
12 Status and Distribution of Chinook Salmon and Steelhead in the Interior Columbia River Basin and Portions of the Klamath River Basin

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Abstract.—This chapter summarizes information on presence, absence, current status, and probable historical distribution of steelhead *Oncorhynchus mykiss* and stream-type (age-1 migrant) and ocean type (age-0 migrant) chinook salmon *O. tshawytscha* in the interior Columbia River basin and portions of the Klamath River basin. Data were compiled from existing sources and via surveys completed by more than 150 biologists working in the region. We developed models to quantitatively explore relationships among fish status and distribution, the biophysical environment, and land management. Biophysical setting was an important determinant of species distributions and habitat suitability. We applied model results to predict fish presence in unsampled areas and mapped expected distributions in more than 3,700 subwatersheds. Chinook salmon and steelhead are extirpated from more than 50% of their potential historical ranges. Most remaining populations are severely depressed; less than 2% of the watersheds in the current range were classified as supporting strong populations of steelhead or stream-type chinook salmon. Wild, indigenous fish are rare; 22% of remaining steelhead stocks and less than 17% of chinook salmon stocks were judged to be genetically unaltered by hatchery-reared fish. Much of the historical production has been eliminated. However, a core for maintaining and rebuilding functional areas remains. Protection of core areas critical to stock persistence and restoration of a broader matrix of productive habitats will be necessary for productive and sustainable fisheries. This effort will require conservation and restoration of sufficient habitats to ensure the full expression of phenotypic and genotypic diversity in chinook salmon and steelhead.

INTRODUCTION

Historically, the Columbia River basin supported immense runs of anadromous salmonids. Diverse stocks included spring, summer, and fall chinook *Oncorhynchus tshawytscha*, sockeye *O. nerka*, coho *O. kisutch*, and chum salmon *O. keta*, and steelhead *O. mykiss*. Chapman (1986) estimated peak runs of Pacific salmon and steelhead in the Columbia River in the late 1800s were about 7.5 million fish. Estimates of annual chinook salmon returns prior to 1850 range from 3.4 to 6.4 million fish (NWPPC 1986). Commercial harvest of chinook salmon in the mainstem Columbia River peaked in 1883 at 2.3 million fish and was about 1.3 million fish annually from 1890–1920 (Mullan et al. 1992). Steelhead have been reported in the commercial Columbia River catch since 1889 and 2.23 million kg of canned steelhead were produced in 1892 (Fulton 1970). Estimates of steelhead

runs were derived after Bonneville Dam was constructed, and, in 1940, 423,000 summer-run steelhead passed the dam (NWPPC 1986). Annual steelhead sport harvests averaged 117,000 summer-run and 62,000 winter-run fish from 1962 to 1966 (Fulton 1970). Many native people in the Columbia River basin shared a significant dependence on anadromous salmonids as a subsistence and ceremonial resource (NWPPC 1986; Mullan et al. 1992). Since European settlement, anadromous salmonids have continued to influence social and economic systems.

Many native stocks of Columbia River anadromous salmonids are now considered imperiled (Williams et al. 1989; Moyle and Williams 1990; Nehlsen et al. 1991; Frissell et al. 1993, 1995). Concern for the persistence of steelhead in the study area culminated in a final rule (Office of the Federal Register 62[August 18, 1997]:43937) listing one evolutionarily significant unit (ESU) as endangered (Upper Columbia River) and one as threatened (Snake River Basin) under the Endangered Species Act of 1973 (ESA). In 1998, a third stock (Lower Columbia River) was listed as threatened (Office of the Federal Register 63[March 19, 1998]:13347). Returns of wild steelhead to the uppermost Snake River dam have declined from more than 80,000 in the 1960s to an estimated 7,900 in 1995 (C. Petrosky, Idaho Department of Fish and Game, personal communication). Snake River spring, summer, and fall chinook and sockeye salmon are listed as threatened or endangered, and Columbia River coho salmon and upper Columbia River spring chinook salmon are candidate species under ESA. In the Snake River, an estimated 1,882 naturally produced stream-type chinook salmon reached Lower Granite Dam in 1994 (NMFS 1995) compared to an estimated production of 1.5 million fish in the late 1880s (Bevan et al. 1994). During 1985–1993 an average of 387 naturally produced ocean-type chinook salmon annually reached Lower Granite Dam (NMFS 1995). Redd counts in four tributaries to the Middle Fork Salmon River in central Idaho have declined from more than 2,000 redds in the 1960s (Hassmer 1993) to 11 in 1995.

Several recent status reviews of Columbia River basin anadromous salmonids exist (Howell et al. 1985a, 1985b; NWPPC 1986; CBFWA 1990; IDFG et al. 1990; WDF et al. 1993; Chapman et al. 1994a, 1994b; Kostow et al. 1994; Anderson et al. 1996; Busby et al. 1996). 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 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.

This chapter summarizes information collected by the Aquatic Science Team of the Interior Columbia River Basin Ecosystem Management Project (ICBEMP) (Lee et al. 1997). In response to the President's directive, the Chief of the Forest Service and the Director of the Bureau of Land Management (BLM) established the 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 consistent evaluation of the status and distribution of fishes throughout the interior Columbia River basin. Here we describe the potential historical range and current status and distribution of chinook salmon and steelhead. We consider the factors that have influenced status and distribution, and opportunities for conservation and restoration.

