Redband Trout: Resilience and Challenge in a Changing Landscape
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Distribution and Status of Redband Trout in the Interior Columbia River Basin and Portions of the Klamath River and Great Basins

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Abstract.—We summarized existing knowledge (circa 1996) of the potential historical range and the current distribution and status of non-anadromous interior redband trout *Oncorhynchus mykiss* ssp. in the U.S. portion of the interior Columbia River Basin and portions of the Klamath River and Great Basins (ICRB). We estimated that the potential historical range included 5,458 subwatersheds and represented about 45% of the species' North American range. Two forms of interior redband trout were considered, those sympatric with steelhead *Oncorhynchus mykiss* ssp. and allopatric forms that evolved outside the range of steelhead. Data were compiled from existing surveys and expert opinions of over 150 biologists during the scientific assessment for the Interior Columbia River Basin Ecosystem Management Project (ICBEMP). We also predicted fish presence and status in unsampled areas, using statistical models to quantitatively explore relationships among redband trout status and distribution, the biophysical environment, and land management. Redband trout had the highest likelihood of being present or supporting strong populations in mid-size or smaller streams, of higher gradients, in highly erosive landscapes with steep slopes, with more solar radiation, and mean annual air temperatures less than 8–9ºC. Variables reflecting the degree of human disturbance within watersheds (road density, land ownership, and management emphasis) were also important. Redband trout remain the most widely distributed native salmonid in the ICBEMP assessment area and the second most widely distributed native fish, occupying 47% of the subwatersheds and 64% of their potential range. Sympatric redband trout are the most widely distributed of the two forms, present in an estimated 69% of their potential range. Despite their broad distribution, important declines in distribution and status are apparent from our analysis, although finer scale extirpations of redband trout populations were more difficult to quantify. Both forms of redband trout have narrower distributions and fewer strong populations than historical populations; neither form supported strong populations in more than 17% of their potential ranges. Habitat degradation, habitat fragmentation, and nonnative species introductions are primary factors that have influenced status and distribution. Because of the likelihood of introgressive hybridization with introduced salmonids, actual status of some strong populations may be worse than suggested. Although much of the potential range has been altered, core areas remain for conserving and rebuilding more functional aquatic systems in order to retain the ecological diversity represented by redband trout. Protection of core areas critical to stock persistence and restoration of a broader matrix of productive habitats will be necessary to ensure the full expression of phenotypic and genotypic diversity in interior redband trout. We recognize the limitations of this database and acknowledge that estimates based on expert opinion and modeling involve inherent uncertainties. A more refined synthesis of redband trout distribution and status will require documentation, consistency, and rigor in sampling and data management that does not currently exist.

Rainbow trout *Oncorhynchus mykiss* are a widely distributed salmonid native to western North America. Little consensus exists on the taxonomic nomenclature for the groups. Currens et al. (2007) suggested the species should be segregated into at least four groups: (1) Columbia River populations; (2) populations from Goose Lake, Warner Lakes, and the Chewaucan Basin; (3) Upper Klamath Lake and River and coastal Klamath Mountain populations; and (4) populations from pluvial lake basins in Oregon. Other taxonomists have suggested three groups (Behnke 1992): (1) Coastal rainbow trout west of the Cascade/Sierra mountain divide; (2) Interior Columbia River redband trout upstream of Celilo Falls, including the Fraser and Athabasca rivers in Canada, the upper Klamath River Basin, and the isolated interior basins of Oregon; and (3) the Sacramento–San Joaquin red-

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band trout. Although the systematics of redband trout are in dispute, genetic and physical characteristics support the view that these groups warrant subspecies recognition (Allendorf 1975; Utter and Allendorf 1977; Allendorf and Utter 1979; Allison and Bond 1983; Berg 1987; Stearley and Smith 1993).

Here we consider the interior redband trout native to the interior Columbia River Basin and portions of the Klamath River and Great Basins. Redband trout have two distinct life histories, anadromous (steelhead) and non-anadromous. In this paper, we confine our analysis to non-anadromous redband trout (*Oncorhynchus mykiss* ssp.). Thurow et al. (2000) describe the distribution and status of steelhead (*Oncorhynchus mykiss* ssp.) in the same assessment area.

Interior redband trout exhibit broad phenotypic diversity including varying age-at-maturity, frequency and timing of spawning, seasonal timing and patterns of migration, longevity, habitat selection, temperature tolerance, and a host of other characteristics. Life histories of redband trout are variable. At least three forms have been described, including adfluvial and fluvial migratory forms and resident forms. Adfluvial redband trout (such as Kamloops rainbow trout) migrate from lentic waters to tributaries and were historically present in Canadian lakes, Crescent Lake, Washington and several isolated lake basins within the Northern Great Basin in Oregon (Moyle et al. 1989; Behnke 1992). Fluvial redband trout remain in flowing waters throughout their entire life cycle and inhabit streams ranging from low-order tributaries to large rivers, compared to resident forms that have more restricted movements. Because redband trout have persisted in a variety of biophysical settings, other life history adaptations may exist (*see* Thorpe 1994). Movement among habitats and populations may be an important mechanism for maintenance of genetic variability in populations (Leary et al. 1992) and for their persistence in variable environments (Rieman and Clayton 1997; Rieman and Dunham 2000). Local adaptation and selection for unique alleles resulting from isolation, however, may also be important to total genetic variability in the species (e.g. Lesica and Allendorf 1995; Gamperl et al. 2002). Introgressed forms of redband trout, hybrids with introduced cutthroat trout *O. clarkii* or coastal rainbow trout, have replaced native redband trout in some areas today (Currens et al. 1997; Neville et al. *in preparation*).

As a result of declines in abundance and distribution, the interior redband trout is considered a species of special concern by the American Fisheries Society (Williams et al. 1989) and in all states within the historical range, and is classified as a sensitive species by the USDA Forest Service (Forest Service) and USDI Bureau of Land Management (BLM). In 1994, the Kootenai River redband trout in northern Idaho and Montana was petitioned for listing under the Endangered Species Act of 1973 (ESA). The USDI Fish and Wildlife Service (USFWS) determined that listing was unwarranted because there was insufficient information to identify the Kootenai River population as a distinct population segment. A 1997 petition to the USFWS to list redband trout in the Catlow, Fort Rock, Harney, Warner Lakes, Goose Lake, and Chewaucan basins of eastern Oregon was also denied. Concerns for the persistence of other redband trout stocks in the interior Columbia River Basin and portions of the Klamath River and Great Basins have culminated in several listings under ESA (www.nwr.noaa.gov/ESA-Salmon-Listings). The final rules list only anadromous forms because of inconclusive data regarding the relationship between steelhead and non-anadromous redband trout. Upper Columbia River steelhead were listed as endangered in 1997 and downgraded to threatened in 2006. Snake River Basin steelhead were listed as threatened in 1997, Lower Columbia River steelhead were listed as threatened in 1998, and Middle Columbia River steelhead were listed as threatened in 1999, with all three listings reaffirmed in 2006.

Despite concerns for the species persistence, the distribution and status of redband trout across their range are poorly defined. One goal of the Interior Columbia River Basin Ecosystem Management Project (ICBEMP) (Quigley and Arbelbide 1997) was a comprehensive evaluation of the status and distribution of fishes (Lee et al. 1997). In this paper we describe the potential historical range and the current (as of 1996) distribution and status of redband trout in the U.S. portion of the interior Columbia River Basin and portions of the Klamath River and Great Basins, hereafter referred to as the ICRB. We also describe 1996 conditions and consider factors likely to influence the species' future.

Methods

The ICBEMP confined our analysis to the United States portion of the interior Columbia River Basin east of the Cascade crest and portions of the Klamath River and Great Basins (Figure 1). The area includes over 58 million ha in Idaho, Montana, Nevada, Oregon, Washington, and Wyoming, of which 53% is administered by the Forest Service or BLM (Quigley et al. 1996). Lee et al. (1997) and Rieman et al. (1997b) provide detailed descriptions of the hierarchical system of subbasins, watersheds, and subwatersheds and the ecological reporting units we used. Topography was used to define subbasins averaging 356,500 ha surface area, watersheds averaging 22,800 ha, and subwatersheds averaging 7,800 ha (Figure 1). Subwatersheds were the smallest sample unit used in our analysis of fish distributions. These divisions follow the hierarchical framework of aquatic ecological units described by Maxwell et al. (1995). The study area also was subdivided into 13 broad geographical regions known as Ecological Reporting Units (ERUs) (Lee et al. 1997) (Figure 2). The ERUs were delineated based primarily on the distribution of potential vegetation types and broad zoogeographical boundaries to aquatic and terrestrial organisms.

