sdt3	Percent lithologies that produce fine-textured sediments
alsi1	Percent felsic lithologies
alsi2	Percent intermediate aluminosilicated lithologies
alsi3	Percent mafic lithologies
alsi4	Percent carbonate lithologies
pprecip	Mean annual precipitation extrapolated to complete coverage using a regional climate simulation model
elev	Mean elevation
mtemp	Mean annual air temperature extrapolated to complete coverage using a regional climate simulation model
solar	Mean annual solar radiation based on topographic shading, latitude, and aspect
streams	Total length of streams within subwatershed based on 1:100,000 scale hydrography
drnden	Drainage density (stream length/watershed area)
anadac	Access for anadromous fish (0 = no, 1 = yes)
hucorder	Number of upstream subwatersheds tributary to the watershed of interest (0 designates a headwater subwatershed)
hk	Soil texture coefficient
baseero	Base erosion index representing relative surface erodability without vegetation
ero	Surface erosion hazard, a derived variable based on baseero and other modifying factors
bank	Streambank erosion hazard, a derived variable representing relative bank stabilities
	Vegetation
vmf	Vegetation amelioration factor, a derived variable representing the relative amount of ground cover in vegetation
vegclus	Current vegetation class (12 possible types) based on structure and composition
	Ownership and management
roaddn	Estimated road density class (5 classes: none–very high)
mgclus	Management class (10 possible types, intense commodity extraction–wilderness) based on ownership and management emphasis

70% of the subwatersheds in the study area (Table 3). Bull trout probably occurred throughout much of the Klamath and the Columbia River basins with the exception of a portion of the Columbia Plateau and the upper reaches of the Snake River basin in Idaho and Wyoming (Figure 4). Bull trout are reported from the geologically isolated sink drainages of the upper Snake River Basin (Hubbs and Miller 1948), but not from other waters of the Snake River basin above Shoshone Falls. Bull trout were reported as present in about 36% of the subwatersheds within the potential range. In about 28% of the potential range, bull trout presence was unknown or unclassified; in another 10% bull trout were known to be present but their status unknown (Table 3).

Both classification models were developed from 2,717 subwatersheds with complete landscape information and known status. The model that was limited to status in spawning and rearing areas (i.e., strong, depressed, absent) had an overall classification success rate of about 82% (Table 4). The model was most successful predicting subwatersheds where bull trout were absent (86%) and performed less well predicting the occurrence of strong (61%) and depressed (70%) populations (Table 4). We used 21 variables, but a major portion of the deviance (a measure of variation in categorical variables) was explained by mean annual air temperature (mtemp), road density (roaddn), and watershed order (hucorder) (Table 5). Bull trout were more likely to occur in colder subwatersheds with lower road densities, and in a midorder to headwater context. For example, bull trout were four times more likely to be present (spawning and rearing) and populations were more than six times more likely to be classified as strong in subwatersheds with a mean annual air temperature less than 5.1°C, than in warmer areas (i.e., the frequency of strong populations was 0.102 where temperatures were below 5.08°C and 0.015 where they exceeded 5.08°C; Table 5). Over 80% of the reported spawning and rearing areas were in the colder subwatersheds. Within the colder subwatersheds, bull trout populations were reported as strong nearly seven times more frequently in those with less than 2.5 miles of road per square mile than those with more (Table 5).

The more general model that was used to predict presence (including transient occupation of seasonal habitats) and absence had a slightly better overall classification success rate (83%; Table 6). We included 19 variables in this model, but the principal variables explaining most of the deviance

TABLE 3.—Summary of classifications (number of subwatersheds) of occurrence and status for bull trout within the interior Columbia River basin and part of the Klamath River basin in Oregon, Washington, Idaho, Montana, and Nevada.