STUDY AREA

The complete study area included all U.S. waters entering the Columbia River basin east of the Cascade Mountains and those portions of the Klamath River basin and Great Basin in Oregon (Figure 12.1). A hierarchical system of subbasins, watersheds, and subwatersheds was defined by topography. Within the 58.3×10^6 ha study area, 164 large subbasins were defined (Figure 12.2). The subbasins were further divided into watersheds which average about 22,820 ha in surface area. The watersheds were ultimately divided into 7,498 subwatersheds averaging 7,800 ha. The hydrologic divisions follow the hierarchical framework of aquatic ecological units described by Maxwell et al. (1995). The delineations and map coverages were provided by the Columbia Basin Project

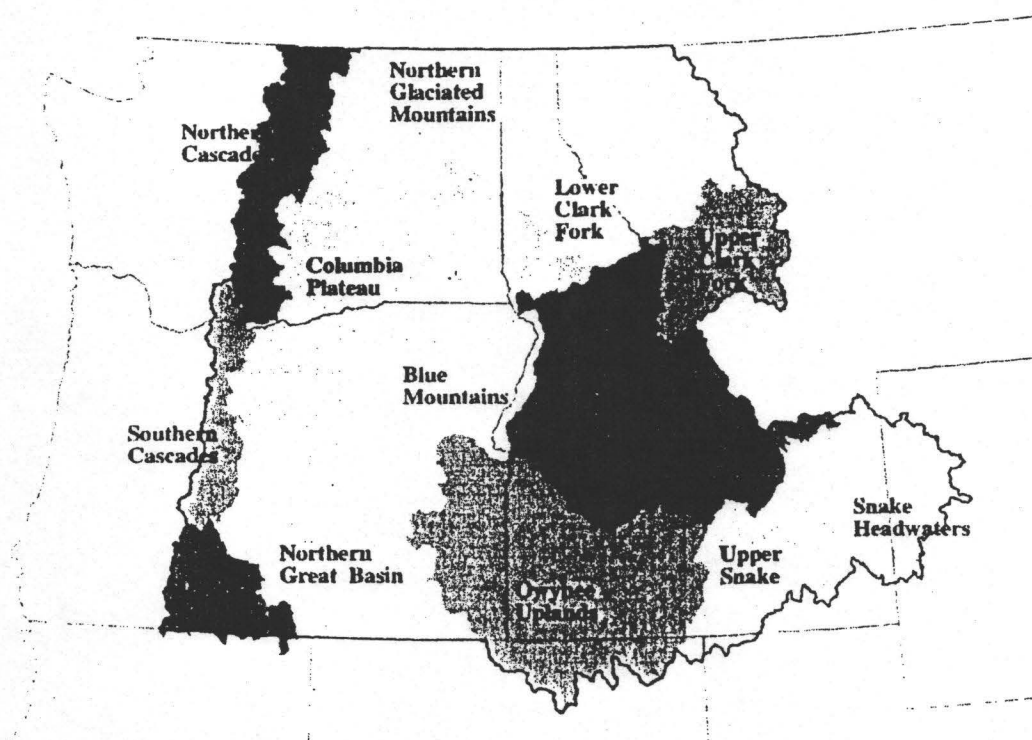


FIGURE 12.1 The interior Columbia River basin in the U.S. and portions of the Klamath River basin and Great Basin represented in this study. Ecological reporting units (ERUs) used to summarize information across broad regions of similar biophysical characteristics are also shown.

(Quigley and Arbelbide 1997). We used the subwatersheds as our basic unit of summary and prediction. Because anadromous fish were not native to the Great Basin those subwatersheds were excluded from further analysis.

We also considered 13 larger landscape classifications defined as ecological reporting units (ERUs) (Figure 12.1) representing distinct land areas of broadly homogeneous biophysical characteristics (Jensen et al. 1997). Chinook salmon and steelhead are distributed over a broad geographic range and have likely evolved under a broad range of environmental conditions. If gene flow has been limited by distance, there is potential for local and unique adaptations to those environments (Lesica and Allendorf 1995). We summarized our results by ERU to consider potentially important differences in the representation of distinct populations and environments.

METHODS

Steelhead, the anadromous form of rainbow/redband trout, are distributed within the study area as two genetically distinct subspecies, coastal (*O. m. irideus*) and inland (*O. m. gairdneri*) (Utter et al. 1980). Coastal steelhead are found primarily below Bonneville Dam in the lower Columbia River and inland steelhead occur primarily from the Deschutes River, Oregon upstream. The two subspecies overlap near the crest of the Cascade Range (K. Kostow, Oregon Department of Fish and Wildlife, personal communication). Coastal steelhead are predominately winter-run and inland steelhead summer-run fish. Within the study area, winter steelhead are found in two tributaries to the lower Columbia River in Oregon, 15-mile Creek and Hood River (Kostow et al. 1994). We summarized information for summer steelhead only.