Sympatric and allopatric forms of non-anadromous redband trout were assessed separately. We considered allopatric redband trout those that evolved outside the historical

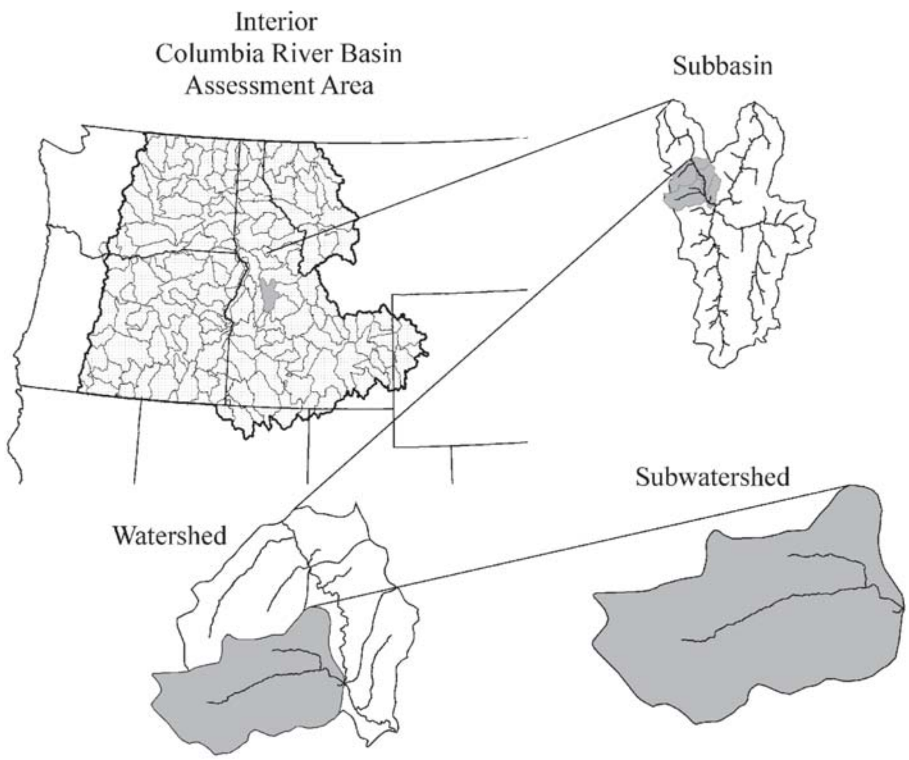

Figure 1.—The interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins and the hierarchy of hydrologic units used in the analysis.

range of steelhead and assumed that this form was evolutionarily distinct from other redband trout because of isolation. We considered sympatric redband trout to be the non-anadromous form historically associated with steelhead. A non-anadromous form is likely to exist in sympatry with steelhead (Busby et al. 1996). Morphologically, anadromous and non-anadromous redband trout juveniles are indistinguishable, so 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 (for example, above natural barriers in 2nd- and 3rd-order streams) was not addressed.

Known Status and Distribution

We held a series of workshops in 1995 and asked more than 150 biologists from across the ICRB to characterize the status and distribution of native salmonids including redband trout. 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 supporting spawning and rearing were further classified as strong or depressed. Strong subwatersheds include those where: (1) all major life histories that historically occurred within the watershed are present; (2) numbers are stable or increasing, and the local population is likely to be at half or more of its historical size or density; and (3) the population or metapopulation within the subwatershed, or within a larger region of which the subwatershed is a part, probably contains at least 5,000 individuals or 500 adults. When no information was available to judge current presence or absence, the subwatershed was classified as status unknown. Because non-anadromous redband trout and juvenile steelhead were indistinguishable and the level of genetic or behavioral segregation between them is unknown (Busby et al. 1996), we classified the status of sympatric redband trout as unknown when steelhead were present. Unknown also was the default classification in the absence of survey responses or information from prior databases, or where there were conflicting responses between the survey and electronic databases that could not be resolved. We asked biologists to rely on biological characteristics and to not infer status from habitat or landscape information or presence of introduced fishes. Where possible, classifications were reviewed by others familiar with the area in question and we attempted to use only the most current information.

The resolution of our data may produce estimates of current distributions that are more optimistic than work based on stream reaches (Rieman et al. 1997b). Redband trout were considered present in the entire subwatershed if they occurred anywhere within it. Because redband trout have the

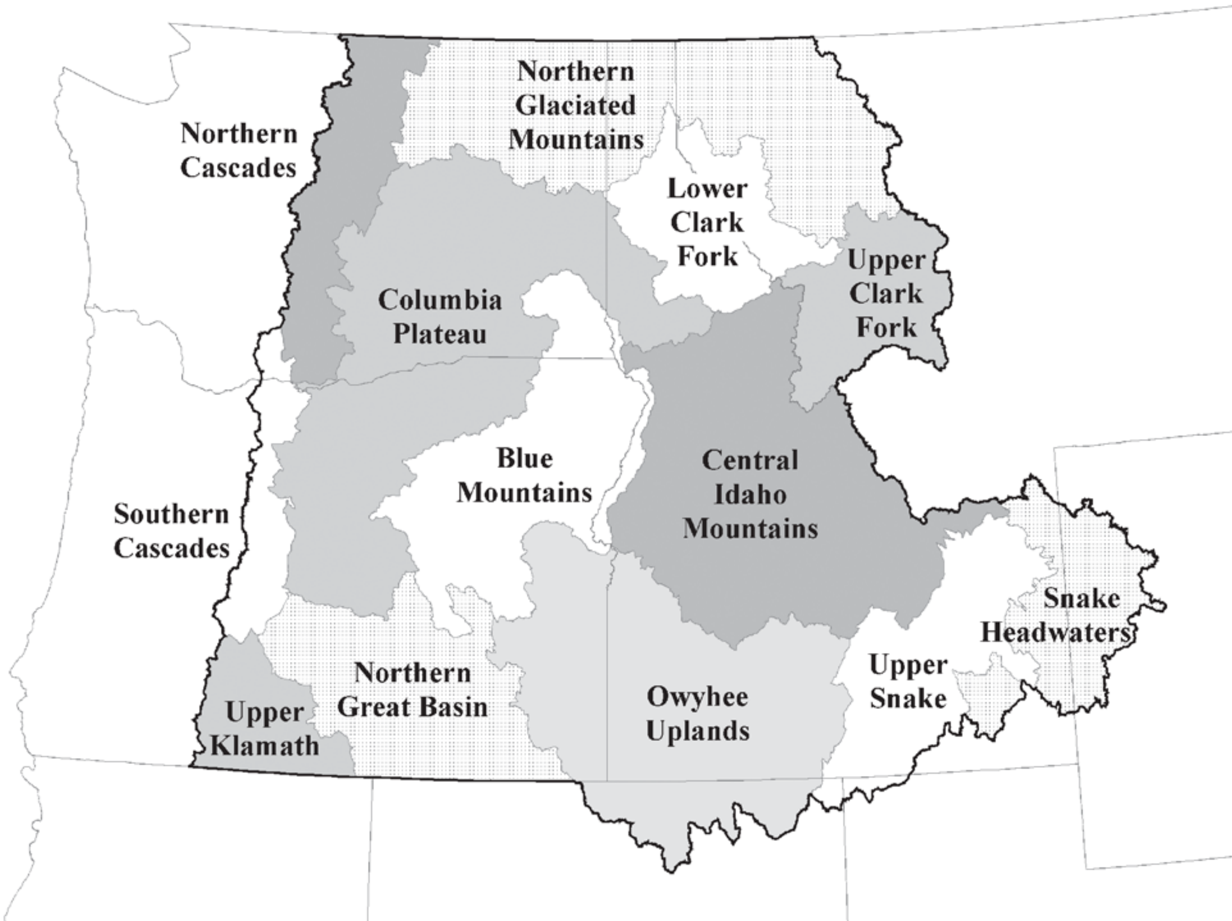

Figure 2.—Ecological reporting units (ERUs) used to summarize information across broad regions of similar biophysical characteristics in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins, adapted from Lee et al. (1997).

potential for extended movement and dispersal (Moyle et al. 1989), subwatersheds provide an appropriate sampling unit for a large-scale analysis. To minimize bias, distributions were based on the number of occupied subwatersheds.

Potential Historical Range

Potential historical ranges, hereafter referred to as potential ranges, were defined as the likely distributions in the ICRB prior to European settlement. Potential ranges were characterized from historical distributions in prior databases and augmented through published and anecdotal accounts. The potential range of all forms of redband trout included freshwaters west of the Rocky Mountains, extending from northern California to northern British Columbia, Canada (Figure 3). What may be a primitive form has been found in the Athabasca and Peace River drainages on the east flank of the Rocky Mountains (Carl et al. 1994). We did not consider the distribution of redband trout in Canada, but they are believed to have been present throughout the upper Columbia River Basin with the exception of the upper Kootenai River Basin above Kootenai Falls (Behnke 1992; E. Parkinson, British Columbia Ministry of Environment, personal communication). Redband trout were widely distributed and occupied most waters from the southern desert basins to the high mountain coniferous forests (Cope 1879, 1889; Jordan 1892; Gilbert and Evermann 1895; Jordan and Evermann 1896; Snyder 1908; Jordan et al. 1930; Behnke 1992). Hubbs and Miller (1948) and Behnke (1992) speculated that a wet cycle in the Pleistocene could have allowed redband trout to move from the Columbia River Basin to the upper Klamath River and several of the closed desert basins along the southern margin of Oregon.