Ecological reporting unit	Total	Potential historical range	Total present	Status where present: Strong	De-pressed	Unknown	Trans-ient	Absent	Unknown or no classifi-cation
Northern Cascades	340	319	144	10	22	90	22	84	91
Southern Cascades	141	80	32	10	6	9	7	40	8
Upper Klamath	175	73	9	0	9	0	0	48	16
Columbia Plateau	1,089	551	59	3	19	17	20	217	275
Blue Mountains	695	442	163	23	72	31	37	177	102
Northern Glaciated Mountains	955	955	316	26	125	77	88	335	304
Lower Clark Fork	415	415	166	4	75	46	41	160	89
Upper Clark Fork	306	306	145	21	109	5	10	84	77
Owyhee Uplands	956	174	7	0	2	1	4	102	65
Central Idaho Mountains	1,232	1,147	567	72	186	167	142	360	220
Entire assessment area	6,304	4,462	1,608	169	625	443	371	1,607	1,247

were subwatershed slope (slope), order (hucorder), and mean elevation (elev). Bull trout were reported more frequently in steeper, higher-elevation watersheds, but were less likely in the lowest-order (i.e., headwater) than in larger streams (Table 7). This indicates that bull trout occur commonly throughout larger stream and river systems, even though they are not found in all of the headwater tributaries.

We used the models to estimate the probability of occurrence of bull trout in subwatersheds in which bull trout presence was unknown (Figure 4) and to predict the status of bull trout in watersheds in which bull trout presence was unknown or in

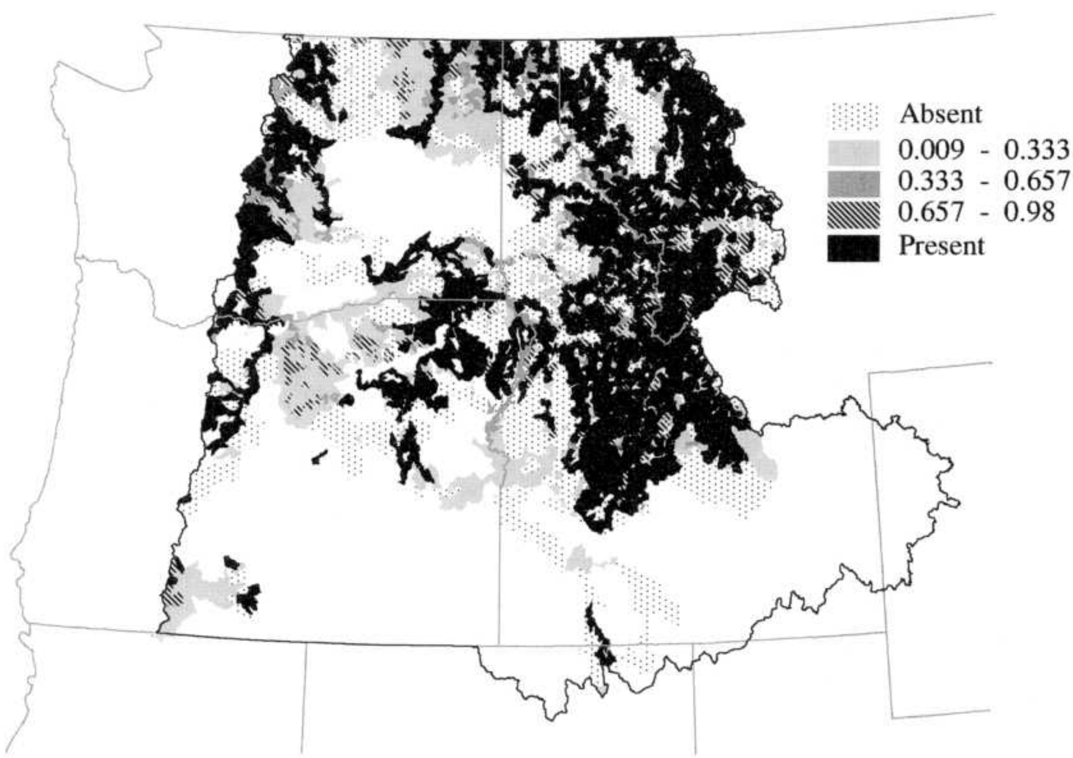

FIGURE 4.—Classified presence, absence, and estimated probability of occurrence of bull trout across the interior Columbia River basin within the United States and part of the Klamath River basin. Areas not shaded represent subwatersheds outside the potential range.