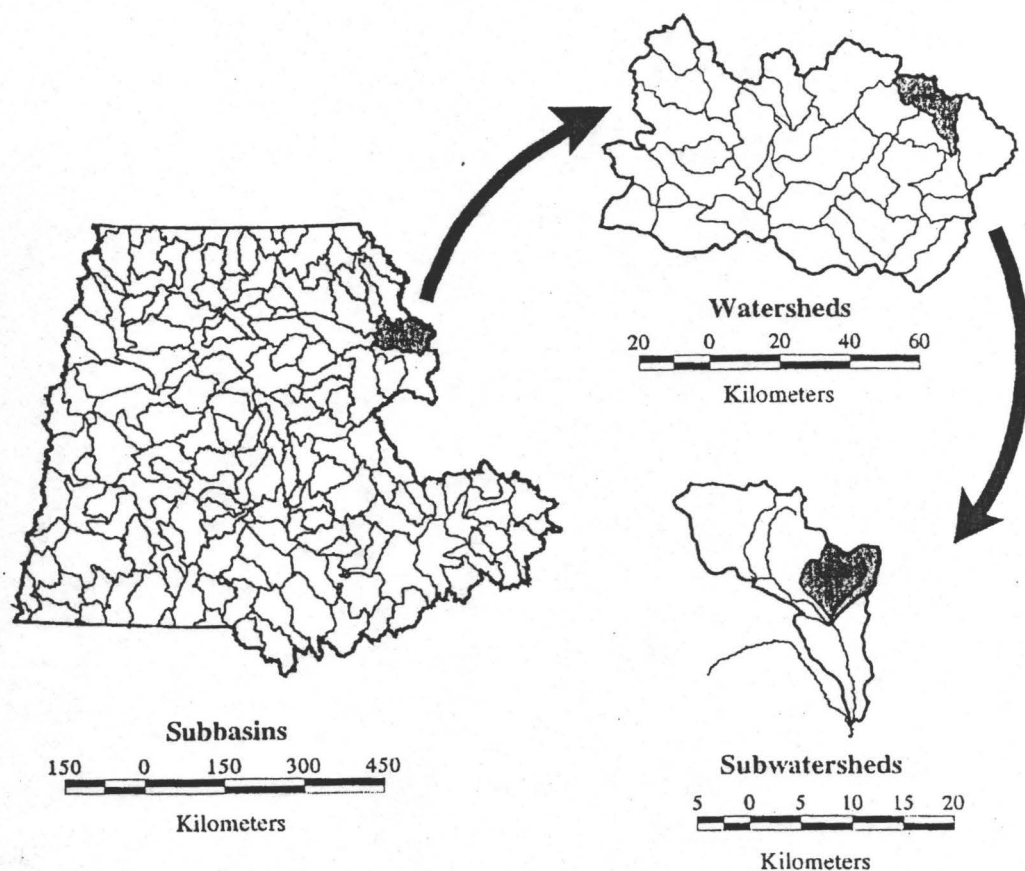


FIGURE 12.2 Hydrologic divisions of subbasins, watersheds, and subwatersheds used to characterize landscape information and classify the status and distribution of salmon and steelhead across the interior Columbia River basin in the U.S. and portions of the Klamath River basin and Great Basin. The hierarchical framework of drainage boundaries was defined from topography as described by Maxwell et al. 1995. Detailed descriptions and derivations are available in Quigley and Arbelbide (1997).

Columbia River basin chinook salmon have traditionally been described as spring, summer, and fall races—separated primarily by their time of passage over Bonneville Dam (Matthews and Waples 1991). Spring chinook salmon cross Bonneville Dam from March to May, summers from June to July, and falls from August to September (Burner 1951). This nomenclature has led to some confusion across the study area because stocks of similar run timing may differ considerably between the Snake and Columbia rivers in their spawning areas, life histories, behavior, and genetic characteristics. Healey (1991) categorized juvenile chinook salmon that migrate seaward after one or more years as stream-type and those that migrate as subyearlings as ocean-type. We adopted these definitions to characterize chinook salmon stocks in the study area. Within the Snake River basin and tributaries to the Columbia River downstream from the Snake River, stream-type chinook salmon include spring- and summer-run fish and ocean-type chinook salmon include fall-run fish (Parkhurst 1950; Gebhards 1959; Fulton 1968; IDFG 1992). Within the Columbia River upstream from its confluence with the Snake River stream-type chinook salmon include spring-run fish and ocean-type chinook salmon include summer- and fall-run fish (Matthews and Waples 1991; Mullan et al. 1992).

KNOWN STATUS AND DISTRIBUTION

Status was summarized by more than 150 private, agency, and tribal fish biologists working across the study area (Lee et al. 1997). Through a series of workshops in 1995, biologists were asked to characterize 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 either spawning and rearing habitat, overwintering and migratory-corridor habitat, or as supporting populations of unknown status. Subwatersheds containing spawning and rearing habitat were further classified as strong or depressed, based on population characteristics. We asked biologists to rely on target species' biological characteristics and not to infer status from habitat or landscape information or presence of introduced fishes.

The following criteria guided classification.

- *Present strong*.—Included those subwatersheds where 1) spawning and rearing occur; 2) all major life history forms that historically occurred are present; 3) numbers are stable or increasing, and the local population is likely to be at half or more of its historical size or density; and 4) the population within the subwatershed, or metapopulation within a larger region of which the subwatershed is a part, contains at least 5,000 individuals or 500 adults.
- *Present depressed*.—Included those subwatersheds where fish are present and use the area for spawning and rearing, but the population is not judged to be strong using the criteria listed above.
- *Absent*.—The species does not inhabit the subwatershed at any life history stage.
- *Present-unknown*.—The species is present, but there is no reliable information to determine current status.
- *Present, migration corridor*.—Migration corridors are habitats that do not support spawning, do not support initial rearing prior to juvenile migration, and function primarily as routes or staging and wintering areas for migrating fish. The mainstem migration routes of the Columbia River and major tributaries are examples of corridors. Some areas currently classified as migration corridors may have been important juvenile rearing areas prior to alteration by human activities (Lichatowich and Mobrand 1995).
- *Unknown*.—No information exists regarding the current presence or absence of the species.

