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Distribution and Status of Seven Native Salmonids in the Interior Columbia River Basin and Portions of the Klamath River and Great Basins

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Abstract.—We summarized presence, absence, current status, and potential historical distribution of seven native salmonid taxa—bull trout *Salvelinus confluentus*, Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri*, westslope cutthroat trout *O. c. lewisi*, redband trout and steelhead *O. mykiss gairdneri*, stream type (age-1 migrant) chinook salmon *O. tshawytscha*, and ocean type (age-0 migrant) chinook salmon—in the interior Columbia River basin and portions of the Klamath River and Great basins. Potential historical range was defined as the likely distribution in the study area prior to European settlement. Data were compiled from existing sources and surveys completed by more than 150 biologists. Within the potential range of potamodromous salmonids, status was unknown in 38–69% of the area, and the distribution of anadromous salmonids was unknown in 12–15%. We developed models to quantitatively explore relationships among fish status and distribution, the biophysical environment, and land management, and used the models to predict the presence of taxa in unsampled areas. The composition, distribution, and status of fishes within the study area is very different than it was historically. Although several of the salmonid taxa are distributed throughout most of their potential range, declines in abundance and distribution and fragmentation into smaller patches are apparent for all forms. None of the salmonid taxa have known or predicted strong populations in more than 22% of their potential ranges, with the exception of Yellowstone cutthroat trout. Both forms of chinook salmon are absent from more than 70% and steelhead from more than 50% of their potential ranges, and all are approaching extirpation in portions of their remaining ranges. If current distributions of the taxa are useful indicators, many aquatic systems are remnants of what were larger and more complex, diverse, and connected systems. Because much of the ecosystem has been altered, areas supporting strong populations or multiple species will be critical for conservation management. Moreover, restoration of a broader matrix of productive habitats also will be necessary to allow fuller expression of phenotypic and genotypic diversity in native salmonids.

Historically, the abundant coldwater streams of the northwestern United States supported a wide variety of salmonids. We identified 15 native salmonid taxa that once flourished in the interior Columbia River basin and portions of the Klamath and Great basins (Lee et al. 1997), including four subspecies of cutthroat trout *Oncorhynchus clarki*; two forms of chinook salmon *O. tshawytscha*; two forms of steelhead *O. mykiss gairdneri* and *O. m. irideus*; coho salmon *O. kisutch*, sockeye salmon *O. nerka*, and chum salmon *O. keta*; interior redband trout *O. mykiss gairdneri*; mountain *Prosopium wiliamsoni* and pygmy whitefish *P. coulteri*; and bull trout *Salvelinus confluentus*. These abundant and widely distributed salmonids shaped the culture of pre-European inhabitants. Runs of anadromous salmonids were immense; Chapman (1986) estimated peak runs of Pacific salmon and steelhead in the Columbia River in the late 1800s at about 7.5 million fish. Early records suggest potamodromous forms were also abundant and widely distributed. Lewis and Clark first recorded cutthroat trout in 1805 (Behnke 1992), and early accounts suggest the species was extremely abundant (Evermann 1893). Redband trout were widely distributed, occupying waters from southern desert basins to mountainous coniferous forests (Cope 1879; Jordan 1892; Gilbert and Evermann 1895). Most native people in the region depended on anadromous (Mullan et al. 1992) or potamodromous salmonids (Turney-High 1941) as subsistence and ceremonial resources. Since European settlement, native salmonids have continued to influence social and economic systems.

Many stocks of native salmonids are now considered imperiled (Williams et al. 1989; Moyle and Williams 1990; Nehlsen et al. 1991; Frissell et al. 1993). Presently, stocks of spring, summer, and fall chinook salmon, sockeye salmon, and steelhead are listed as threatened or endangered under the U.S. Endangered Species Act of 1973 (ESA). Lahontan cutthroat trout *Oncorhynchus clarki hen-*

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shawi are listed as threatened under the ESA, coho salmon are designated as a candidate species, and bull trout are proposed for listing. Coastal cutthroat trout *O. c. clarki* are under review for ESA listing. Most other native salmonids have been identified by federal or state agencies as species of concern (Lee et al. 1997).

Several status reviews address salmon and steelhead (Howell et al. 1985a, 1985b; NWPPC 1986; CBFWA 1990; WDF et al. 1993; Chapman et al. 1994a, 1994b; Kostow et al. 1994) or native trouts and chars (Liknes and Graham 1988; Rieman and Apperson 1989; Thomas 1992; Young 1995) in the Columbia River basin. Different methods, lack of spatially explicit information, and focus on either declining stocks (Nehlsen et al. 1991) or healthy stocks (Huntington et al. 1996), have prevented a synthesis of data across the Columbia River basin. Frissell (1993) completed an extensive analysis of native fish extinctions within the Pacific Northwest, but provided little resolution below the scale of major river subbasins. The work was based primarily on published records of well-documented forms.

In July 1993, the President of the United States directed the Forest Service to "develop a scientifically sound and ecosystem-based strategy for management of Eastside forests," referring to forests east of the Cascade Mountains. To accomplish this, the Chief of the Forest Service and the Director of the Bureau of Land Managment (BLM) established the Interior Columbia River Basin Ecosystem Management Project (ICBEMP), which includes a scientific assessment of ecological, social, cultural, and economic systems; two environmental impact statements; and an evaluation of impact statement alternatives. One goal of the assessment was a comprehensive evaluation of the status and distribution of fishes throughout the area (Lee et al. 1997). Rieman et al. (1997, this issue) describe the distribution, status and trends of bull trout in detail. Here we consider the individual and composite distributions and status of seven native salmonid taxa: bull trout, westslope cutthroat trout *O. clarki lewisi,* Yellowstone cutthroat trout *O. c. bouvieri,* redband trout, steelhead (subspecies *gairdneri*), ocean type (age-0 migrant) chinook salmon, and stream type (age-1 migrant) chinook salmon. We describe their potential historical range and current distribution and status in the interior Columbia River basin and portions of the Klamath River and Great basins. We consider those factors that have influenced the status and distribution of the seven taxa, and we address application of our results to conservation and restoration strategies.

Methods

The study area included the interior Columbia River basin east of the Cascade Mountains and smaller portions of the Klamath River and Great basins. The area includes over 58.3×10^6 ha in Idaho, Montana, Nevada, Oregon, Washington, and Wyoming, of which 53% is administered by the Forest Service or BLM (Quigley et al. 1996). Rieman et al. (1997) provide a study area map and a detailed description of the hierarchical system of subbasins, watersheds, and subwatersheds we used; their paper is the primary source for the methods we applied.

Within the study area, the seven salmonid taxa studied include distinct species, subspecies, and life history forms. Bull trout, westslope cutthroat trout, and Yellowstone cutthroat trout are taxonomically and geographically distinct. Redband trout and chinook salmon each are represented by two life history forms. Interior redband trout include potamodromous redband trout and anadromous steelhead. For purposes of this analysis, redband trout designates the potamodromous form, which we further divided into sympatric and allopatric populations. We defined allopatric redband trout as those that evolved outside the historical range of steelhead, and we assumed this form was evolutionarily distinct from other redband trout because of isolation. We considered sympatric redband trout to be the nonanadromous form historically derived from or associated with steelhead. A potamodromous form is likely to exist in sympatry with steelhead; however, the level of genetic or behavioral segregation between forms is unknown (Busby et al. 1996). Morphologically, anadromous and potamodromous redband trout juveniles are indistinguishable, and we relied on knowledge of established barriers to anadromy to define the range for the allopatric form. The distribution of small populations of allopatric redband trout isolated from but within the general range of steelhead was not addressed. Chinook salmon have been described as spring, summer, and fall races, which are separated primarily by their time of passage over Bonneville Dam (Matthews and Waples 1991). To avoid confusion among stocks in the Snake and Columbia rivers, we adopted Healey's (1991) definitions of chinook salmon that migrate seaward after one or more years in freshwater as stream type and those that migrate as subyearlings as ocean type.