We included all subwatersheds that were accessible as potential range based on known current and historical occurrences because redband trout can be highly mobile, moving through subwatersheds, watersheds, subbasins, and basins at different life stages seasonally (Moyle et al. 1989). Subwatersheds that were known to be historically isolated by barriers to movement were excluded from potential ranges. We recognize that, within subwatersheds, the potential range may be further restricted by elevation, temperature, and local channel features but did not attempt to define potential ranges at a finer resolution.

Figure 3.—Native range of interior redband trout in North America. Distributions outside the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins were adapted from Behnke (1992).

Predictive Models

We produced a set of predictions using statistical models, called classification trees (Breiman et al. 1984), that reflect the likelihood of redband trout presence, or the likely status of the population, within unsampled or unknown subwatersheds. Our objective was to generate a complete picture of the current distribution and status of redband trout by quantitatively exploring relationships among fish distribution, the biophysical environment, and land management. Lee et al. (1997) and Rieman et al. (1997b) provide a detailed description of classification trees and the fitting, cross-validation, and pruning routines. We summarized 28 variables with the potential to influence aquatic systems from more than 200 landscape variables available across the ICRB (Lee et al. 1997). Quigley and Arbelbide (1997) describe the variables and their derivations in detail. Rieman et al. (1997b) list the categorical and continuous variables we used to represent vegetative communities, climate, geology, landform and erosive potential, land management history, and relative intensity of human disturbance.

Two separate classification tree models were built for redband trout. In the first tree (Presence model), 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 (Status model) was constructed with a trinomial response to distinguish spawning and rearing areas (present-strong or present-depressed) from non-spawning areas. Present-strong and present-depressed were retained as two separate responses, while migration corridors and absence were combined into a third response as absent. Trees were used to estimate the probability of presence or absence of redband 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.

We summarized known and predicted status and distribution of redband trout across the ICRB. We estimated the percentage 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 percentage 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 a geographic information system (GIS). To estimate the proportion of the current distribution in protected status, we summarized the number of occupied subwatersheds within National Park Service lands and in designated wilderness areas.

Results

Potential Historical Range

The potential range of redband trout included 77% of the ERUs and 73% of the subwatersheds in the ICRB (Tables 1, 2). This area includes 5,458 subwatersheds and represents about 45% of the species' North American range (Figure 3). The only major areas of the ICRB that did not support redband trout were the Snake River upstream from Shoshone Falls, tributaries to the Spokane River above Spokane Falls, Rocky Mountain basins in Montana excluding the Kootenai River, and portions of the northern Great Basin in Oregon (Figure 4). Only six subwatersheds were identified exclusively as corridors (Tables 1, 2). Sympatric redband trout were the most widely distributed form, occupying an estimated 59% of all subwatersheds and all but four ERUs (Table 1, Figure 4). Allopatric redband trout were less widely distributed, occupying an estimated 40% of all subwatersheds (Table 2, Figure 4).

Known Status and Distribution

Based on our synthesis, redband trout appear to have remained relatively widely distributed. We estimated that they were known to be present in 55% of the subwatersheds in the potential range (Table 1, 2). Populations of redband trout remained in some portion of all ERUs in the potential range. Sympatric redband trout were believed present in 59% of the potential range (Table 1, Figure 4). Strong populations of the sympatric form were judged to be present in 5% of the potential range and 9% of the current range. Allopatric redband trout were estimated to be present in 40% of the potential range, with strong populations in 7% of the current range (Table 2, Figure 4).

Despite their broad occurrence, the distribution and status of redband trout was unclassified or unknown in many subwatersheds. About 27% of the sympatric redband trout potential range and 39% of the allopatric redband trout potential range was not classified (Table 1, 2). Another 41% of the sympatric redband trout potential range and 23% of the allopatric redband trout potential range was judged to support redband trout, but too little information was available to evaluate status. As described above, our inability to differentiate juvenile steelhead and sympatric redband trout was a principal reason for the unknown status of sympatric redband trout.

Predictive Models

Two classification models were developed from 1,793 subwatersheds with complete fish status and landscape in-

Table 1.—Summary of classifications (number of subwatersheds) of occurrence and status for sympatric redband trout throughought Ecological Reporting Units of the study area.

				Status where present					
Ecological Reporting Unit	Total	Potential historical range	Total present	Strong	Depressed	Unknown	Transient in migration corridor	Absent	Unknown or no classification
Northern Cascades	340	292	222	5	4	213	0	7	63
Southern Cascades	141	125	107	25	38	44	0	19	4
Upper Klamath	175	35	8	0	0	8	0	0	27
Northern Great Basin	506	0	0	0	0	0	0	0	0
Columbia Plateau	1,089	796	398	23	94	278	3	148	250
Blue Mountains	695	643	534	35	69	427	3	23	86
Northern Glaciated Mountains	955	258	180	21	3	156	0	31	47
Lower Clark Fork	415	98	67	3	17	47	0	8	23
Upper Clark Fork	306	0	0	0	0	0	0	0	0
Owyhee Uplands	956	898	279	38	154	87	0	283	336
Upper Snake	301	0	0	0	0	0	0	0	0
Snake Headwaters	387	0	0	0	0	0	0	0	0
Central Idaho Mountains	1,232	1,051	693	66	146	481	0	43	315
Entire study area	7,498	4,196	2,488	216	525	1,741	6	562	1,151

Table 2.—Summary of classifications (number of subwatersheds) of occurrence and status for allopatric redband trout throughought Ecological Reporting Units of the study area.

				Status where present					
Ecological Reporting Unit	Total	Potential historical range	Total present	Strong	Depressed	Unknown	Transient in migration corridor	Absent	Unknown or no classification
Northern Cascades	340	48	31	0	0	31	0	2	15
Southern Cascades	141	0	0	0	0	0	0	0	0
Upper Klamath	175	140	36	0	10	26	0	0	104
Northern Great Basin	506	405	99	2	49	48	0	165	141
Columbia Plateau	1,089	254	67	1	62	4	0	62	125
Blue Mountains	695	52	40	13	26	1	0	10	2
Northern Glaciated Mountains	955	198	101	4	10	87	0	21	76
Lower Clark Fork	415	1	1	0	0	1	0	0	0
Upper Clark Fork	306	0	0	0	0	0	0	0	0
Owyhee Uplands	956	58	32	2	13	17	0	4	22
Upper Snake	301	0	0	0	0	0	0	0	0
Snake Headwaters	387	0	0	0	0	0	0	0	0
Central Idaho Mountains	1,232	106	93	13	2	78	0	1	12
Entire study area	7,498	1,262	500	35	172	293	0	265	497