To map areas of potential importance as wild, indigenous gene pools, we asked biologists to identify chinook salmon and steelhead spawning and rearing areas they judged to be unaltered by hatchery stocking, regardless of whether the populations were strong or depressed. Hatchery programs may erode genetic diversity and alter co-adapted gene complexes characteristic of locally adapted stocks (Waples and Do 1994; Reisenbichler 1997). The effects may include a loss of fitness or performance (such as growth, survival, and reproduction) and a loss of genetic variability important to long term stability and adaptation in varying environments. Because data describing genetic purity of populations was not available across the study area, we chose not to rely solely on genetic analysis. Instead, we defined wild, indigenous areas as subwatersheds with a low probability of non-indigenous strays spawning with indigenous fish and as

1. subwatersheds that had no history of hatchery-reared or non-indigenous introductions; or
2. subwatersheds that had been stocked rarely with hatchery-reared or non-indigenous fish, but where evidence suggested poor survival of stocked fish and a low probability of introgression; or
3. subwatersheds that had been stocked regularly in the past, but genetic analyses found existing wild fish identical to the original wild gene pool.

We submitted status classifications for review by others familiar with the area in question and attempted to use only the most current information. We summarized fish distribution information from existing state databases to validate and augment presence or absence classifications. We restricted our use to databases that had been created or updated after 1993. In general, biologists provided information in addition to and directly supporting that already available from the databases. When there was no survey response, no information in electronic databases, or conflicting responses between the survey and electronic databases that could not be resolved, unknown was the default classification.

Despite the criteria provided for classification, an element of subjectivity remains in the data (Rieman et al. 1997). Most of the information represented by the classifications is not published or peer-reviewed. Inconsistencies probably occur in classifications and the quality of available information may vary. Recognizing the potential for errors, we believe these data represent as complete a summary of the current (or recent), collective knowledge of these species as is possible. The resolution of our data may also produce more optimistic estimates of current distributions than work based on stream reaches. That is, if chinook salmon or steelhead occurred anywhere in a subwatershed they were considered present in the entire subwatershed. An analysis at the subwatershed level of resolution was necessary simply because of logistical and computational constraints imposed by the scale of our study. We believe, however, because of the potential for extended movement and dispersal and the structuring of populations within tributaries, subwatersheds are actually the most appropriate level for our analysis. We believe that subwatersheds will best approximate the distributions of potentially discrete groups or local populations and thus represent a better summary unit than stream reaches. To minimize any potential bias all estimates of the distributions were based on the number of subwatersheds and not area.

POTENTIAL HISTORICAL RANGE

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. In some cases, the potential ranges remain speculative; few records are available to ascertain the historical range of chinook salmon and steelhead in the Bruneau River subbasin, for example, because a 1906 dam blocked access prior to detailed population surveys (IDFG 1992). For a complete description of the data sources used to infer potential ranges for chinook salmon and steelhead, see Lee et al. (1997). We included all subwatersheds that were accessible as potential range based on the known current and historical occurrences because chinook salmon and steelhead are highly mobile, moving seasonally through subwatersheds, watersheds, subbasins, and basins at different life stages (Withler 1966; Healey 1991, 1994). Subwatersheds that were known to be historically isolated by barriers 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 scale.

PREDICTIVE MODELS

Our knowledge of the current status of chinook salmon and steelhead was limited to areas that have been sampled. We attempted to generate the most complete picture of the current distribution of these fishes for unsampled areas by quantitatively exploring relationships among fish status and distribution, the biophysical environment, and land management. We produced a set of predictions that reflect the likelihood of a species' presence, or alternatively, the likely status of the population within a subwatershed. The predictions arose from statistical models, called classification trees (Breiman et al. 1984), which elucidate the relationship between a set of predictor variables and a single response variable. Tree-based models represent a nonparametric alternative to conventional linear models that have more constraining assumptions about data structure (see Breiman et al.

1984; Clark and Pregibon 1992; Crawford and Fung 1992; Taylor and Silverman 1993). For more information on the advantages of tree-based models, see Lee et al. (1997).

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

All analyses involving classification trees were performed using the Splus² programming language, following the procedures outlined in Clark and Pregibon (1992). We used ERU as a variable and summarized 29 additional predictor variables (Table 12.1) from more than 200 coverages representing landscape characteristics across the study area. We limited our variables to those with potential influence on aquatic ecosystems and generally eliminated many of those that were strongly correlated with or directly derived from others (Lee et al. 1997). The variables were both categorical and continuous, representing vegetative communities, climate, geology, landform and erosive potential, and past management or the relative intensity of human disturbance (Table 12.1). Much of the information used in developing the landscape variables was developed from continuous 90-meter digital elevation data, 1-km vegetation data (from satellite imagery), 1:100,000 hydrography, state geologic maps, land ownership and activity maps, and extrapolated landscape characteristics derived from aerial photographs. Detailed descriptions of the complete landscape coverages, variables and their derivations can be found in Quigley and Arbelbide (1997) and Lee et al. (1997).

We present the classification tree for stream-type chinook salmon (Table 12.2) to illustrate the general procedure that we followed for stream-type and ocean-type chinook salmon and steelhead. Status of stream-type chinook salmon (*stc*), was used as the response. Four possible values indicated whether the species was absent (A), present in spawning and rearing areas at depressed levels (D), present in spawning and rearing areas at strong levels (S), or transient in migration corridors (T). The tree-fitting routine produced a full model that used 22 of the 29 potential predictor variables. The model had 64 terminal nodes and many of the nodes near the termini of the full tree added little to change the predictions or reduce the deviance. The next step was to prune the tree by removing the least important nodes. Breiman et al. (1984) developed a process of cross-validation which uses the full set of observations to build the full model, and mutually exclusive subsets of the data to iteratively prune and test the tree. For stream-type chinook salmon, a tree with 26 nodes was selected (Table 12.2). A smaller tree may predict responses equally well, but we chose to keep the additional nodes for the insight they provide.