TABLE 4.—Cross-classification comparison of predicted and reported status of bull trout within spawning and rearing areas across the potential historical range among subwatersheds of the interior Columbia River basin and part of the Klamath River basin in Oregon, Washington, Idaho, Montana, and Nevada.

Reported status	Predicted status in spawning and rearing area		
	Absent	Depressed	Strong
Absent	1,789	99	36
Depressed	267	335	22
Strong	31	48	90

TABLE 6.—Cross-classification comparison of predicted and reported occurrence of bull trout within the potential historical range among subwatersheds of the interior Columbia River basin and part of the Klamath River basin in Oregon, Washington, Idaho, Montana, and Nevada.

Reported occurrence	Predicted occurrence across range	
	Absent	Present
Absent	1,326	228
Present	226	937

which they were present but their status was unknown (Figure 5). Predictions were made for a total of 927 subwatersheds. By combining the known and predicted classifications we estimated that bull trout occurred in about 44% of the potential range and 26% of the entire study area. We estimated that subwatersheds supporting spawning and rearing bull trout (strong or depressed populations) were about 25% of the potential range while those supporting strong populations were about 6% (Tables 3, 8). The model predictions tended to be spatially correlated with known conditions. That is, predicted strong populations were likely to occur in proximity to known strong populations, and predicted depressed populations in proximity to known depressed populations (Figure 5). These patterns probably emerged because of spatially correlated landscape characteristics and indicate that suitable habitats are likely to be clumped across larger areas.

Our summary of status and distribution shows a substantial variation in conditions across the potential range. We estimated that of the 270 subwatersheds classified or predicted as having strong populations, about one third fell within lands protected by special-use designations (Table 8). The Central Idaho Mountains represented the most secure part of the distribution. In contrast, the Upper Klamath and Owyhee Uplands ERUs had the fewest estimated occurrences and contained no subwatersheds classified as having strong populations (Table 8).

Discussion

Current Status and Distribution

Our analysis indicated that bull trout remain widely distributed across the species' potential range. Although many areas support only remnant populations, bull trout still were reported or predicted to occur in most of the subbasins within the potential range. Lee et al. (1997) found that of 66 native species occurring within the region, bull trout were the seventh most widely reported. Although this might result, in part, from the differential sampling intensity targeted at different spe-

TABLE 5.—The first nine nodes of a classification tree, showing discriminating variables and splitting criteria, and associated frequency distributions for bull trout status (absent, depressed, strong) within spawning and rearing areas in 2,717 subwatersheds used to develop the models. The nodes, variables, and observed distributions of the classifications are displayed in hierarchical fashion representing the structure of the tree. For example, the first, or root, node represents the complete distribution. The first split based on mean annual air temperatures less than 5.08°C (node 2) or greater than 5.08°C (node 3) produced two subdistributions that are further, and independently, subdivided. For further information on the development and application of classification trees see Brieman et al. (1984), Clark and Pregibon (1992), and Lee et al. (1997).

Node	Variable and criteria	Sample size	Deviance	Modal class	Relative frequency		
					Absent	Depressed	Strong
(1)	root	2,717	4103.000	A	0.708	0.230	0.062
(2)	mtemp < 5.08°C	1,474	2726.000	A	0.558	0.340	0.102
(4)	roaddn < 2.5	539	1131.000	A	0.475	0.304	0.221
(8)	hucorder < 35.5	500	1070.000	A	0.434	0.328	0.238
(9)	hucorder > 35.5	39	0.000	A	1.000	0.000	0.000
(5)	roaddn > 2.5	935	1466.000	A	0.606	0.360	0.033
(3)	mtemp > 5.08°C	1,243	995.000	A	0.886	0.099	0.015
(6)	baseero < 47.03	1,121	704.600	A	0.917	0.074	0.009
(7)	baseero > 47.03	122	211.100	A	0.598	0.328	0.074

TABLE 7.—The first nine nodes of a classification tree showing discriminating variables and associated frequency distributions for bull trout presence or absence in 2,717 subwatersheds used to develop the models. The nodes, variables, and observed distributions of the classifications are displayed in hierarchical fashion representing the structure of the tree.