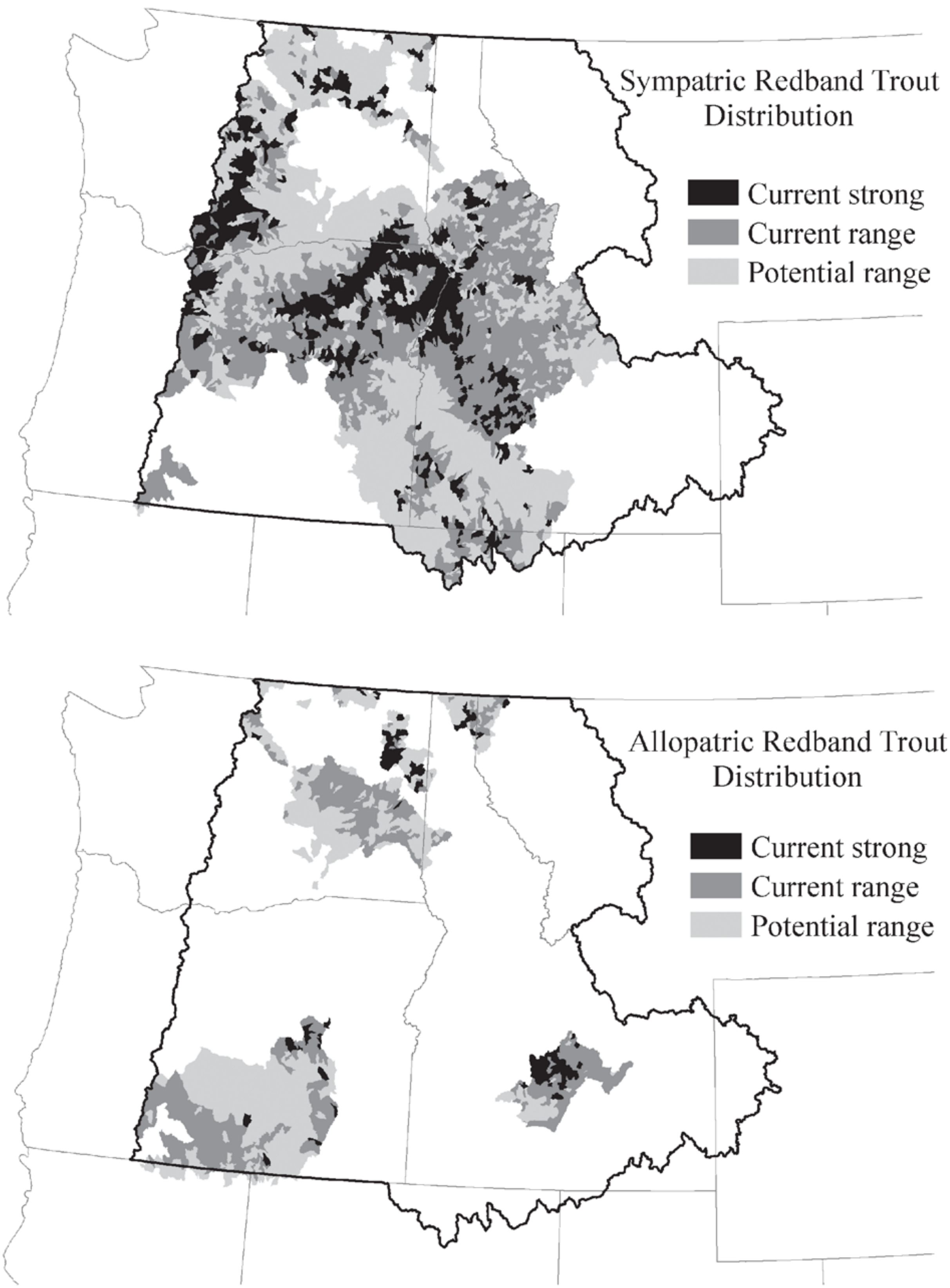

Figure 4.—The potential historical range, known and predicted current range, and known and predicted strong populations of sympatric redband trout (top) and allopatric redband trout (bottom) within the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

formation. The Status model for classifying status of redband trout in spawning and rearing areas (strong, depressed, absent) had an overall classification success rate of 76% and was most successful classifying absent (83%) followed by depressed (74%) and strong (58%) (Table 3). Nineteen variables were used in the model and five explained a major portion of the deviance (a measure of variation in categorical variables, Lee et al. 1997) (Table 4). Variables were: *management class* based on land ownership and management emphasis, *slope* was area-weighted average midslope based on 90 m digital elevation maps, *anadromous access* was accessible to anadromous fish (yes or no), *ecological reporting unit*, and *hucorder* was the number of upstream subwatersheds tributary to the subwatershed of interest. Redband trout were more likely to be present in spawning and rearing areas in mid-size or smaller streams within landscapes with steep slopes in certain ERUs. The relationship between redband trout status and anadromous access was less clear. As explained above, we considered the status of sympatric redband trout unknown when steelhead were present. Biologists were able to classify redband trout status in 119 subwatersheds with anadromous access, and redband trout had similar likelihood of being present (0.54) as absent (0.46) in spawning and rearing areas (Table 4). Variables potentially reflecting the degree of human disturbance within watersheds (management class) were also important. Redband trout were four times less likely to be present in spawning and rearing areas and more than five times less likely to be strong in subwatersheds within private and federal grazing lands and private agricultural lands compared to private and federal forest lands, moderately grazed Forest Service lands, or tribal lands (Table 4).

Table 3.—Cross classification comparison of predicted and reported status and occurrence of both forms of redband trout pooled across the study area. Tables represent comparisons for a model of status within spawning and rearing areas (top) and for presence and absence (bottom) across the potential historical range.

	Predicted status in spawning and rearing areas			
Reported status	Absent	Depressed	Strong	Total
Absent	688	134	9	831
Depressed	117	525	70	712
Strong	32	73	145	250

Misclassification error rate = 435/1793 = 24%

	Predicted occurrence across range		
Reported occurrence	Absent	Present	Total
Absent	749	76	825
Present	255	713	968

Misclassification error rate = 331/1793 = 18%

The second model had an overall classification success rate of 82% when limited to presence or absence (Table 3). Of the sixteen variables used in this model, five explained a major portion of the deviance: *mean annual precipitation* in mm; *base erosion index* representing relative surface erodability without vegetation; *mean annual solar radiation* based on topographic shading, latitude, and aspect; *ecological reporting unit*, and *mean annual air temperature* (Table 5). Redband trout were more likely to be present in subwatersheds with precipitation greater than about 38 cm, highly erosive landscapes, higher solar radiation, and mean air temperatures less than 8.7ºC (Table 5).

Overall, the patterns suggested by the classification models were consistent with our understanding of redband trout biology and habitat use. The frequency of physiographic and geophysical predictor variables within the models suggests that biophysical setting is an important determinant of redband trout distribution and habitat suitability. The importance of management class suggested a negative influential effect of human disturbance.

Based on these analyses we used the two models to estimate the probability of occurrence of sympatric redband trout in 1,151 subwatersheds that were previously unclassified and to predict status (strong, depressed, absent.) in those subwatersheds and an additional 1,741 subwatersheds where fish were present of unknown status (Table 1, Figure 5). We used the classification models to estimate the probability of occurrence of allopatric redband trout in 497 subwatersheds that were previously unclassified and to predict status in those subwatersheds and an additional 293 subwatersheds where fish were present of unknown status (Table 2, Figure 6).

Known and Predicted Status and Distribution

After combining the known and predicted subwatershed classifications, we estimated that sympatric and allopatric redband trout jointly occupy 47% of the ICRB and remain in 64% of their combined potential historical range (Figure 4, Tables 6, 7). Sympatric redband trout are the most widely distributed of the two forms; their estimated distribution includes 69% of the potential range (Table 6, Figure 5). The largest areas of unoccupied potential habitat include the Owyhee Uplands and Columbia Plateau**.** Allopatric redband trout are not as widely distributed and are currently estimated in 49% of the potential range (Table 7, Figure 4). Allopatric redband trout are least well distributed in the Northern Great Basin and Columbia Plateau, where they are believed absent in 72% of the potential range (Table 7).

Despite their broad distribution, relatively few strong redband trout populations were identified. We estimated that 78% of the subwatersheds in the current range of sympatric redband trout supported spawning and rearing and 31% were classified as strong (Table 6). Strong populations were present in 17% of the potential range and 24% of the current range. Allopatric redband trout had fewer strong populations. We estimated that 94% of the subwatersheds in the

Table 4.—The first 11 nodes of a classification tree for redband trout status (absent, depressed, strong) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within spawning and rearing areas in 1,793 subwatersheds used to develop the model. Nodes and accompanying data are hierarchical and represent the structure of a tree. The root node represents the complete distribution. The first split occurs at mngclus (management class, based on ownership and management emphasis) and produces nodes 2 and 3 that are further independently subdivided. Node 2 includes BLM (BR) and private (PR) grazed lands, Forest Service high impact lands with grazing (FH), and private agricultural lands (PA). Node 3 includes Forest Service moderately impacted and grazed lands (FG) and high impact lands with no grazing (FM), managed wilderness (FW), Forest Service and private forest lands (PF), and tribal lands (TL). Other variables included: slope (area weighted average midslope), eru (ecological reporting unit), hucorder (number of upstream subwatersheds), and anadac (access for anadromous fish). See Lee et al. (1997) for further information.

				Relative frequencies		
Node (Variable and criteria)	Sample size	Deviance	Modal class	Absent	Depressed	Strong
1) root	1793	3578.0	A	0.4635	0.3971	0.1394
2) mngclus: BR, FH, PA, PR	1254	2107.0	A	0.5981	0.3437	0.05821
4) slope < 9.9835	757	961.5	A	0.7411	0.2417	0.01717
8) eru: 4,7,10	464	460.5	A	0.8362	0.1487	0.01509
9) eru: 1,2,5,6,13	293	444.2	A	0.5904	0.3891	0.02048
5) slope > 9.9835	497	964.0	D	0.3803	0.4990	0.1207
10) hucorder < 144	460	887.5	D	0.3304	0.5391	0.1304
11) hucorder > 144	37	0.0	A	1.0000	0.0000	0.0000
3) mngclus: FG, FM, FW, PF, TL	539	1067.0	D	0.1503	0.5213	0.3284
6) anadac < No	420	716.6	D	0.0619	0.5857	0.3524
7) anadac > Yes	119	252.4	A	0.4622	0.2941	0.2437

current range of the allopatric form supported spawning and rearing and 20% were classified as strong (Table 7). Strong populations were estimated in 9% of the potential range and 20% of the current range. Model predictions tended to be spatially correlated with known conditions. That is, predicted strong populations were more likely to occur in proximity to known strong populations and predicted depressed populations in proximity to known depressed populations (Figure 5).

Table 5.—The first 11 nodes of a classification tree for redband trout presence (P) or absence (A) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within 1,793 subwatersheds used to develop the model. Nodes and accompanying data are hierarchical and represent the structure of a tree. The root node represents the complete distribution. The first split occurs at pprecip (mean annual precipitation), node 2 is < 380.3 mm compared to node 3 that is >380.3 mm. These two nodes are further independently subdivided. Other variables included: baseero (base erosion index), solar (mean annual solar radiation), and mtemp (mean annual air temperature). See Lee et al. (1997) for further information.