Known status and distribution.—We held a series of workshops in 1995 and asked more than 150 biologists from across the study area to characterize the status and distribution of the seven salmonid taxa. Participants were asked to use existing information to classify the status of naturally reproducing populations in each subwatershed within their jurisdiction. If populations were supported solely by hatchery-reared fish, naturally spawning fish were considered absent. Biologists classified subwatersheds where fish were present as spawning or rearing habitat, overwintering or migratory corridor habitat, or as supporting populations of unknown status. Subwatersheds containing spawning and rearing habitat were further classified as supporting strong or depressed populations. Because potamodromous redband trout and juvenile steelhead were indistinguishable, and the level of genetic or behavioral segregation between them is unknown (Busby et al. 1996), we considered the status of sympatric redband trout unknown when steelhead were present. Rieman et al. (1997) describe the criteria we provided biologists. We asked biologists to rely on biological characteristics and not to infer status of the seven taxa from habitat or landscape information or presence of introduced fishes.

Potential historical range.—Potential historical ranges, hereafter referred to as potential ranges, were defined as the likely distributions in the study area prior to European settlement. Potential ranges were characterized from historical distributions in prior databases and augmented through published and anecdotal accounts. Rieman et al. (1997) describe the data sources used to define the potential range for bull trout. For a complete description of the data sources used to define potential ranges for all seven salmonid taxa see Lee et al. (1997). We included all subwatersheds that were accessible as potential range based on the known current and historical occurrences because the seven taxa are highly mobile, moving through subwatersheds, watersheds, subbasins, and basins at different life stages seasonally (Bjornn and Mallet 1964; Withler 1966; Varley and Gresswell 1988; Rieman and Apperson 1989; Healey 1991). Subwatersheds that were known to be historically isolated by barriers to movement of the seven taxa were excluded from potential ranges. We recognize that, within subwatersheds, the potential range may be restricted further by elevation, temperature, and local channel features, but we did not attempt to define potential ranges at a finer scale.

Predictive models.—We produced a set of predictions using statistical models, called classification trees (Breiman et al. 1984), that reflect the likelihood of a species presence or the likely status of the population within an unsampled subwatershed. Our objective was to generate a complete picture of the current distribution of the salmonid taxa by quantitatively exploring relationships among fish distribution, the biophysical environment, and land management. See Rieman et al. (1997) for a description of the classification trees for bull trout and the fitting, cross-validation, and pruning routines used for all taxa.

Two separate classification trees were built for the potamodromous salmonids. In the first tree, known status was reduced to a binomial variable by combining all presence calls (present–strong, present–depressed, or transient in migration corridor) into a single present call (Lee et al. 1997). 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 migration corridors. Present–strong and present–depressed were retained as separate responses; transient and absent were combined in the third permissible response. For the anadromous salmonids, single trees were built using a four-level response: present–strong, present–depressed, transient, and absent.

We summarized known and predicted status and distribution for the salmonid taxa across the study area. We estimated the percent of the potential range currently occupied by comparing the number of occupied subwatersheds to the total subwatersheds in the potential range. Because areas supporting strong populations are potentially critical for short-term persistence and long-term recovery, we summarized subwatersheds supporting known or predicted strong populations and defined them as strongholds. We estimated the percent of the potential and current range supporting strongholds by comparing subwatersheds with strongholds to the total number of subwatersheds in the potential and current ranges. We mapped distributions and strongholds using geographic information systems (GIS). This represents the first attempt to develop a spatially explicit database across the study area that synthesizes collective knowledge of the status and distribution of the seven salmonid taxa.

Results

Potential Historical Range

The seven salmonid taxa were once broadly distributed in the study area. Their combined poten-

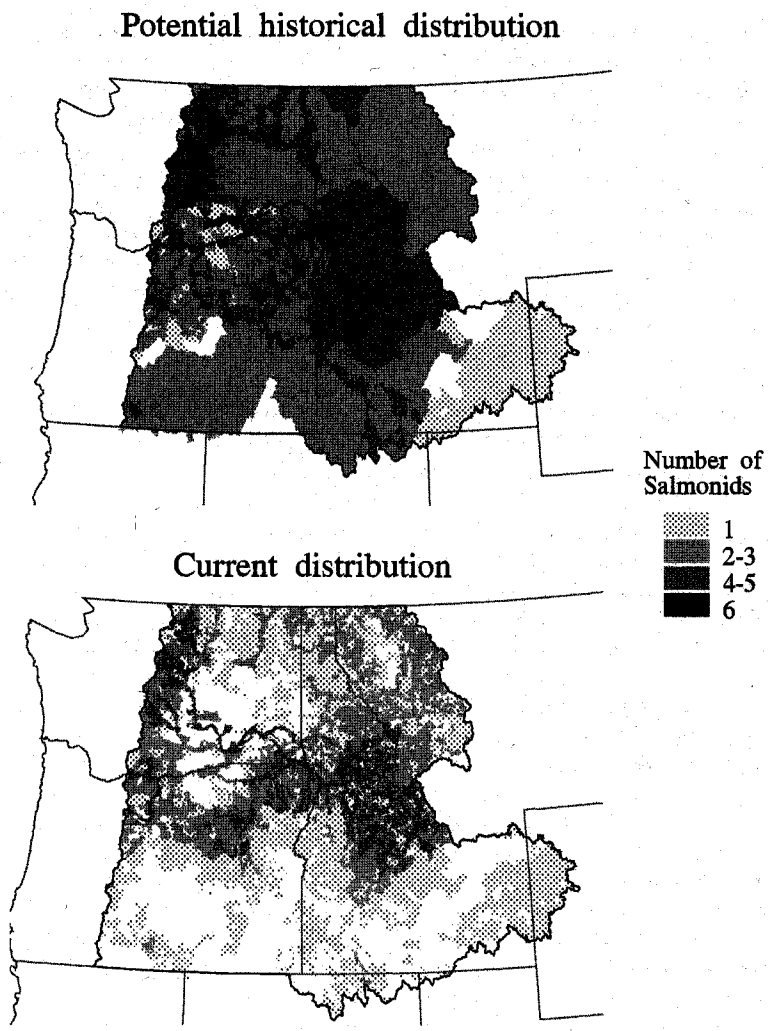

FIGURE 1.—Historical number of salmonid taxa potentially present (top) and current number of salmonids known or predicted to be present (bottom) in subwatersheds within the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

tial ranges included 97% of the 7,498 subwatersheds (Figure 1). The central Idaho mountains, northern Cascades, and western Montana, along with the river corridors connecting all of the subwatersheds accessable to anadromous fish, supported multiple taxa. We estimate that 74% of the subwatersheds may have supported two or more of the salmonid taxa, and about 2% may have supported six (Figure 1). Potential ranges varied by taxon (Table 1). The most narrowly distributed forms included ocean type chinook salmon (7% of the subwatersheds) andYellowstone cutthroat trout (9%; Table 1). The most broadly distributed taxa were bull trout, sympatric redband trout, steelhead, and stream type chinook salmon. The potential ranges of these four species included about 50% of the subwatersheds.