Part A of Table 12.2 lists the variables used in the reduced tree and summarizes overall performance. Part B of Table 12.2 provides a complete listing of the tree structure and identifies each node, the variables and ranges defining each split, the number of observations, the deviance (a measure of within-node heterogeneity), the modal response (most frequent response), and the relative frequencies of each response level at that node. When used in a predictive fashion, these frequencies are equivalent to a probability of a given response. Normally, the modal response is equivalent to the predicted value. With the status data, however, three of the responses indicate different levels of presence (D, S, or T) in contrast to a single absent value (A). Thus, we chose to predict absence only when the relative frequency was greater than or equal to 0.5. The probability of presence was defined as one minus the probability of absence.

Classification trees were used to estimate the probability of chinook salmon or steelhead presence or absence in subwatersheds classified as unknown and to predict status in subwatersheds classified as unknown or in subwatersheds with fish of unknown status. All estimates and predictions were limited

TABLE 12.1

Descriptions of landscape variables used to build classification trees in the analysis of chinook salmon and steelhead distribution and status. All values for physiographic, geophysical, and vegetation variables were summarized for subwatersheds from complete coverages with a pixel resolution of 1 km². All values expressed as percents refer to the percent area of the subwatershed. Detailed descriptions and derivations are described in Quigley and Arbelbide (1997).

Variable Name	Description
ERU	Ecological Reporting Unit (see text and Figure 12.2)
Physiographic and Geophysical	
<i>slope</i>	area weighted average midslope based on 90 m digital elevation maps
<i>slope2</i>	percent of area in slope class 2 (slopes >10%, <30%)
<i>con1</i>	percent weakly-consolidated lithologies
<i>con2</i>	percent moderately-consolidated lithologies
<i>con3</i>	percent strongly-consolidated lithologies
<i>sdt1</i>	percent lithologies that produce coarse-textured sediments
<i>sdt2</i>	percent lithologies that produce medium-textured sediments
<i>sdt3</i>	percent lithologies that produce fine-textured sediments
<i>alsi1</i>	percent felsic lithologies
<i>alsi2</i>	percent intermediate aluminosilicated lithologies
<i>alsi3</i>	percent mafic lithologies
<i>alsi4</i>	percent carbonate lithologies
<i>pprecip</i>	mean annual precipitation extrapolated to complete coverage using a regional climate simulation model
<i>elev</i>	mean elevation
<i>mtemp</i>	mean annual air temperature extrapolated to complete coverage using a regional climate simulation model
<i>solar</i>	mean annual solar radiation based on topographic shading, latitude, and aspect
<i>streams</i>	total length of streams within subwatershed based on 1:100,000 scale hydrography
<i>drnden</i>	drainage density (stream length/watershed area)
<i>anadac</i>	access for anadromous fish (0 = no, 1 = yes)
<i>dampass</i>	number of intervening dams
<i>hucorder</i>	number of upstream subwatersheds tributary to the watershed of interest (0 designates a headwater subwatershed)
<i>hk</i>	soil texture coefficient
<i>baseero</i>	base erosion index representing relative surface erodability without vegetation
<i>ero</i>	surface erosion hazard, a derived variable based on <i>baseero</i> and other modifying factors
<i>bank</i>	streambank erosion hazard, a derived variable representing relative bank stabilities
Vegetation	
<i>vmf</i>	vegetation amelioration factor, a derived variable representing the relative amount of ground cover in vegetation
<i>vegclus</i>	current vegetation class (12 possible types) based on structure and composition
Ownership and Management	
<i>roaddn</i>	estimated road density class (5 classes: none to very high)
<i>mngclus</i>	management class (10 possible types, intense commodity extraction to wilderness) based on ownership and management emphasis

TABLE 12.2

The pruned classification tree for stream-type chinook salmon status (absent (A), depressed (D), transient (T), strong (S)) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within spawning and rearing areas in 1,262 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 hucorder (number of upstream watersheds tributary to the watershed of interest), node 2 is <30 compared to node 3 that is >30. These two nodes are further independently subdivided. See text and Table 12.1 for a description of other variables and Lee et al. (1997) for further information.

A. Summary

Variables actually used in tree construction:

hucorder	pprecip	dampass	streams	mtemp	eru
mngclus	alsi1	solar	alsi3	con3	

Number of terminal nodes: 26
Residual mean deviance: 0.8282

Misclassification error rate: 0.1672 = 211/1262

B. Tree structure

Node) Split criterion	Sample size	Deviance	Modal response	Relative frequencies			
				Absent	Depressed	Transient	Strong
1) root	1262	2718.00	A	0.43900	0.36450	0.190200	0.006339
2) hucorder < 30	991	1652.00	A	0.54990	0.41370	0.028250	0.008073
4) hucorder = 0	500	622.40	A	0.75800	0.22200	0.020000	0.000000
8) pprecip < 601	145	93.04	A	0.92410	0.03448	0.041380	0.000000 *
9) pprecip > 601	355	473.80	A	0.69010	0.29860	0.011270	0.000000
18) dampass < 4	23	13.59	D	0.08696	0.91300	0.000000	0.000000 *
19) dampass > 3	332	418.60	A	0.73190	0.25600	0.012050	0.000000
38) streams < 23	145	112.40	A	0.88280	0.11030	0.006897	0.000000 *
39) streams > 23	187	274.20	A	0.61500	0.36900	0.016040	0.000000
78) mtemp < 6.9	158	242.70	A	0.54430	0.43670	0.018990	0.000000
156) streams < 43.6	122	177.00	A	0.63110	0.35250	0.016390	0.000000
312) pprecip < 960.7	52	50.68	A	0.84620	0.13460	0.019230	0.000000 *
313) pprecip > 960.7	70	106.00	D	0.47140	0.51430	0.014290	0.000000 *
157) streams > 43.6	36	49.04	D	0.25000	0.72220	0.027780	0.000000
314) streams < 64.1	31	32.40	D	0.12900	0.83870	0.032260	0.000000 *
315) streams > 64.1	5	0.00	A	1.00000	0.00000	0.000000	0.000000 *
79) mtemp > 6.9	29	0.00	A	1.00000	0.00000	0.000000	0.000000 *
5) hucorder > 0	491	841.50	D	0.33810	0.60900	0.036660	0.016290
10) eru: 5,7	116	117.80	A	0.81900	0.17240	0.008621	0.000000
20) mngclus: BR,PA,PF,PR	106	85.95	A	0.87740	0.11320	0.009434	0.000000
40) alsi1 < 1.56	77	18.55	A	0.97400	0.02597	0.000000	0.000000 *
41) alsi1 > 1.56	29	45.20	A	0.62070	0.34480	0.034480	0.000000 *
21) mngclus: FG,FH,FM,TL	10	10.01	D	0.20000	0.80000	0.000000	0.000000 *
11) eru: 1,2,6,13	375	568.10	D	0.18930	0.74400	0.045330	0.021330
22) mngclus:BR,PA,PR	68	129.60	A	0.45590	0.44120	0.102900	0.000000
44) mtemp < 10.54	62	94.79	A	0.50000	0.48390	0.016130	0.000000 *
45) mtemp > 10.54	6	0.00	T	0.00000	0.00000	1.000000	0.000000 *