Node (Variable and criteria)	Sample size	Deviance	Modal class	Absent	Present
1) root	1793	2474.00	P	0.46010	0.53990
2) pprecip<380.296	840	1021.00	A	0.70360	0.29640
4) baseero<5.637	432	372.80	A	0.84490	0.15510
8) eru:2,5,6,7	99	126.00	A	0.66670	0.33330
9) eru:4,10	333	219.60	A	0.89790	0.10210
5) baseero>5.637	408	560.90	A	0.55390	0.44610
10) mtemp<8.707	254	349.50	P	0.44880	0.55120
11) mtemp>8.707	154	180.50	A	0.72730	0.27270
3) pprecip>380.296	953	1062.00	P	0.24550	0.75450
6) solar<277.231	258	357.40	A	0.51550	0.48450
7) solar>277.231	695	576.20	P	0.14530	0.85470

Of the 3,500 subwatersheds that supported either form of redband trout, about 10% were in protected status within National Park Service or designated wilderness (Tables 6, 7). About 9% of the 816 subwatersheds supporting strongholds for either redband trout form were in protected status. For sympatric redband trout, 12% of the present distribution and 10% of the strongholds were within lands of protected status (Table 6). The most secure portions of the distribution were found within the Central Idaho Mountains (25% of the current range and 15% of the strongholds in protected status), the Northern Cascades, and the Blue Mountains ERUs. For allopatric redband trout, less than 4% of the current range and less than 3% of the strongholds were within lands of protected status (Table 7). Subwatersheds supporting allopatric redband trout were secure only within the Northern Cascades ERU, where 55% of the current range and the one stronghold were in protected status.

Discussion

Limitations of our Approach

Our analysis has several important limitations. As described above, the ICBEMP (Quigley and Arbelbide 1997) mandated a comprehensive evaluation of the status and distribution of fishes within a clearly defined area. Consequently, we described the potential historical range and the current distribution and status of redband trout only within the interior Columbia River Basin and portions of the Klamath River and Great Basins, and omitted other important areas within the range of redband trout (i.e., in California and Canada).

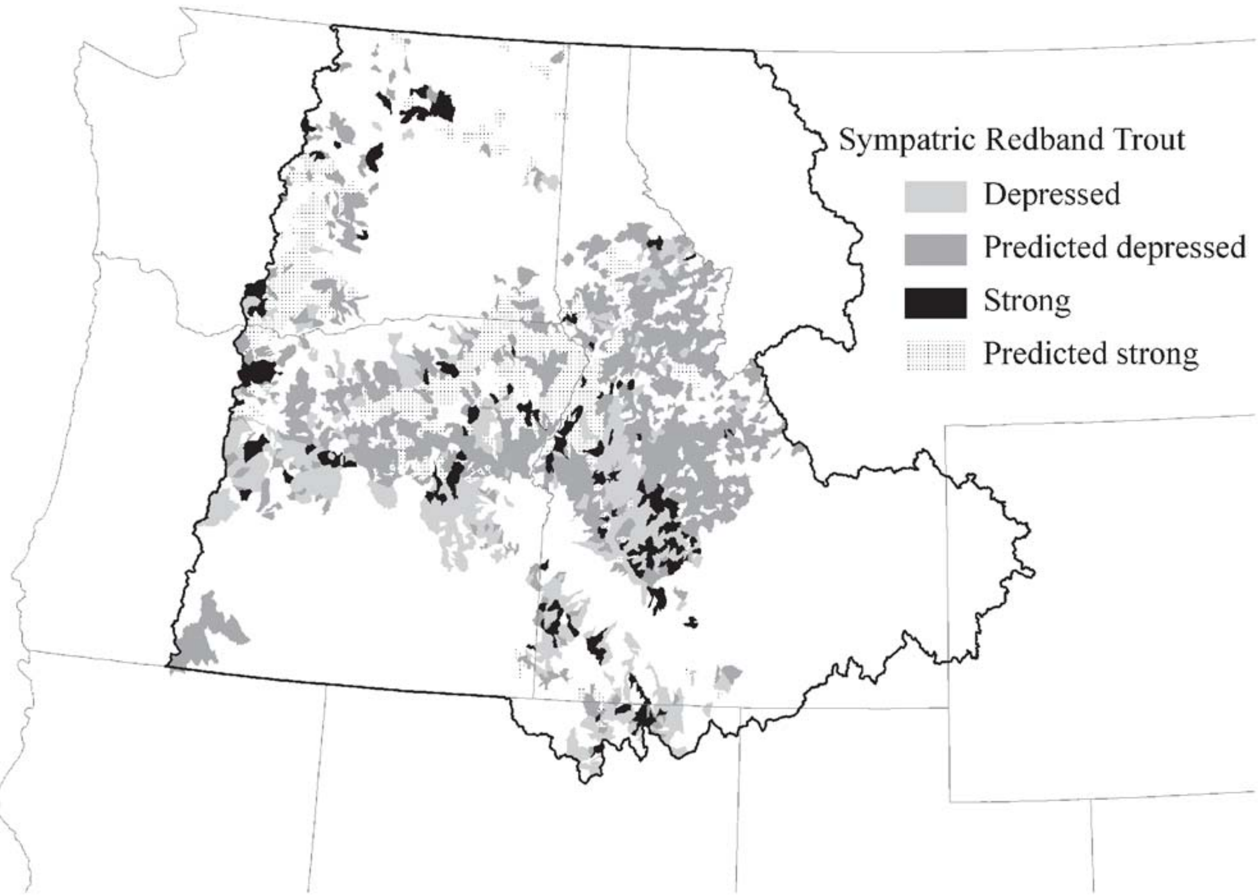

Figure 5.—Known and predicted classifications of status for sympatric redband trout within spawning and rearing areas in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

Secondly, many of the "known" subwatershed classifications relied on expert opinion rather than actual surveys. We predicted fish presence and status in areas classified as "unknown," using statistical models to quantitatively explore relationships among redband trout status and distribution, the biophysical environment, and land management. As noted above, where possible, classifications were reviewed by others familiar with the area in question and we attempted to use the most current (circa 1996) information. Despite criteria for classification and review, an element of subjectivity remains in the data and inconsistencies in judgment undoubtedly occurred.

To explore potential errors associated with "expert-based" analyses, we summarized a 2001 attempt to update the 1995 classification. In 2001, a group of biologists were asked to review and update our classifications within a subset of the watersheds we addressed. Some of the biologists participated in our original 1995 workshops; others were new to the process. Criteria for classification and review were intended to be the same as in 1995. Deadlines required that the 2001 update be completed in a much shorter time than our original 1995 classifications. Results of the 2001 update suggested that the 1995 classifications for sympatric populations of redband trout and other native salmonids were similar. Notable inconsistencies were present in the classifications for allopatric redband trout, however, particularly in the number of "strong" populations. In 1995, 35 subwatersheds were classified as strong versus 126 similarly classified in 2001. Additional information provided in the 2001 update indicated that 60% of those changes were a result of new data and 25% of the changes were due to "errors" in the 1995 data. It was unclear, however, how many changes were a result of differing interpretations of the criteria and data between the two classifications. Conversations with participants in the 2001 update suggested that some of the upgrades from depressed to strong status were based on inferred population status from improvements in habitat quality as a result of management actions (e.g. following improvements in grazing management). Our 1995 criteria explicitly stated that status must not be inferred from habitat conditions. No attempt was made to investigate the basis for such discrepancies or to resolve inconsistencies between the two classifications on a subwatershed by subwatershed basis.

The inconsistencies between the 1995 and 2001 classifications and the large number of subwatersheds classified as "unknown" are both symptomatic of the lack of quantitative information available for redband trout in the ICRB.