Node	Variable	Sample size	Deviance	Modal class	Relative frequency	
					Absent	Present
(1)	root	2,717	3,710.000	A	0.572	0.428
(2)	slope < 20.68	1,325	1,467.000	A	0.758	0.242
(4)	hucorder < 0.5	621	420.600	A	0.894	0.106
(8)	elev < 5,449 m	495	192.100	A	0.951	0.048
(9)	elev > 5,449 m	126	160.400	A	0.667	0.333
(5)	hucorder > 0.5	704	921.800	A	0.638	0.362
(3)	slope > 20.68	1,392	1,868.000	P	0.395	0.605
(6)	hucorder < 1.5	857	1,187.000	A	0.520	0.480
(7)	hucorder > 1.5	535	527.000	P	0.194	0.806

cies, even accounting for such a bias bull trout appear to be distributed far more widely than many native fishes.

A broad distribution does not mean there have not been important declines. We estimated that strong populations occur in only 6% of the potential range, or about 24% of the estimated spawning and rearing subwatersheds (i.e., strong + depressed). If we consider all of the subwatersheds in the historical range with an estimated mean annual air temperature (mtemp) less than 5.1°C (i.e., the subwatersheds supporting most of the identified spawning and rearing) as the historical spawning and rearing habitat, bull trout were estimated as strong in 12% and present in 44% of subwatersheds. We cannot estimate the actual decline in

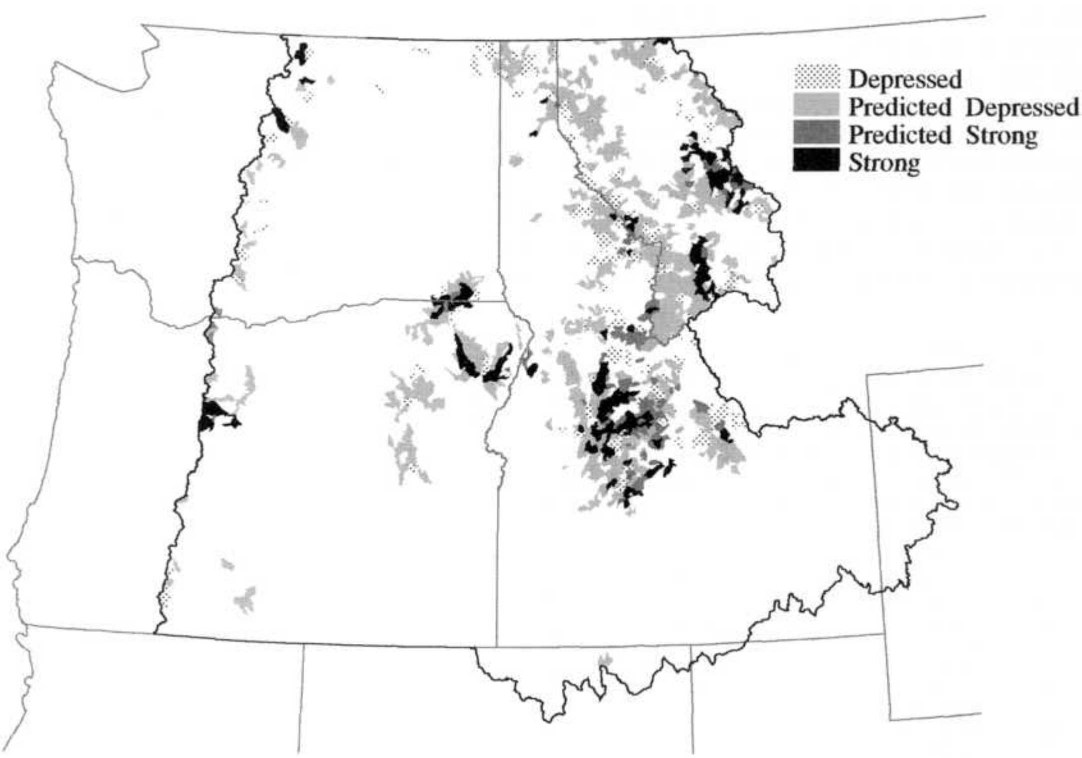

FIGURE 5.—Known and predicted classifications of status of bull trout within spawning and rearing areas and the potential range across the interior Columbia River basin within the United States and part of the Klamath River basin.