TABLE 12.2 (continued)

The pruned classification tree for stream-type chinook salmon status (absent (A), depressed (D), transient (T), strong (S)) showing discriminating variables, sample sizes, splitting criteria, and frequency distributions within spawning and rearing areas in 1,262 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 hucorder (number of upstream watersheds tributary to the watershed of interest), node 2 is <30 compared to node 3 that is >30. These two nodes are further independently subdivided. See text and Table 12.1 for a description of other variables and Lee et al. (1997) for further information.

B. Tree structure (continued)							
Node) Split criterion	Sample size	Deviance	Modal response	Relative frequencies			
				Absent	Depressed	Transient	Strong
23) mngclus: FG,FH,FM,FW,PF,TL	307	394.20	D	0.13030	0.81110	0.032570	0.026060
46) dampass < 4	56	82.10	D	0.10710	0.75000	0.000000	0.142900
92) solar < 330.6	30	8.77	D	0.03333	0.96670	0.000000	0.000000 *
93) solar > 330.6	26	53.37	D	0.19230	0.50000	0.000000	0.307700
186) pprecip < 535.2	10	13.86	A	0.50000	0.50000	0.000000	0.000000 *
187) pprecip > 535.2	16	22.18	D	0.00000	0.50000	0.000000	0.500000 *
47) dampass > 4	251	280.20	D	0.13550	0.82470	0.039840	0.000000
94) hucorder < 4	130	149.20	D	0.22310	0.76920	0.007692	0.000000 *
95) hucorder > 3	121	105.00	D	0.04132	0.88430	0.074380	0.000000
190) mngclus: FG,FM	51	0.00	D	0.00000	1.00000	0.000000	0.000000 *
191) mngclus: FH,FW,PF	70	88.31	D	0.07143	0.80000	0.128600	0.000000 *
3) hucorder > 30	271	334.40	T	0.03321	0.18450	0.782300	0.000000
6) hucorder < 58	74	138.00	T	0.09459	0.39190	0.513500	0.000000
12) eru: 5,7	10	12.22	A	0.70000	0.00000	0.300000	0.000000 *
13) eru: 1,6,13	64	88.16	T	0.00000	0.45310	0.546900	0.000000
26) alsil < 59.7	52	65.73	T	0.00000	0.32690	0.673100	0.000000
52) alsil < 0.37	9	6.28	D	0.00000	0.88890	0.111100	0.000000 *
53) alsil > 0.37	43	44.12	T	0.00000	0.20930	0.790700	0.000000 *
27) alsil > 59.7	12	0.00	D	0.00000	1.00000	0.000000	0.000000 *
7) hucorder > 57	197	155.60	T	0.01015	0.10660	0.883200	0.000000
14) dampass < 3	16	19.87	D	0.00000	0.68750	0.312500	0.000000 *
15) dampass > 2	181	99.13	T	0.01105	0.05525	0.933700	0.000000
30) con3 < 0.49	90	19.18	T	0.02222	0.00000	0.977800	0.000000 *
31) con3 > 0.49	91	63.00	T	0.00000	0.10990	0.890100	0.000000 *

* denotes terminal node

to the potential range. We summarized both the known and predicted information by ERU and across the study area. Known and predicted information was summed to estimate current status and distribution. To estimate how much of the current distribution was protected by special land-use designations, we summarized the number of occupied subwatersheds that were found within designated wilderness or National Park Service lands. We also summarized occupied subwatersheds on federally administered lands. Chinook salmon and steelhead distributions were mapped using a geographic information system (GIS). The GIS coverages depicting the subwatersheds, land ownership, and management status were developed as part of the landscape information noted above (Quigley and Arbelbide 1997).