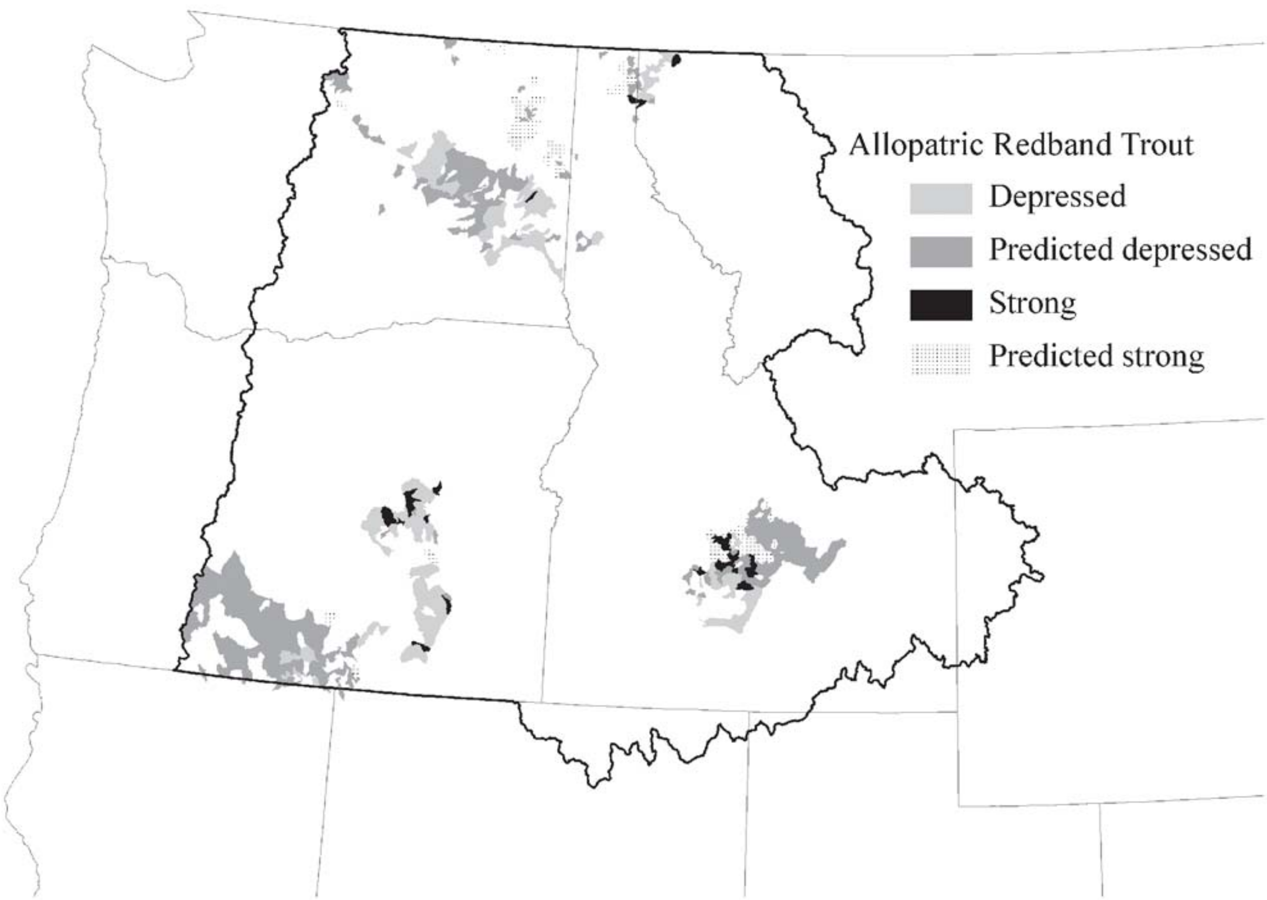

Figure 6.—Known and predicted classifications of status for allopatric redband trout within spawning and rearing areas in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins.

Our analysis was the first comprehensive attempt to describe the broad scale distribution and status of redband trout in the ICRB. A more precise synthesis of species distributions will require consistent and rigorously maintained field surveys and data management protocols that at present simply do not exist at this scale of analysis. Other recent species surveys have used approaches similar to ours (e.g. Shepard et al. 2005); emerging research suggests that traditional sampling approaches also have important limitations (Peterson et al. 2005; Rosenberger and Dunham 2005; Thurow et al. 2006).

Status and Distribution

Redband trout were judged to be the most widely distributed native salmonid in the ICRB, occupying 64% of the combined potential range of the two forms. Some redband trout populations remained in portions of all the ERUs that are part of the potential range. Of 66 native fishes in the ICRB, redband trout were the second most widely distributed (Lee et al. 1997). Although redband trout remained distributed in much of their potential range, important declines in distribution and status are apparent from our analysis. We were unable to quantify extirpations of redband trout populations, however, because much of the potential range is too speculative. Attempts to quantify extirpations are further confounded because it is unlikely that redband trout occupied all reaches of all accessible streams.

The distribution of many redband trout populations was likely restricted by elevation, temperature, and local channel features. Mullan et al. (1992) suggested that some redband trout avoid water temperatures exceeding 22ºC (lower elevational limit) and that the distribution of steelhead may be restricted to stream reaches that exceed 1,600 annual temperature units (upper elevational limit). Platts (1974) similarly reported an upper elevational limit in the South Fork Salmon River; redband trout populations were not found above 2,075 m. In contrast, other redband trout forms in the southern margins of the range exhibit tolerance to high water temperatures (Kunkel 1976; Johnson et al. 1985; Behnke 1992; Zoellick 1999).

Our analysis suggests that both forms of redband trout have more limited distributions and fewer strongholds than historically. Model results suggest it is unlikely that new population strongholds will be identified in areas spatially disjunct from known strongholds, because unknown areas generally have habitat conditions that are less likely to support populations than areas where observations were available (Lee et al. 1997). If redband trout are abundant, we

Table 6.—Summary of total known + predicted classifications (number of subwatersheds) for occurrence and status of sympatric redband trout in all subwatersheds and within "Protected" areas (National Park Service lands and designated wilderness) within the study area. The numbers predicted are based on the classification trees for redband trout within the range of summer steelhead and are shown in parentheses. Fifty-five subwatersheds classified as unknown did not have a prediction.

	Total known + predicted				Known + predicted within "Protected" areas	
Ecological Reporting Unit	Present	Strong	Depressed	Absent	Present	Strong
Northern Cascades	258 (36)	93 (88)	35 (31)	34 (27)	49 (1)	7 (5)
Southern Cascades	111 (4)	46 (21)	56 (18)	14 (0)	9 (0)	2 (0)
Upper Klamath	23 (15)	0 (0)	31 (31)	8 (8)	0 (0)	0 (0)
Northern Great Basin	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Columbia Plateau	457 (59)	73 (50)	305 (211)	339 (191)	0 (0)	0 (0)
Blue Mountains	579 (45)	249 (214)	241 (172)	64 (41)	50 (1)	38 (31)
Northern Glaciated Mountains	181 (1)	42 (21)	12 (9)	75 (44)	3 (0)	2 (2)
Lower Clark Fork	68 (1)	14 (11)	50 (33)	30 (22)	4 (0)	1 (0)
Upper Clark Fork	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Owyhee Uplands	336 (57)	54 (16)	213 (59)	513 (230)	2 (0)	2 (0)
Upper Snake	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Snake Headwaters	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Central Idaho Mountains	870 (177)	131 (65)	613 (467)	181 (138)	221 (67)	20 (13)
Entire study area[a]	2,883 (395)	702 (486)	1,556 (1,031)	1,258 (701)	338 (69)	72 (51)

[a] There were 7,498 subwatersheds in the study area and 4,196 in the potential range

generally know of their presence. Sympatric redband trout were known or predicted to be widely distributed in large patches of suitable habitat in the Northern Cascades, Blue Mountains, and Central Idaho Mountains. These watersheds represent the core of the sympatric distribution and appear to be relatively secure. Known or predicted populations in watersheds within the Southern Cascades, Upper Klamath, Owyhee Uplands, and Northern Glaciated Mountains were recently (since 1900) isolated from steelhead by dams. These latter populations appeared to be more fragmented in the remaining distribution. Allopatric redband trout within the Northern Great Basin, and portions of the Northern Glaciated Mountains, the Columbia Plateau, Central Idaho Mountains, and the Owyhee Uplands have been isolated from steelhead over geologic time. Remaining populations appeared to be severely fragmented and restricted to small patches of known or potential habitat. These areas likely represent a critical element of the evolutionary history for this species and a major challenge in conservation management. Introgression with introduced rainbow trout is potentially a serious but unevaluated threat for both redband trout forms.

Other status reviews in Idaho, Oregon, and Montana similarly report declines in redband trout populations (Moskowitz and Rahr 1994; Anonymous 1995; Kostow 1995; Perkinson 1995; Dambacher and Jones 2007; Gerstung 2007; Stuart et al. 2007). As described above, concern for the persistence of redband trout has increased efforts to conserve remaining populations. Our analysis and other work suggest that habitat degradation, habitat fragmentation, and introductions of non-native species and rainbow trout are primary factors that have influenced the status and distribution of redband trout and are likely to influence future species trends.

Factors Influencing Status and Distribution

Despite the limitations of the analysis, we believe that the general patterns provide some insight on redband trout. In general they appear to occupy a wide array of habitats, suggesting that they evolved over a wider range of environmental conditions than other native salmonids in the ICRB (Lee et al. 1997). Currens et al. (2007) suggest that redband trout include more major evolutionary linkages or subspecies than previously recognized, which contributes to ecological and evolutionary diversity. Redband trout are often found in more extreme conditions than those associated with other salmonids. Populations in the southern margin of the ICRB inhabit turbid and alkaline waters with minimum temperatures near freezing and maximum temperatures from 25–29ºC (Kunkel 1976; Johnson et al. 1985; D. Buchanan, Oregon Department of Fish and Wildlife, personal communication). Behnke (1992) and Zoellick (1999) reported red-

Table 7.—Summary of total known + predicted classifications (number of subwatersheds) for occurrence and status of allopatric redband trout in all subwatersheds and within "Protected" areas (National Park Service lands and designated wilderness) within the study area. The numbers predicted are based on the classification trees for redband trout outside the range of summer steelhead and are shown in parentheses. Forty-nine subwatersheds classified as unknown did not have a prediction.