Known Status and Distribution

The known distributions of the salmonid taxa also varied by species. Stream type and ocean type chinook salmon were known in 21% and 25% of their potential ranges, respectively (Table 1). Westslope cutthroat trout occupied the largest portion of their potential range (74%). Depending on the taxon, presence or absence was unknown or unclassified in 7–39% of the subwatersheds, and 4–42% of the areas with known presence had pop-

TABLE 1.—Summary of potential historical ranges and known and predicted classifications of occurrence and status (number of subwatersheds) for seven salmonid taxa. The numbers of subwatersheds for which predictions were made are in parentheses. There were 7,498 subwatersheds in the study area. The omitted subwatersheds had incomplete information.

Species	Potential historical range	Current known and predicted range	Known and predicted status where present			Unknown or no classification	Absent known and predicted	Omitted from analysis
			Strong	Depressed	Unknown			
Bull trout	4,462	1,965 (357)	270 (101)	813 (187)	443	1,247	2,484 (877)	13
Yellowstone cutthroat trout	662	436 (49)	209 (34)	173 (55)	89	171	182 (78)	44
Westslope cutthroat trout	2,646	2,251 (303)	587 (255)	1,485 (494)	574	426	393 (121)	2
Redband trout								
Sympatric	4,196	2,883 (395)	702 (486)	1,556 (1,031)	1,741	1,151	1,258 (701)	55
Allopatric	1,262	617 (117)	114 (79)	465 (293)	293	497	596 (331)	49
Combined	5,458	3,500 (512)	816 (565)	2,021 (1,324)	2,034	1,648	1,854 (1,032)	104
Steelhead	3,754	1,711 (478)	23 (0)	1,431 (462)	289	279	2,021 (68)	22
Stream type chinook salmon	3,461	958 (224)	8 (0)	668 (198)	141	281	2,495 (190)	8
Ocean type chinook salmon	553	161 (23)	25 (4)	71 (14)	20	50	387 (42)	5

ulations of unknown status (Table 1). The distribution of anadromous salmonids was known more thoroughly than the distribution of potamodromous salmonids. Despite their broad distribution, we knew less about the current distribution of redband trout than any of the other taxa. About 27% of the sympatric redband trout potential range and 39% of the allopatric redband trout potential range was not classified. Another 42% of the sympatric redband trout potential range and 23% of the allopatric redband trout potential range was judged to support redband trout of unknown status.

Predictive Models

Classification trees were successful in distinguishing status and distribution in sampled subwatersheds using landscape information. The overall misclassification error rates were 7.6–16.8% for the anadromous taxa and 13.7–24.2% for the potamodromous forms (Table 2). Absent was most often confused with depressed and rarely confused with strong, and strong was confused primarily with depressed (Table 2). Because the models assumed no ordinal relationships among the responses, a priori, reasonable patterns in the errors reinforce the conclusion that the models identified meaningful relationships (Lee et al. 1997).

Overall, the patterns suggested by the classification trees were consistent with our understanding of salmonid biology and habitat use. Variables related to geographic location, temperature, stream size, slope, vegetative cover, precipitation, and solar radiation provided important discrimination in the analyses (Table 2). The frequency of physiographic and geophysic predictor variables within the models suggested that biophysical setting was an important determinant of species distributions.

Although our models were not designed to test correlations between specific subwatershed characteristics and taxon status, variables reflecting the degree of human disturbance within subwatersheds (road density, land ownership and management emphasis, number of dams) were useful predictors of fish status (Table 2). The number of main-stem dams in migratory corridors, for example, showed a consistent, negative association with chinook salmon. In no instance was increased disturbance of natural landscapes interpreted to have a positive effect on salmonids.

Current Status and Distribution

Bull trout.—Bull trout were known or predicted to occur in 44% of subwatersheds in the potential range (Table 1). We found bull trout less widely distributed within the potential range than the other potamodromous salmonids. Subwatersheds believed or predicted to support strong populations represented only 6% of the potential range. Rieman et al. (1997) describe bull trout in detail.

Yellowstone cutthroat trout.—Yellowstone cutthroat trout were narrowly distributed within the study area. The known and predicted distribution included about 66% of the potential range (Table 1; Figure 2). Large-river populations, in particular, have declined or disappeared. Concomittant to declines in natural distributions of Yellowstone cutthroat trout, stocking activities have expanded the species range, particularly in mountain lakes throughout Idaho and Montana. Introductions have established the species in at least 140 subwatersheds outside their potential range. Yellowstone cutthroat trout are now found in central and northern Idaho and western Montana (Figure 2). We estimated that Yellowstone cutthroat trout had the

TABLE 2.—Cross-classification of the observed status calls with the predicted values for seven salmonid taxa, and list of leading predictor variables. Transient populations in migration corridors were grouped with absent calls in building the models for potamodromous salmonids, but they are separated here to demonstrate classification patterns (for example, spawning and rearing bull trout are predicted to be absent from most migration corridors). Leading predictor variables accounted for the largest amount of variance in the models and are listed in order of the relative proportion of variance accounted for.

Species	Predicted status	Observed values: Absent (A)	Present–depressed (D)	Present–strong (S)	Transient (T)	Leading predictor variables[a]
Bull trout	A	1,445	267	31	344	mtemp, roaddn, hucorder, pprecip, ERU, baseero
	D	81	335	48	18	
	S	28	22	90	8	
Yellowstone cutthroat trout	A	97	9	0	0	ERU, solar, mtemp, pprecip
	D	3	96	29	4	
	S	1	11	141	2	
Westslope cutthroat trout	A	165	33	9	38	ERU, vmf, mgclus, roaddn, hucorder
	D	84	896	103	12	
	S	22	59	218	1	
Redband trout	A	685	117	32	3	mgclus, slope, anadac, hucorder, solar, ERU
	D	132	525	73	2	
	S	8	70	145	1	
Steelhead	A	124	30	0	2	hucorder, ERU, drnden, mgclus
	D	53	870	9	28	
	S	0	2	11	0	
	T	1	29	0	196	
Ocean type chinook salmon	A	89	5	0	2	hucorder, ERU, mgclus, dampass
	D	2	47	2	1	
	S	1	0	17	2	
	T	1	0	1	54	
Stream type chinook salmon	A	440	40	0	12	hucorder, dampass, slope, elev, ERU
	D	112	401	8	19	
	S	0	0	0	0	
	T	2	19	0	209	

[a] Abbreviations: anadac = access for anadromous fish; baseero = base erosion index; dampass = number of intervening dams fish must pass; drnden = drainage density; elev = mean elevation; ERU = ecological reporting unit; hucorder = number of upstream subwatersheds tributary to the watershed of interest; mgclus = management class; mtemp = mean annual air temperature; pprecip = mean annual precipitation; roaddn = estimated road density; slope = average midslope; solar = mean annual solar radiation; vmf = vegetation amelioration factor. All but dampass are described more fully by Rieman et al. (1997).

largest proportion of strong populations of any salmonid taxa. Subwatersheds known or predicted to support strong populations represented 32% of the potential range (Table 1), and 48% of the current distribution (Figure 2).