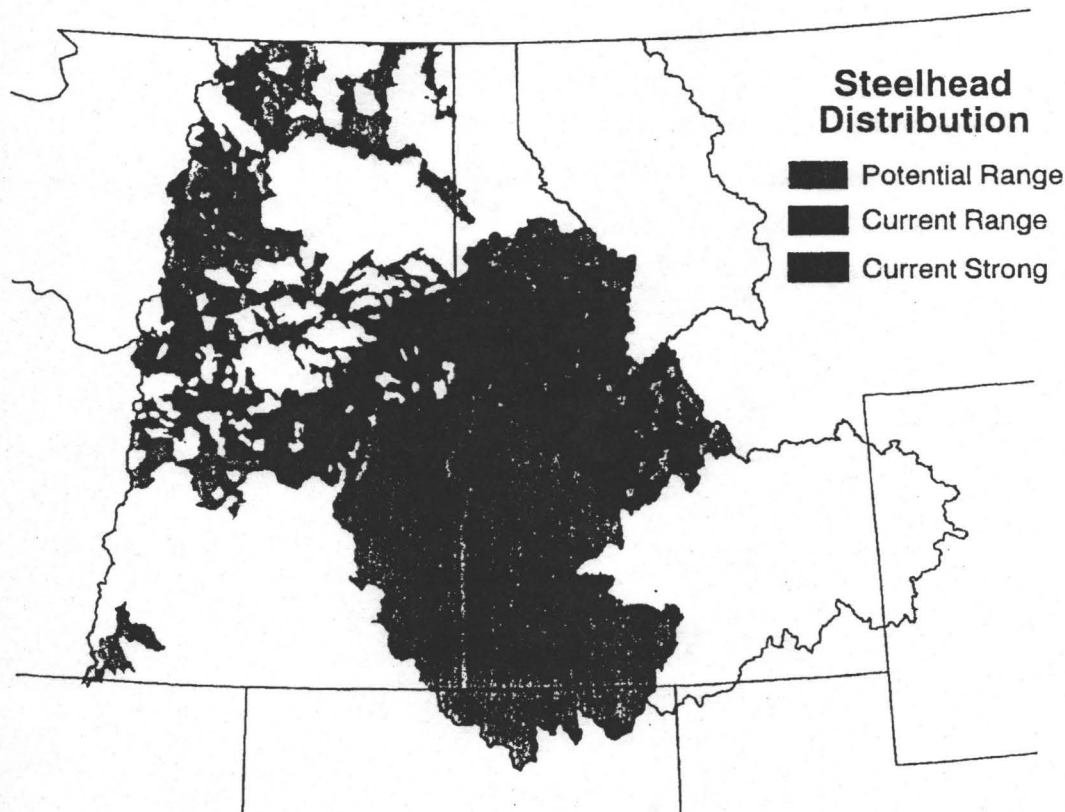


FIGURE 12.3 Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of steelhead within the interior Columbia River basin in the U.S. and portions of the Klamath River basin.

RESULTS

STEELHEAD

Potential Historical Range.—The broad potential range of steelhead is well documented (Howell et al. 1985b; NWPPC 1986). Steelhead were present in most streams—both perennial and intermittent—that were accessible to anadromous fish including all accessible tributaries to the Snake (Evermann 1896; Parkhurst 1950) and Columbia rivers (Fulton 1970; Howell et al. 1985b; Bakke and Felstner 1990) (Figure 12.3). Steelhead formerly ascended the Snake River and spawned in reaches of Salmon Falls Creek, Nevada, more than 1,450 km from the ocean. Approximately 16,935 km of stream were accessible to steelhead in the Columbia River basin, including Canada (NWPPC 1986). Steelhead occupied about 50% of the subwatersheds and nine of the 13 ERUs in the study area (Table 12.3). The largest areas of unoccupied habitat were waters above Spokane Falls on the Spokane River and above Shoshone Falls on the Snake River.

Known Status and Distribution.—Steelhead were reported as present in about 33% of the subwatersheds within the potential range, with strong populations present in 1.9% of the current known range and <1% of the potential range (Table 12.3). The distribution of steelhead was unknown or unclassified in 7% of the potential range (279 subwatersheds) and reported as present but of unknown status in another 289 subwatersheds.

TABLE 12.3

Summary of the potential historical range and known (as reported by biologists) and predicted classifications of current range and status (number of subwatersheds) for summer steelhead. The numbers predicted are based on the classification trees and are shown in parentheses. Known status is the remainder of known and predicted minus predicted. Twenty-two subwatersheds classified as unknown had incomplete information and were omitted from analysis. Transient refers to transient in migration corridors. Wild indigenous subwatersheds were those judged to be unaltered by hatchery programs.

Ecological Reporting Unit	Total sub- watersheds	Potential historical range	Current known range	Current known and predicted range	Known and predicted status				Wild indigenous
					Where present			Absent	
					Strong	Depressed	Transient		
Northern Cascades	340	274	123	201 (78)	1 (0)	192 (77)	8 (1)	65 (7)	3
Southern Cascades	141	67	38	42 (4)	0	37 (4)	5 (0)	25 (0)	0
Upper Klamath	175	35	0	0	0	0	0	35 (0)	0
Columbia Plateau	1,089	554	295	392 (97)	6 (0)	289 (89)	97 (8)	160 (22)	56
Blue Mountains	695	584	364	378 (14)	13 (0)	326 (14)	39 (0)	206 (2)	169
Northern Glaciated Mountains	955	193	21	24 (3)	0	9 (3)	15 (0)	169 (10)	0
Lower Clark Fork	415	98	0	0	0	0	0	98 (0)	0
Owyhee Uplands	956	898	0	0	0	0	0	887 (0)	0
Central Idaho Mountains	1,232	1,051	392	674 (282)	3 (0)	578 (275)	93 (7)	376 (27)	150
Entire Assessment Area	7,498*	3,754	1,233	1,711 (478)	23 (0)	1,431 (462)	257 (16)	2,021 (68)	378

*This total includes 4 ERUs with no potential range

TABLE 12.4

Cross classification comparison of predicted status with observed status for chinook salmon and steelhead, and list of leading predictor variables. Correct classifications match on a diagonal from left to right. 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 (see Table 12.1 for variable descriptions).