TABLE 8.—Summary of total known plus predicted classifications (number of subwatersheds) of occurrence and status of bull trout across all subwatersheds and "protected lands" of the interior Columbia River basin and part of the Klamath River basin in Oregon, Washington, Idaho, Montana, and Nevada. The number of subwatersheds where the classification was predicted is shown in parentheses.

Ecological reporting unit	Known + predicted[a]				Known + predicted within "protected lands"	
	Present	Strong	Depressed	Absent	Present	Strong
Northern Cascades	172 (28)	10 (0)	34 (12)	144 (60)	49	8
Southern Cascades	33 (1)	14 (4)	6 (0)	47 (7)	2	1
Upper Klamath	16 (7)	0	14 (5)	57 (9)	1	0
Columbia Plateau	124 (65)	3 (0)	22 (2)	426 (209)	0	0
Blue Mountains	200 (37)	28 (5)	83 (11)	242 (65)	35	15
Northern Glaciated Mountains	365 (49)	38 (12)	156 (31)	582 (247)	75	18
Lower Clark Fork	197 (31)	8 (4)	107 (32)	218 (58)	14	2
Upper Clark Fork	197 (52)	26 (5)	128 (19)	109 (25)	26	6
Owyhee Uplands	7 (0)	0	2 (0)	167 (65)	2	0
Central Idaho Mountains	654 (87)	143 (71)	261 (75)	492 (132)	175	39
Entire assessment area[a]	1,965 (357)	270 (101)	813 (187)	2,484 (877)	379	89

[a] Thirteen subwatersheds within the potential historical range are omitted because of incomplete information.

the distribution of bull trout because we do not know how much of the potential range was occupied. Bull trout distributions are patchy even in pristine environments (Rieman and McIntyre 1993) and it is unlikely that all of the available habitat was ever occupied at any one time (Rieman and McIntyre 1995). More refined predictions of suitable habitats are needed to clarify the magnitude of change.

Despite the uncertainty, these and other results suggest important declines have occurred. First, depressed classifications were three times more common than strong. Second, the association between bull trout occurrence and estimated road density suggests a trend of environmental disruption and biological response. Because human disruption and roads are widespread, such effects may be widespread as well. Third, as noted earlier, other work at finer scales of resolution showed local declines in abundance, local extinctions, and loss of migratory life histories.

A general goal in the conservation of any species is to maintain a broad representation of viable populations across both local and regional scales to conserve both biological diversity and adaptive capacity (Leary et al. 1993; Lesica and Allendorf 1995; Li et al. 1995; Noss et al. 1995; Allendorf et al. 1997), and to minimize the risks of local and regional extinctions (Rieman and McIntyre 1993). The current distribution suggests that bull trout have fared better and are currently more secure in some areas than in others. For example, we noted that bull trout are very poorly represented in the Upper Klamath and Owyhee Uplands ERUs. Because these two regions represent the extreme southern margins of the species range, the populations here may be adapted to unique environments and may represent a disproportionate part of the total diversity within the species (Scudder 1989; Lesica and Allendorf 1995). From a broad conservation perspective, these two areas could be particularly important.

There are sound reasons for concern about other regions as well. General criteria for evaluating priorities in conservation have been based on rarity at the particular scales of interest (e.g., Noss et al. 1995) and on gaps in protection across a range (e.g., Kiester et al. 1996). For example, Nature Conservancy standards consider regions supporting fewer than six "viable elements" to be the highest level of concern, those supporting 6–20 elements at the second level, and those supporting more than 100 to be "apparently secure" (Noss et al. 1995). Subwatersheds of the size we used approximate the boundaries of local populations of bull trout (see Rieman and McIntyre 1995). If we consider only those classified or predicted as having strong populations, or only those falling within protected lands to be viable elements, in either case only the Central Idaho Mountains ERU could be considered secure (Table 8).

Future Trends

We suggest three factors are likely to influence the future trends in bull trout distribution and status: further habitat degradation, the expansion of exotic species, and existing and future habitat fragmentation.