Westslope cutthroat trout.—Westslope cutthroat trout remained widely distributed within their potential range. We estimated that westslope cutthroat trout were present in about 85% of the potential range (Table 1; Figure 3). Despite the broad distribution, there were few remaining strong populations outside the central Idaho mountains and, possibly, the northern Cascades in western Washington. We estimated that 22% of the potential range was classified or predicted as strong (Table 1; Figure 3).

Redband trout.—Redband trout remained the most widely distributed native salmonid, with sympatric and allopatric forms occupying about 47% of the study area. We estimated that they occurred in 64% of their combined potential range (Table 1; Figure 4). Despite their broad distribution, we know less about the current distribution of redband trout than that of any of the salmonids. Sympatric redband trout were the most widely distributed of the two forms, the known and predicted distribution included 69% of the potential range (Table 1). The largest areas of apparently unoccupied habitat are in waters of southwestern Idaho, southeastern Oregon, and northern Nevada and in waters of southern Washington and northern Oregon (Figure 4). Despite their broad distribution, relatively few strong sympatric redband trout populations were identified (Figure 4). Known or pre-

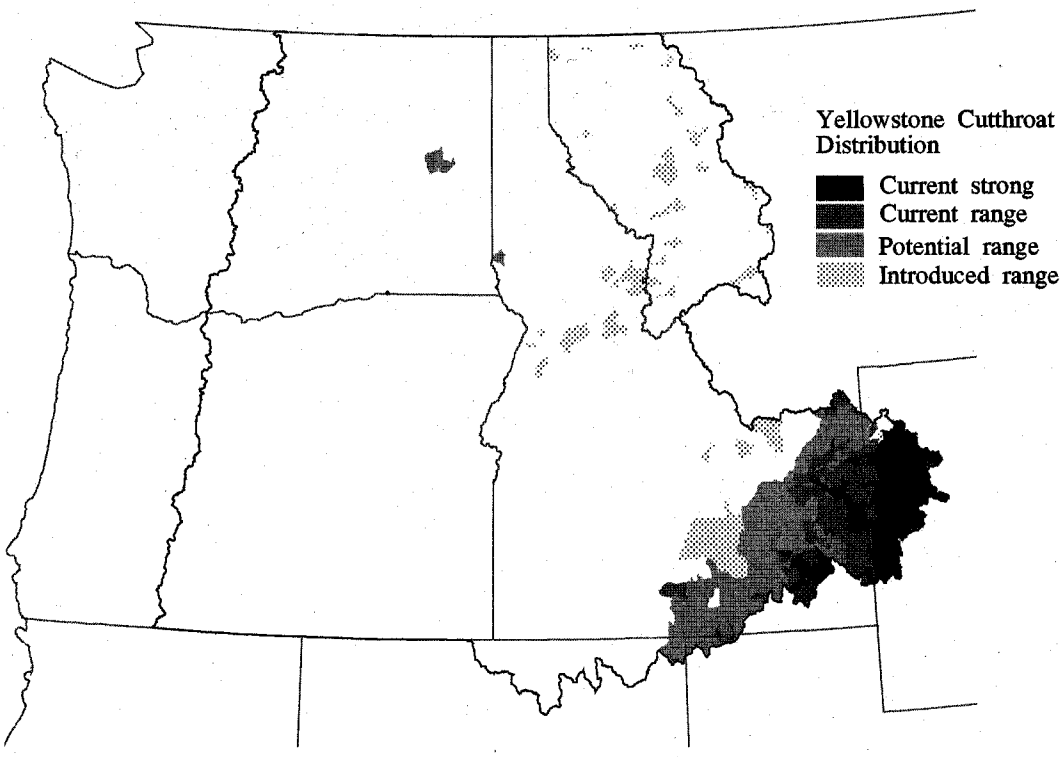

FIGURE 2.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of Yellowstone cutthroat trout in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

dicted strong areas included 17% of the potential range (Table 1). Allopatric redband trout were less widely distributed and were present or predicted in 49% of the potential range (Table 1). Allopatric redband trout had fewer strong populations (9% of the potential range; Table 1). Allopatric redband trout populations were least well-distributed in the Oregon Great Basin and southern Washington (Figure 4), where they were believed to be absent in most of the potential range, with few strong populations known or predicted within the present distribution.

Steelhead.—Steelhead remained widely distributed; however, they were absent from large portions of their potential range and few strong populations existed (Figure 5). The current known and predicted distribution included about 46% of the potential range (Table 1). Subwatersheds known or predicted to support strongholds represented 0.6% of the potential range and 1.3% of the current range (Table 1; Figure 5).

Chinook salmon.—Chinook salmon have been extirpated in most of their potential range. Current known and predicted distributions of stream and ocean type chinook salmon included 28% and 29%, respectively, of the potential range (Table 1; Figures 6, 7). Most remaining stocks were depressed; subwatersheds supporting strong populations represented 0.2% of the potential range and 0.8% of the current range of stream type chinook salmon (Table 1; Figure 6). Strong populations represented 5% of the potential range and 15% of the current range of ocean type chinook salmon (Table 1; Figure 7). The North Fork of the John Day River in north central Oregon contained the only reported strong population of stream type chinook salmon (Figure 6). The northern Cascades and mid-Columbia River in western Washington supported the remaining core of ocean type chinook salmon strongholds (Figure 7).

Summary.—Although some of the taxa, notably cutthroat trout and redband trout, remain in most of their potential range, declines in abundance, reductions in distribution, and fragmentation into smaller patches are apparent for all forms examined. We estimated that about 74% of the subwatersheds supported at least one salmonid taxon, less than 38% supported two or more taxa, and

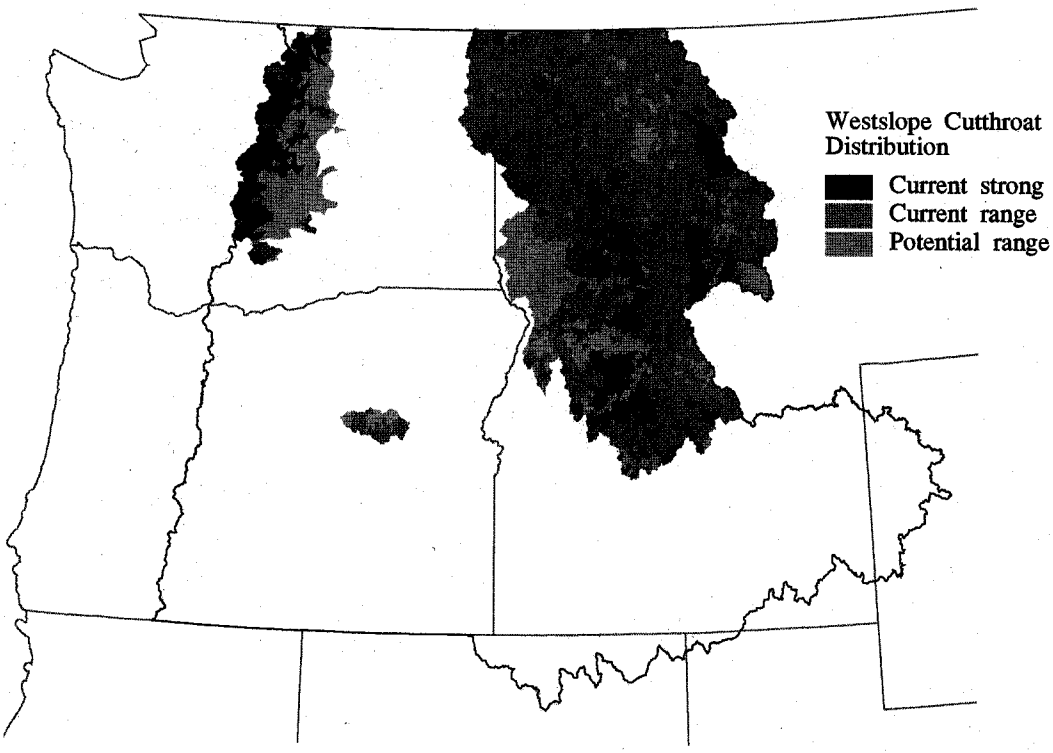

FIGURE 3.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of westslope cutthroat trout in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