	Total known + predicted				Known + predicted within "Protected" areas	
Ecological Reporting Unit	Present	Strong	Depressed	Absent	Present	Strong
Northern Cascades	31 (0)	1 (0)	12 (12)	16 (14)	17 (0)	1 (0)
Southern Cascades	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Upper Klamath	111 (75)	0 (0)	112 (102)	15 (15)	2 (2)	0 (0)
Northern Great Basin	117 (18)	5 (3)	89 (40)	258 (93)	1 (0)	0 (0)
Columbia Plateau	72 (5)	1 (0)	120 (58)	182 (120)	0 (0)	0 (0)
Blue Mountains	42 (2)	15 (2)	27 (1)	10 (0)	0 (0)	0 (0)
Northern Glaciated Mountains	102 (1)	44 (40)	27 (17)	92 (71)	0 (0)	0 (0)
Lower Clark Fork	1 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)
Upper Clark Fork	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Owyhee Uplands	39 (7)	2 (0)	23 (10)	19 (15)	0 (0)	0 (0)
Upper Snake	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Snake Headwaters	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Central Idaho Mountains	102 (9)	46 (33)	54 (52)	4 (3)	2 (0)	2 (2)
Entire study area[a]	617 (117)	114 (79)	465 (293)	596 (331)	22 (2)	3 (2)

[a] There were 7,498 subwatersheds in the study area and 1,262 in the potential range

band trout in tributaries to the Snake and Owyhee river basins tolerating maximum temperatures from 28 to 29ºC. Growth has been positively associated with temperature in forested streams (Mullan et al. 1992), and redband trout are often found in warmer waters than other salmonids. The apparent persistence of redband trout in some heavily disturbed basins might suggest that some populations are less strongly influenced by habitat disruption than other salmonids. If redband are more resistant, the loss of a population may be an indication of substantial habitat disruption. Persistence in a disturbed basin, however, could be influenced by several factors, including emigration of fish from adjacent areas or a time lag in population response (Rieman and Clayton 1997; Rieman and Dunham 2000).

Habitat degradation.—Anthropogenic disturbance has influenced redband trout status and distribution. We found no instances of a positive association with increased human disturbance. Although our models were not designed to test linkages between specific watershed characteristics and species status, variables reflecting the degree of human disturbance within watersheds (roads and management class) were useful predictors of redband trout status. A supplemental road analysis described in Lee et al. (1997) found decreasing likelihood of redband trout occupancy and a decreasing likelihood of strongholds if occupied, with increasing road density in forested landscapes. The lowest mean road density values were associated with strong population status. Redband trout status was negatively associated with increasing road density within forested, higher-elevation areas (Lee et al. 1997).

Work at finer scales has also described the result of habitat degradation. Interior redband trout habitats have been altered by a host of land use practices (Williams et al. 1989; Moskowitz and Rahr 1994; Anonymous 1995; Perkinson 1995). Diverting water for irrigation threatens many populations in the southern portion of the range through dewatering of stream reaches, loss of fish in unscreened diversions, blockage of migration corridors, and alteration of stream channels. The loss or conversion of riparian cover has been caused by grazing, timber harvest, mining, urbanization, and agriculture (Meehan 1991). Although removal of canopy by fire may benefit production in colder, high elevation streams (Rieman et al. 1997a), in warmer and dryer environments the loss of riparian cover has been associated with excessive temperature and reduced abundance and production (Li et al. 1994; Tait et al. 1994). Channel alterations associated with attempts to control flooding, develop floodplains, and construct roads have been extensive and adversely affect stream hydraulics (Bottom et al. 1985), nutrient pathways (Schlosser 1982), invertebrate production (Benke et al. 1985), and fish production. In Idaho, unaltered stream reaches supported 8 to 10 times the densities of redband trout observed in altered channels (Thurow 1988). Habitat alterations may reduce the resilience and stability of the entire aquatic assemblage (Pearsons et al. 1992). Declines of fluvial forms in particular, have been most common in larger low-elevation streams that have historically been the focus of agricultural, residential, and other forms of development.

Fragmentation.—Many systems that support redband trout remain as remnants of what were larger, more complex, diverse, and connected systems. With the exception of the Central Idaho Mountains, the Blue Mountains, and the Northern Cascades, most of the important areas for redband trout exist as patches of scattered watersheds. Many are not well connected or are likely restricted to smaller areas than existed historically. Where watershed disturbances such as construction of dams, irrigation diversions, or other migration barriers result in loss of connectivity, remaining redband trout populations have been progressively isolated into smaller and smaller patches of habitat. Corridors that provide habitat for migration, rearing, and overwintering may be critical to the conservation of species where connections among population are important (Hanski and Gilpin 1991; Rieman and Dunham 2000). Such effects can be exaggerated by climate change. In the Goose Lake basin, Oregon, adfluvial redband trout find refuge in tributaries when the lake dries and recolonize the lake when it fills (Gerstung 2007; Tinniswood 2007). Factors that isolate tributaries from Goose Lake would increase the risk of extinction during dry cycles. The loss of genetic variability through genetic drift may be a particularly important factor in the more isolated watersheds in the southern range of redband trout (Wallace 1981; Berg 1987). The loss of spatial diversity in population structure and of the full expression of life-history pattern may lead to a loss of productivity and stability important to long term persistence (Lichatowich and Mobrand 1995).

Non-native species introductions.—Redband trout are part of a native community that includes cottids, catostomids, cyprinids, and salmonids including westslope cutthroat trout *Oncorhynchus clarkii lewisi*, bull trout *Salvelinus confluentus*, mountain whitefish *Prosopium williamsoni*, steelhead, and Chinook salmon *O. tshawytscha* (Lee et al. 1997). The Columbia River basin harbors 52 native freshwater species. Thirteen of these natives are endemic to the system (Hocutt and Wiley 1986). The introduction and expansion of non-native species has influenced redband trout. Displacement may occur through competition, predation, and hybridization (Fausch 1988; Leary et al. 1993) and by introduction of diseases (Nehring and Walker 1996). About 50 non-native species have been introduced within the range of redband trout (Lee et al. 1997). At least 25 foreign species (not native to U.S.) have been introduced in Idaho, Oregon, Washington, and Montana, and 67 native species have been transplanted to systems where they are not indigenous (Fuller et al. 1999). Introduced rainbow trout, brook trout *Salvelinus fontinalis*, and brown trout *Salmo trutta* are widely distributed in lowland and alpine lakes and streams. Introduced rainbow trout were reported in 78% of the watersheds in the ICRB (Figure 7), and brook trout in about 50% (Lee et al. 1997), making them the most widely distributed fishes in the ICRB. Brown trout were found in 23% of the watersheds (Lee et al. 1997). Many other salmonids have been introduced outside their natural range and hatchery-reared forms have also been widely stocked. These include Lahontan *O. c. henshawi*, Yellowstone *O. c. bouvieri*, and westslope cutthroat trout; interior redband trout and coastal forms of rainbow trout; Chinook and coho salmon *O. kisutch*; kokanee *O. nerka*; and steelhead.

The effects of introductions on genetic integrity of redband trout have not been thoroughly assessed. Because of the potential for genetic introgression, we suspect that our assessment of strong populations may be optimistic. The long history of stocking rainbow trout within the ICRB, and the proclivity for redband trout and rainbow trout to hybridize (Allendorf et al. 1980; Wishard et al. 1984; Berg 1987; Currens et al. 1990; Leary et al. 1992; Moskowitz and Rahr 1994; Anonymous 1995; Williams et al. 1996), support concerns about the distribution and status of the original redband trout genotype. Introgressive hybridization is viewed as one of the most pervasive problems in the management of other non-anadromous native salmonids (Allendorf et al. 2001, 2004) and may be a serious threat to many fishes in general (Campton 1987). The effects may include a loss of fitness and a loss of genetic variability important to long-term stability and adaptation in varying environments.

Information is also lacking on the factors influencing the spread of diseases from fish introductions. Whirling disease (caused by *Myxobolus cerebralis*) has emerged as an issue of controversy and concern for its potential effects on wild redband trout populations in the western U.S. (Hulbert 1996). Although several ecological factors appear to influence disease epidemics, these relationships are not clearly defined. Nehring and Walker (1996) suggest that without a disease sampling protocol, whirling disease effects can be masked by other factors including angler harvest and other sources of natural mortality. The authors suggest that rainbow trout are among the most susceptible salmonids to mortality caused by whirling disease.