Habitat degradation.—Bull trout appear sensitive to habitat changes associated with land use management and other effects on channel conditions, water quality, and water temperature (Shepard et al. 1984; Bond 1992; Henjum et al. 1994; Dambacher and Jones 1997). Disruptive land uses threaten many stream fishes (see papers in Salo and Cundy 1987 and in Meehan 1991) in ways that we may or may not mitigate with more careful management (Frissell and Bayles 1996). Because bull trout appear to have relatively specific habitat requirements (Rieman and McIntyre 1993), they may be particularly sensitive to land management activities. Human populations and demands for forest-based commodities and recreational access are expected to increase, not decrease, in the future. We could anticipate increasing risks for bull trout as well.

Introduced species.—There are now at least 30 introduced species within the range of bull trout in our study area (Lee et al. 1997). Although a number of these may interact with bull trout, there is particular concern that lake trout *Salvelinus namaycush* and brook trout *Salvelinus fontinalis* can and have displaced bull trout in lakes (Donald and Alger 1992) and streams (Leary et al. 1993), respectively. Brook trout, in particular, are now widely distributed in the region and have been reported from most of the watersheds within the current distribution of bull trout (see Thurow et al. 1997). Although brook trout may not invade all waters important to bull trout, the potential for interaction across much if not most of the range is clear.

Fragmentation.—Fragmentation of habitat and populations is a growing issue in the conservation management of many species (Gilpin 1987; Simberloff 1988; Mangel et al. 1996), including bull trout and other fishes (Rieman and McIntyre 1993, 1995; Li et al. 1995; Reeves et al. 1995; Schlosser and Angermeier 1995; Dunham et al. 1997, this issue). In general, as populations are restricted to smaller and more isolated habitats, the risks of both local and regional extinctions are expected to increase. The loss in distribution likely will not be directly proportional to the loss of habitat area. Rather, further loss of habitat could accelerate rates of extinction above the rate of habitat loss (Rieman and McIntyre 1995). Existing fragmentation may be a particularly relevant issue to conservation of bull trout. Barriers (i.e., dams, water withdrawals) and habitat degradation in river corridors have affected migratory patterns, either isolating remnant nonmigratory populations or restricting movements to smaller areas (Ratliff and Howell 1992; Ziller 1992; Rieman and McIntyre 1993; Jakober 1995; Swanberg 1996). Loss of habitat and a progression of local extinctions may have created a similar effect through a patchwork of remnant populations that have become progressively more isolated by distance (Frissell et al. 1993). Our analysis showed that much of the range is represented by patchy or disjunct distribution (Figures 4, 5). Other trends may aggravate that pattern. Expansion of brook trout and other species into bull trout habitats can lead to greater isolation (Ziller 1992; Adams 1994). The association of bull trout distributions with temperature leads us to anticipate a similar effect with climate change (for similar discussions regarding other native *Salvelinus* populations, see Meisner 1990; Flebbe 1993; Nakano et al. 1996).

Regardless of whether the patterns of fragmentation result from natural or anthropogenic effects, the smaller and more isolated parts of the range likely face higher risks in the long term. Local extinctions through stochastic processes are natural, even common, events for many species, and perhaps for bull trout (Rieman and McIntyre 1993, 1995). Where regional populations lack the redundancy and connectivity to refound or support local populations prone to extinction, such losses represent an uncompensated, incremental drift toward regional extinction. Even with no further habitat loss, local extinctions and erosion of the broad distribution may continue.

Conclusions

Bull trout occur widely across a major portion of the potential range. At the broad scale, they are better represented than some other native fishes, and populations in some parts of the range are relatively secure. Despite the broad distribution, however, declines and local extinctions have occurred. Current patterns in the distribution and other empirical evidence, when interpreted in view of emerging conservation theory, lead us to believe that further declines and extinctions are likely. Because of a strong association with colder environments (and the potential for climate change) and the pervasive occurrence of introduced fishes, rates of loss could accelerate in the future. Bull trout are not currently threatened with extinction across all of the range, but effective conservation management will be necessary to preempt that outcome.

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