about 0.5% supported six (Figure 1). The largest remaining regions of high salmonid diversity are associated with the central Idaho mountains, the Blue mountains, the northern Cascades, and their connecting river corridors. Two or more species are still found in subwatersheds scattered throughout Montana and a patchwork of subwatersheds and river corridors throughout the study area. Of 7,498 subwatersheds evaluated, we identified 1,693 with strongholds (Table 1; Figure 8). Less than 0.01% of the subwatersheds supported strong populations of three salmonids, 3% supported two, and 20% supported one. Most strongholds were found on Forest Service administered lands (75%) and a substantial portion (29%) were within designated wilderness areas or national parks (Lee et al. 1997). Strongholds occupied 27% of the Forest Service and BLM lands in the study area, and 12% of the strongholds were on private lands.

Discussion

Although the seven native salmonid taxa remain relatively widely distributed in the study area, our analysis suggests important changes in distribution and status have occurred. Because much of the potential range of the seven taxa remains speculative, we cannot quantify the number of populations that have been extirpated. The resolution of our potential historical ranges also was not sufficient to consider distributional boundaries in individual subwatersheds. Quantification of the extent of extirpation is further complicated by the likelihood that distributions may be restricted by elevation, temperature, and local channel features, in addition to the migration barriers we considered. The distributions of redband trout, steelhead, chinook salmon (Mullan et al. 1992), and bull trout (Rieman et al. 1997), for example, appear to be restricted by local climate or water temperature.

Despite these limitations, when compared to our estimates of the potential historical condition, the seven taxa now have narrower distributions, fewer areas supporting high diversity of taxa, and low percentages of strongholds. Four of seven taxa are present in less than 50% of their potential ranges. The number of subwatersheds supporting more than two taxa is about 50% of the potential dis-

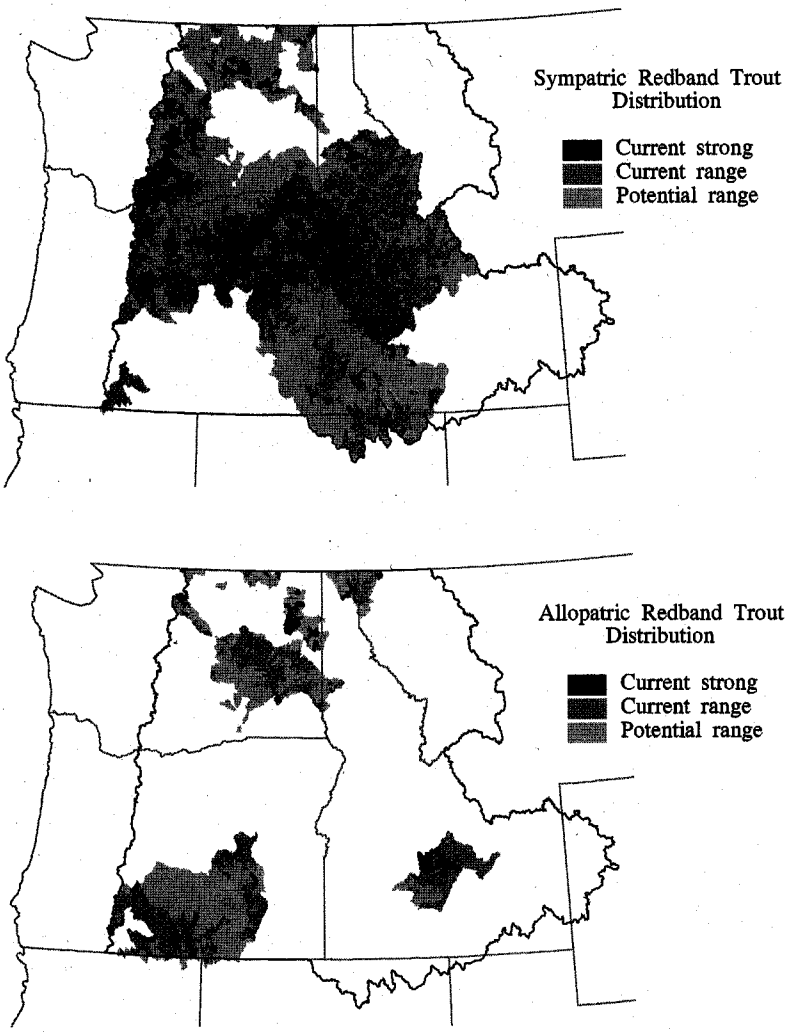

FIGURE 4.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of sympatric redband trout (top) and allopatric redband trout (bottom) in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

tribution, and the number of subwatersheds supporting six or more taxa is about 25% of the potential distribution. With few exceptions, strongholds are rare and not well distributed across the landscape. Model results suggest areas with unknown presence or unknown status are less likely to support populations than areas where better information is available (Lee et al. 1997). That is, unidentified population strongholds in the study area are unlikely; if fish are there in abundance, we generally know of their presence.

Changes in the distribution and status of the salmonid taxa also have been reported in other status reviews cited above. Extirpations of salmon and steelhead in the study area, for example, are well documented in areas upstream from human-caused barriers (NWPPC 1986). These reviews and other work suggest the current distribution of the salmonids has been influenced by a variety of human activities including habitat degradation, habitat fragmentation, nonnative species introductions, and harvest. Our results suggest that portions of the study area have been severely altered; however, results also highlight areas that retain their historical species diversity and ecological structure. Opportunities for watershed conservation and restoration are dictated in part by the current distribution of the best remaining watersheds,