Conservation and Restoration Opportunities

To conserve the ecological diversity represented by the many life history patterns of redband trout, we suggest it will be critical to (1) conserve remaining healthy populations, (2) conserve unique populations, and (3) restore a broader mosaic of productive habitats. A general consensus of aquatic conservation strategies is that conservation and rehabilitation should focus first on the best remaining examples of biological integrity and diversity (Moyle and Sato 1991; Reeves and Sedell 1992; Doppelt et al. 1993; Frissell et al. 1993; Rieman and McIntyre 1993; Lee et al. 1997). Though the historical distribution and status of redband trout

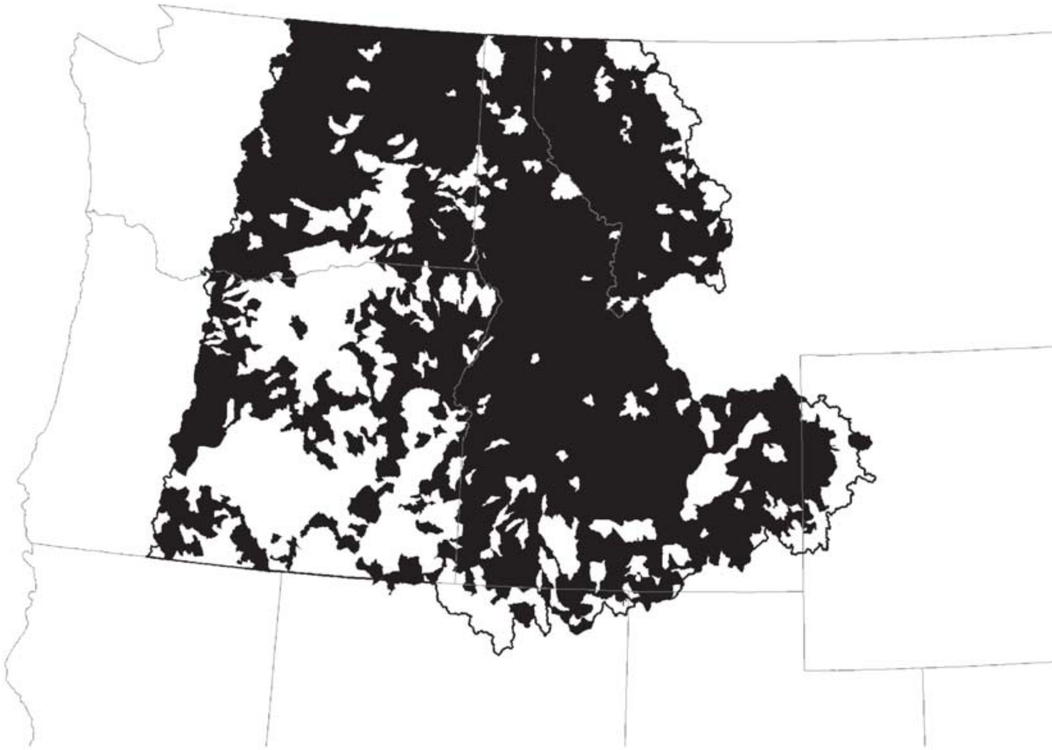

Figure 7.—Current range of introduced rainbow trout in the interior Columbia River Basin in the U.S. and portions of the Klamath River and Great Basins by watershed.

has declined, key areas remain for rebuilding and maintaining more functional aquatic systems. We suggest that core areas for conservation can be represented by subwatersheds supporting strong populations and locally adapted populations with unique phenotypic or genotypic characteristics.

Subwatersheds that support strong populations likely represent a fortuitous balance of habitat quality, climatic and geologic constraint, and geographic location that effectively minimize cumulative threats (Thurow et al. 1997). Where migratory life-history forms remain, the occurrence of strongholds may also indicate the relative integrity of a larger system of watersheds. Strongholds 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 (Schlosser and Angermeier 1995).

Isolated and locally adapted populations, particularly those on the margins of the species range, may represent a disproportionate part of the total genetic variability in species (Scudder 1989; Lesica and Allendorf 1995). Although the large variation in morphological characteristics of redband trout has discouraged firm taxonomic boundaries within the group (Behnke 1992), researchers report genetic differentiation among populations, particularly in allopatric forms within isolated basins (Berg 1987; Currens et al. 2007). Isolated populations may represent evolutionarily distinct lineages and important components of the genetic variability of the species. Examples include redband trout native to Upper Klamath Lake, Oregon desert basins (Malheur, Catlow, Fort Rock, Chewaucan, Warner Lake, and Goose Lake), Idaho's Wood River, and the Kootenai River in Idaho and Montana. Unique characteristics of some isolated redband trout, lacustrine fish in Upper Klamath Lake for example (Behnke 1992; Hemmingsen and Buchanan 1993), suggest that some populations may warrant identification as separate evolutionary units or subspecies (Williams et al. 1989).

Although protection of core areas including strongholds and unique populations is critical, it will not be sufficient. Such reserves will never be large or well distributed enough to maintain biological diversity (Franklin 1993). Because redband trout are relatively broadly distributed, recovery of habitats outside core areas will be essential to secure more strong populations representative of the broad diversity of the species and its life history patterns. 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.

Management of federal lands will have a major influence on the success of conservation and restoration efforts. About 55% of the distribution of redband trout occurs on federal land (Lee et al. 1997). Fifty-six percent of the strongholds occur on Forest Service and BLM lands. Small portions of the current range of redband trout are on lands managed under protected status. About 10% of the subwatersheds in the current range and 9% of the strongholds are secure within National Park Service lands or designated wilderness. The most secure portions of the distribution were found within the Central Idaho Mountains, the Northern Cascades, and the Blue Mountains ERUs.

In addition to the need for watershed restoration and more ecologically compatible land use policies, conservation and restoration of redband trout populations will need to address the effects of non-native species introductions. In some cases, introductions of non-native trout continue and could be curtailed to avoid effects on native redband trout. Recently, concern about the effects of introductions on wild salmonids and the costs of hatchery programs have caused many state agencies to restrict stocking of non-native species to areas that will not support naturally reproducing salmonid populations (Van Vooren 1994). In many cases, however, non-native fishes are established and many are desirable to anglers. As a result, removal may be infeasible or socially unacceptable (Lee et al. 1997). Where non-native species are well established, containment of the potential effects of these forms may be the only reasonable goal.

Importantly, conserving and restoring healthy populations of non-anadromous redband trout may also be critical to the persistence or restoration of some steelhead stocks. Although the relationship between the two forms is not well understood (Busby et al. 1996), there is evidence that some progeny of non-anadromous forms migrate to sea and some progeny of steelhead remain in freshwater (Shapovalov and Taft 1954; Burgner et al. 1992; Olsen et al. 2006). Steelhead confined above barriers adopt a non-anadromous lifestyle appropriate to the habitats available (Moffitt and Bjornn 1984). Mullan et al. (1992) also reported that steelhead progeny in very cold streams residualized and adopted a non-anadromous life history but suggested that these fish retained the ability to produce anadromous offspring. Mullan et al. (1992) reported that blockage of the Methow River by a dam for 14 years exterminated coho salmon but not steelhead. If sympatric redband trout have the potential to refound steelhead, that has application for the recovery of unique populations of steelhead eliminated by human-caused barriers. The maintenance of such distinct life histories may be an adaptation to variable environments (Gross 1991). For example, in watersheds that were periodically blocked by stochastic events, sympatric redband trout populations that retained the ability to produce anadromous progeny would have been able to refound steelhead. Perhaps in recognition of this potential, the National Marine Fisheries Service (NOAA) stated that it believed non-anadromous redband trout could help buffer extinction risks to an anadromous population and believed available evidence suggested that resident rainbow trout should be included in listed steelhead ESUs in certain cases (Office of the Federal Register 62[August 18, 1997]:43937). Since 1997, however, NOAA has reversed its position and only steelhead are currently included in the ESA listing (www.nwr.noaa.gov/ESA-Salmon-Listings).

Conversely, losses of steelhead may pose serious consequences for sympatric redband trout. Steelhead may facilitate gene flow between the two forms, and if this flow is eliminated, non-anadromous forms may diverge (Currens et al. 2007). The questions regarding phenotypic diversity and life history plasticity between steelhead and redband trout forms might be addressed in a series of field experiments. For example, redband trout populations above barriers and within the range of steelhead might be supplemented with nutrients to accelerate growth followed by monitoring of out-migrants. Conversely, steelhead might be introduced into a trout-barren stream within the range of redband trout and monitored for production of out-migrants and adaptation to freshwater residence. Olsen et al. (2006) observed that because it is possible that steelhead and redband trout may be restored from each other, both forms should be conserved.

Conclusions

Redband trout and are the most widely distributed native salmonid in the ICRB, and populations of both sympatric and allopatric forms appear to be relatively secure in some ERUs. Despite their broad distribution, local extirpations and important declines have occurred; both forms have more limited distribution and fewer strongholds than historically. Habitat degradation and fragmentation and the pervasive introduction of non-native species suggest that further declines are likely. Focused conservation and restoration efforts will be necessary to retain the remarkable ecological diversity expressed by redband trout.

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