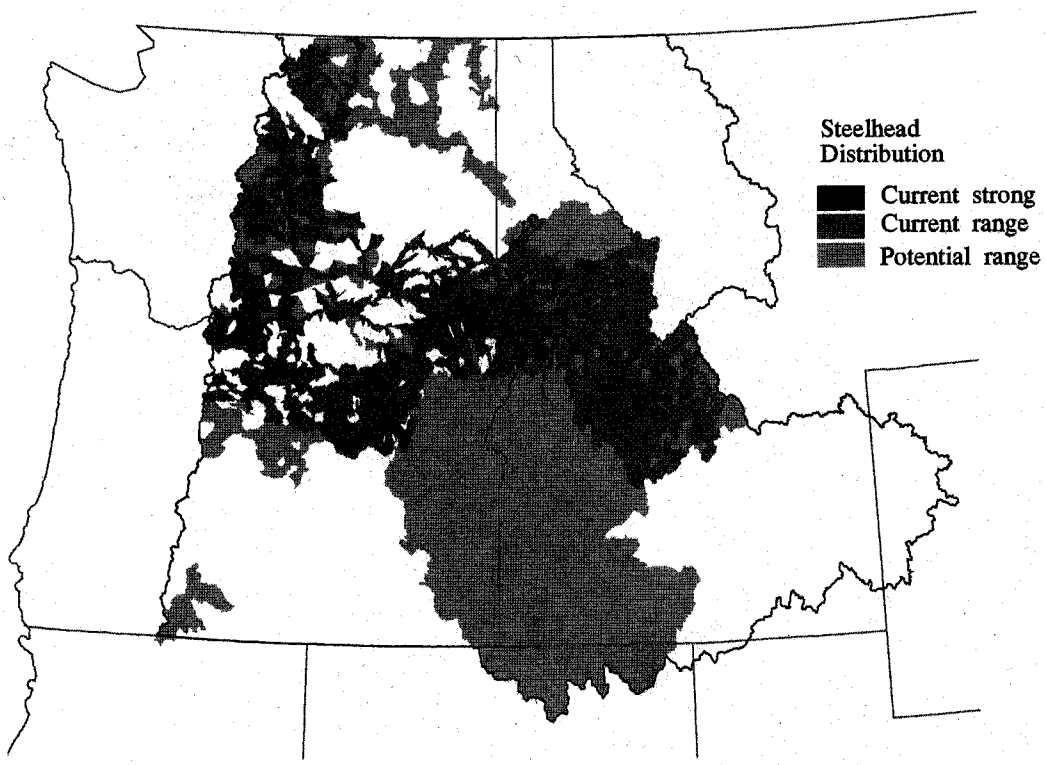

FIGURE 5.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of steelhead in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

strongest populations, and areas of highest taxa diversity.

Factors Influencing Status

Degradation of freshwater habitats is a consistent and pervasive problem facing the productivity and persistence of aquatic faunas in the study area and throughout much of the western United States (Williams et al. 1989; Meehan 1991; Nehlsen et al. 1991; Young 1995).

Salmonids generally have persisted in the areas least influenced by humans. Lee et al. (1997) reported a negative trend between the likelihood of finding strongholds and increasing road density. On Forest Service lands, the proportion of strongholds declined from 0.58 in roadless subwatersheds to 0.16 in subwatersheds with more than 4 km road/km^2 (Lee et al. 1997). Except for the upper Snake River in Wyoming and the southern Cascades in Washington, subwatersheds with strongholds were 20 to 76% unroaded. Subwatersheds with strongholds in the central Idaho mountains and the Snake River headwaters in Wyoming reflect the large wilderness, national park, and unroaded areas with the largest percentages of unroaded area in the study area (72 and 76%, respectively). Occurrence of strongholds highlights the ecological importance of unroaded areas in other reports (FEMAT 1993; Henjum et al. 1994) as well as in our assessment (Lee et al. 1997). Unroaded areas have the potential to maintain natural processes unaltered by land management activities and may be important refugia for strongholds of salmonids. We found designated wilderness and unroaded areas to be important anchors for strongholds throughout the study area (Lee et al. 1997). Remoteness of portions of the native range of Yellowstone cutthroat trout, for example, probably contributed to the preservation of remaining populations. In much of this area, public ownership in the form of parks and reserves has provided habitat protection that is lacking in low-elevation portions of the range (Varley and Gresswell 1988). Similarly, strong populations of westslope cutthroat trout in Idaho and Montana occur largely in roadless and wilderness areas or national parks (Liknes and Graham 1988; Marnell 1988; Rieman and Apperson 1989).

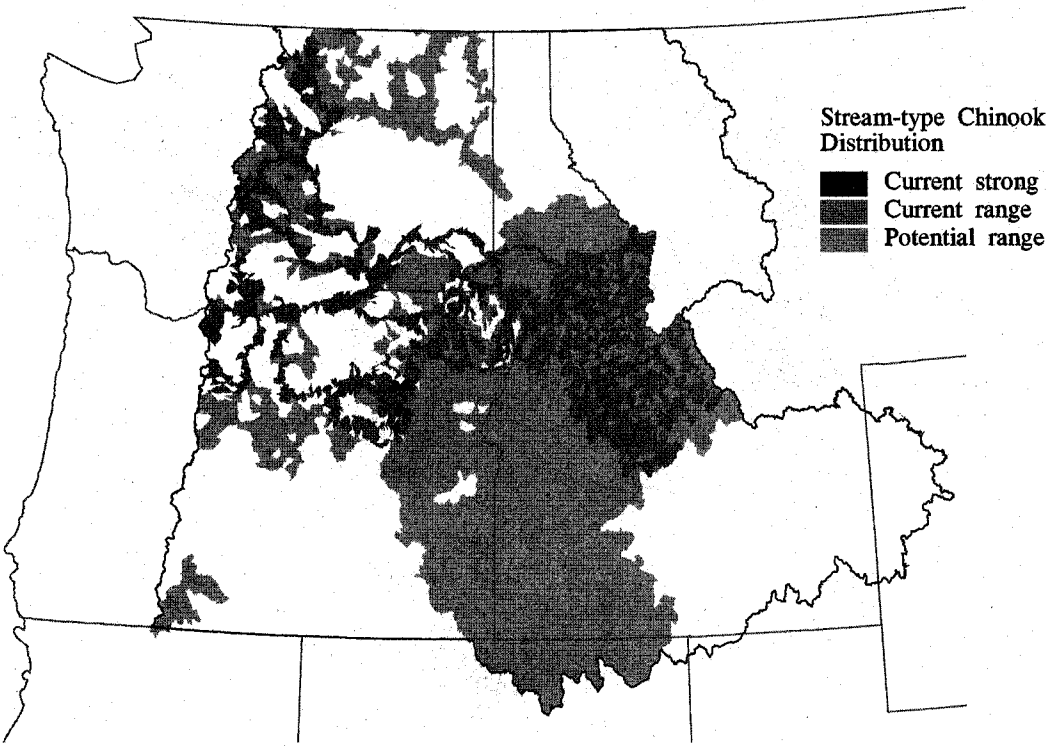

FIGURE 6.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of stream type chinook salmon in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

Work at finer scales has also noted the importance of habitat degradation. The effects of water diversions, grazing, mineral extraction, and timber harvest activities have caused extirpations of Yellowstone cutthroat trout (Varley and Gresswell 1988; Gresswell 1995). Declines have been most common in larger, low-elevation (>3rd order) streams (Hanzel 1959). Low-elevation areas historically have been the focus of agricultural and residential development. Easy access has encouraged angler harvest and nonnative species introductions. Habitat degradation has influenced similarly the current abundance of westslope cutthroat trout (Liknes and Graham 1988; Rieman and Apperson 1989; Behnke 1992) and redband trout (Williams et al. 1989). Their broad distribution suggests redband trout evolved over a wider range of environmental conditions than the other seven salmonid taxa examined, and may have less specific requirements. For example, redband trout exhibit tolerances to temperatures over 25°C (Kunkel 1976), and their apparent persistence in heavily disturbed basins suggests some populations are less strongly influenced by habitat disruption than other salmonids. The loss of a redband trout population, then, may be an indication of substantial habitat disruption. Population declines for salmon and steelhead similarly can be associated with a variety of human-caused factors including habitat disruption linked to land management and watershed development for hydropower and irrigation. The construction of dams and reservoirs and their complex effects on migration and survival is viewed as the single greatest threat to the persistence of salmon and steelhead in the upper basins (CBFWA 1990). Raymond (1979) describes the effects of the dams and impoundments on migrant survival. Until passage problems are resolved, however, the resilience and persistence of remaining stocks will be largely dependent on the quality and diversity of remaining stream habitats. Because of the losses associated with dams, only the most productive populations may have the resilience to persist in stochastic environments facing natural and human-caused disturbance (Emlen 1995; National Research Council 1996).

If current distributions of salmonids are good indicators of aquatic ecosystem health, many sys-

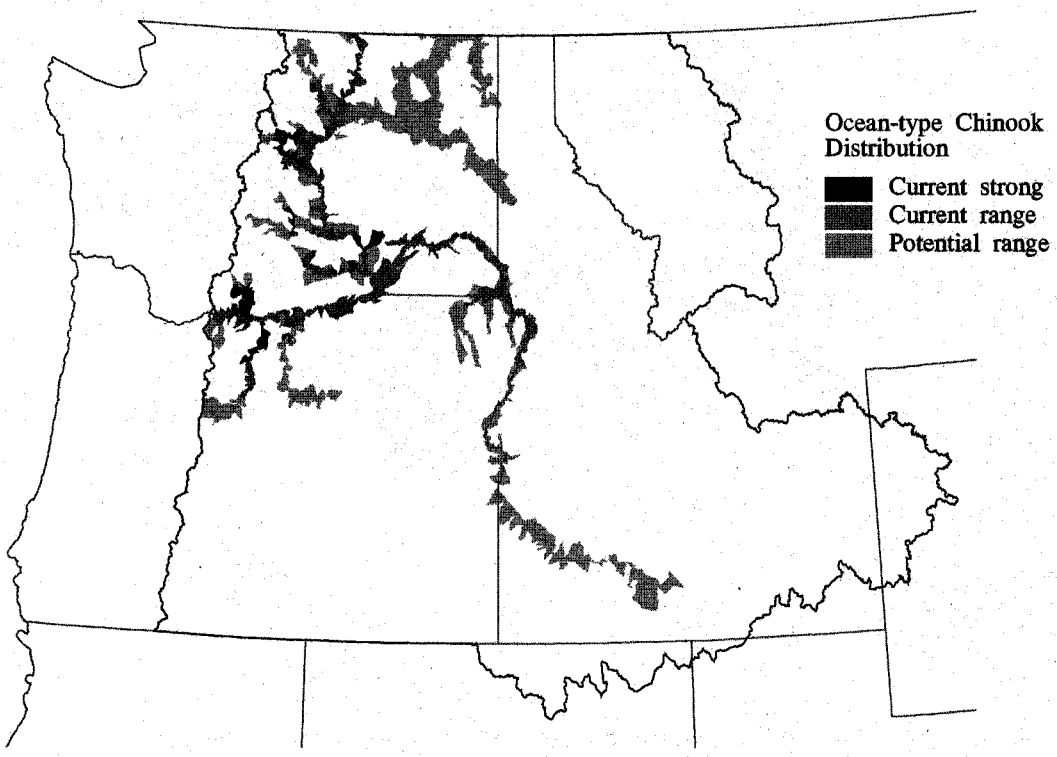

FIGURE 7.—Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of ocean type chinook salmon in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

tems remain only as remnants of what were larger and more complex, diverse and connected systems. With the exception of the central Idaho Mountains, Snake River headwaters, and perhaps the northern Cascades, most of the important areas for salmonids exist as patches of scattered subwatersheds.

Extensive construction of dams, irrigation diversions, or other migration barriers has isolated or eliminated habitats that once were available to migratory salmonids. One of the most substantial changes is associated with efforts to store, control, and direct water. Thousands of dams, ranging from small stock ponds to large hydroelectric facilities on the Columbia River have blocked access to migratory forms. There are about 1,239 dams with storage capacity in excess of 62,000 m^3 within the area (Lee et al. 1997), and chinook salmon and steelhead have been extirpated from 50–70% of their potential range. Although potamodromous salmonids may persist in isolated segments of streams, the loss of the migratory life history and the connection with other populations potentially important to gene flow or metapopulation dynamics may seriously compromise the potential for long-term persistence (Dunham et al. 1997, this issue; Rieman et al. 1997). The loss of spatial diversity in population structure and of the full expression of life history patterns may lead to a loss of productivity and stability important to long-term persistence (Lichatowich and Mobrand 1995). If connectivity among populations is limited by a matrix of poor-quality habitats interspersed among remaining high-quality areas, gene flow and the potential for refounding or demographic support among populations also will be limited. Local extinctions may occur through random events even in high-quality environments with no further habitat change, but in many cases the spatial and life history diversity necessary to mitigate the losses may no longer be present.

The introduction and expansion of nonnative species and use of hatcheries has influenced the status of native salmonids. Introduced species may displace native salmonids through competion, predation, and hybridization (Fausch 1988; Leary et al. 1993). Introgressive hybridization is viewed as a pervasive problem (Allendorf and Leary 1988; Liknes and Graham 1988). Hatchery programs

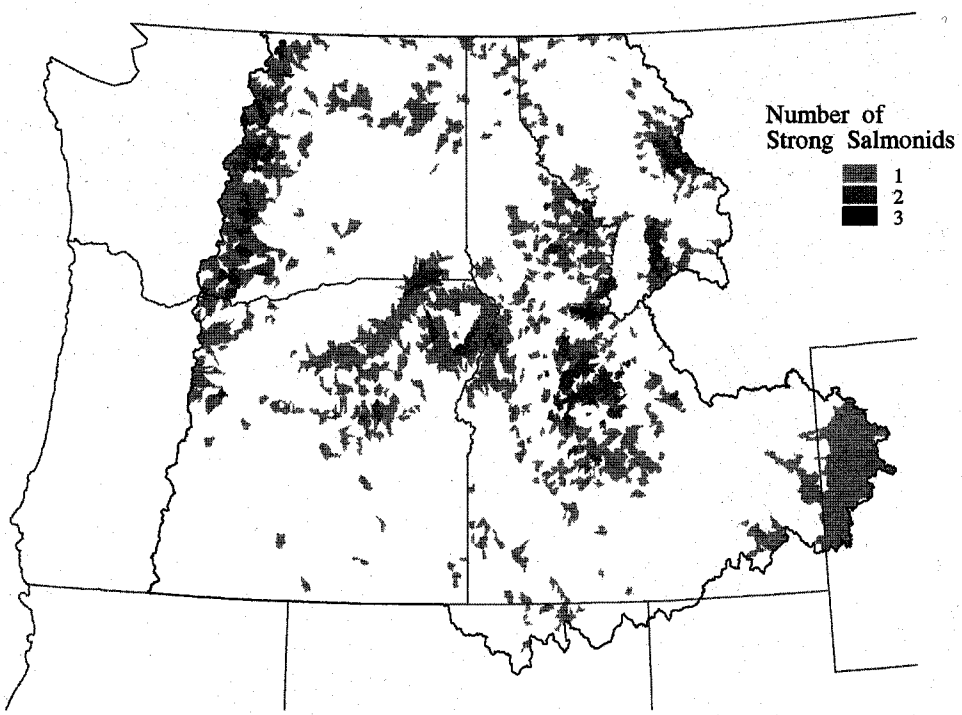

FIGURE 8.—Number of salmonid taxa classified or predicted to be strong in subwatersheds in the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

may erode genetic diversity and alter locally adapted stocks (Waples and Do 1994; Reisenbichler 1997). The effects may include a loss of fitness and a loss of genetic variability important to long term stability and adaptation in varying environments.

About 50 nonnative species have been introduced within the range of the seven salmonids examined (Lee et al. 1997). Introduced rainbow trout *Oncorhynchus mykiss,* brook trout *Salvelinus fontinalis,* and brown trout *Salmo trutta* are distributed widely in lowland and alpine lakes and streams. Introduced rainbow trout were reported in 78% of the watersheds in the study area, and brook trout in about 50% (Figure 9), making them the most widely distributed fishes. Brown trout were found in 23% of the watersheds (Figure 9). Many native salmonids have been introduced outside their natural range via stocking of hatchery-reared forms. These include Lahontan, Yellowstone, and westslope cutthroat trout, redband trout and other forms of rainbow trout, chinook and coho salmon, kokanee *O. nerka,* and steelhead.

The effects of introductions on the community ecology and genetic integrity of native salmonids have not been assessed thoroughly. As a result, our estimates of strong populations (Table 1) may be overly optimistic. Varley and Gresswell (1988), for example, estimated that genetically pure populations of Yellowstone cutthroat trout occur in about 10% of the historical stream habitat and about 85% of the historical lacustrine habitat. Liknes and Graham (1988) estimated that westslope cutthroat trout were pure in 2.5% of the historical range in Montana. The long history of stocking rainbow trout within the study area, and the proclivity for redband and rainbow trout to hybridize (Allendorf et al. 1980; Wishard et al. 1984; Berg 1987; Currens et al. 1990; Leary et al. 1992), raise similar concerns about the distribution and status of the original redband trout genotype. While information is not available across the study area to judge the effects of hatchery releases on genetic structure of steelhead (Busby et al. 1996) and chinook salmon, wild stocks appear to be rare. Biologists judged wild stocks of steelhead and stream and ocean type chinook salmon that were unaltered by hatchery releases to be present in 10, 4, and 5% of the potential range, respectively (Lee et al. 1997).

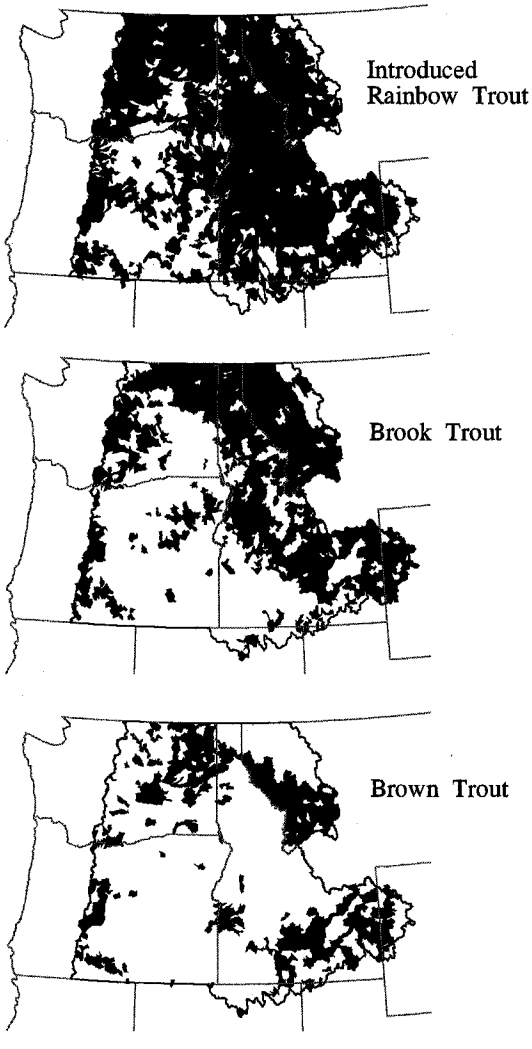

FIGURE 9.—Current distribution of introduced rainbow trout, brook trout, and brown trout in watersheds within the interior Columbia River basin in the United States and portions of the Klamath River and Great basins.

Opportunities for Conservation and Restoration

Though the historical distribution and status of native salmonids has declined, key areas remain for rebuilding and maintaining more functional aquatic systems. Native species still occur in much of the study area (Lee et al. 1997). A core of habitats and populations for maintaining, and perhaps restoring, much of the biological diversity associated with historical aquatic communities still may exist. We suggest that important elements for conservation can be represented by subwatersheds supporting strong populations. Subwatersheds supporting high diversity of salmonid taxa also will be important.

Subwatersheds supporting strong populations of salmonids likely represent a fortuitous balance of habitat quality, climatic and geologic constraint, and geographic location which effectively minimizes cumulative threats. Because full life history expression was part of our criteria for defining strong populations, the occurrence of strongholds also may indicate the relative integrity of the larger system of watersheds. The most productive, abundant, and diverse populations are likely to be most resistant and resilient to environmental disturbance, and are most likely to survive stochastic events. Thus, they are more likely to serve as sources for the support of weak or at-risk populations, refounding of locally extinct populations, or refounding of habitats made available through restoration (see Schlosser and Angermeier 1995). Delineation of strongholds provides a spatially explicit, robust, and extensive area from which any conservation strategy could proceed.

The largest areas of contiguous or clustered subwatersheds supporting strongholds are within the major river subbasins in the central Idaho mountains, the Snake River headwaters, the northern Cascades, and their connecting river corridors (Figure 8). These are also the largest remaining regions of high salmonid taxa diversity (Figure 1). Other important strongholds and areas of taxa diversity are found in the Blue mountains, northern Idaho, and western Montana, but these are scattered or generally restricted to portions of interior river subbasins (Figures 1, 8). With the exception of the central Idaho mountains and northern Cascades, there are few clusters of subwatersheds likely to provide highly productive habitat for multiple taxa, but collections of taxa still exist within larger subbasins. Because salmon and steelhead have very few strongholds, subwatersheds supporting naturally reproducing populations may represent the only areas available from which to anchor a conservation strategy. Conservation of such locally adapted and marginal populations will be critical for maintaining species genetic diversity (Scudder 1989).

Strategies have been proposed for the development of habitat networks designed to conserve species and aquatic biological diversity (Moyle and Sato 1991; Reeves and Sedell 1992; Doppelt et al. 1993; Frissell et al. 1993; Rieman and McIntyre 1993). A general consensus is that conservation and rehabilitation should focus first on the best remaining examples of aquatic biological

integrity and diversity. Special emphasis areas which provide high-quality habitat and stable populations are a cornerstone of conservation strategies for most species.

Ultimately, conservation of native salmonids throughout the Pacific Northwest will require a more integrated, broad-scale view of management than has been practiced historically. The emerging principle of ecosystem management is a new approach to solve current forest, watershed, and aquatic health issues. An assumed goal of ecosystem management is to maintain or rehabilitate the integrity of aquatic ecosystems and to provide for the long-term persistence of native and desirable nonnative fishes and other species (Grumbine 1994). Achieving this goal will require the maintenance or rehabilitation of a network of well-connected, high-quality habitats that support a diverse assemblage of native species, the full expression of potential life histories and dispersal mechanisms, and the genetic diversity necessary for long-term persistence and adaptation in a variable environment. Protection of emphasis areas, such as the strongholds we have identified, will not be sufficient. Such reserves never will be large or well distributed enough to maintain biological diversity (Franklin 1993). Watershed rehabilitation and the development of more ecologically compatible land use policies are also required to ensure the long-term productivity of many systems. Ecosystem management, then, also implies using active management to reestablish more complete or natural structure, function, and processes whenever possible. Identical goals in terrestrial ecology, and the inextricable link between terrestrial and aquatic systems, suggest that management efforts in one should benefit the other. The challenge is to coordinate management of terrestrial and watershed systems rather than to work at cross purposes.

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