Species	Predicted status	Observed status				Leading predictor variables
		Absent (A)	Present-depressed (D)	Present-strong (S)	Transient in migration corridor (T)	
Steelhead	A	124	30	0	2	hucorder, ERU, drnden, mngclus
	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, mngclus, 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	

Predictive Models.—A total of 1,355 subwatersheds within the current range, with both complete landscape information and known status, were used to develop the predictive models. We excluded all subwatersheds in the potential range that were no longer accessible. The overall model predictive success rate was 88.6% (Table 12.4). The model was most successful in classifying present-depressed (93%) and migration corridors (87%) and least successful in discriminating strong populations (55%). Variables including hucorder, ERU, slope, solar radiation, vegetation, management clusters, and variables related to lithology and sensitivity to erosion were useful in discriminating subwatersheds supporting steelhead (Table 12.4). Our results suggest that spawning and rearing areas for steelhead were likely to be found within specific ERUs, in small to mid-size streams, in erosive land types and in steeper, higher elevation subwatersheds. Spawning and rearing occurred primarily on Forest Service lands. Migration corridors represented probable steelhead occurrence in larger mainstem streams at lower elevations. Disturbance-related variables had a relatively minor influence in the model classifications. Management cluster and the number of dams steelhead must pass enroute to the ocean were useful but not dominant predictors.

Current Status and Distribution.—Steelhead were known or predicted to presently occur in 46% of their potential range and 23% of the subwatersheds in the study area (Table 12.3; Figure 12.3). Steelhead have been extirpated from large portions of their potential range, however, and are no longer present in the Upper Klamath, Lower Clark Fork, and Owyhee Uplands ERUs. In ERUs that still support steelhead, much of the potential range is no longer accessible.

Despite their relatively broad distribution, very few strong steelhead populations exist and many populations have been influenced by non-indigenous forms. We estimated about 39% of the potential range still supports spawning and rearing, but only 2% of those subwatersheds were classified as supporting strong populations (Table 12.3; Figure 12.3). None of the unknown or unclassified subwatersheds were predicted to support strong populations, suggesting that we know the distribution of most strong populations. Wild, indigenous steelhead, unaltered by hatchery stocks, are

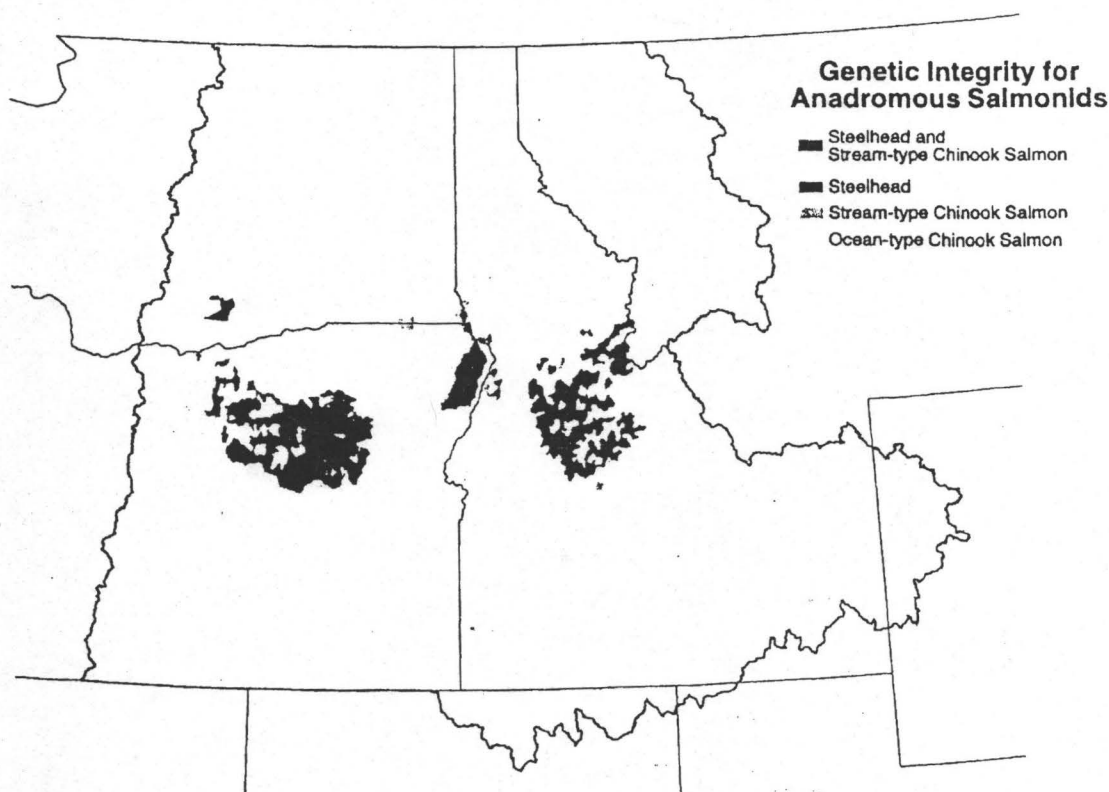


FIGURE 12.4 Map of genetically unaltered stocks of steelhead, stream-type chinook salmon, and ocean-type chinook salmon within the interior Columbia River basin in the U.S.

rare (Figure 12.4) and present in 10% of the potential range and 22% of the current distribution. Remaining wild stocks are concentrated in reaches of the Salmon River in central Idaho and the John Day River basin in Oregon. Although few wild stocks were classified as strong, the only subwatersheds classified as strong were those sustaining wild stocks (6%). About 9% of strong populations were found in designated wilderness and 70% were found on Forest Service or BLM lands.

CHINOOK SALMON

Potential Historical Range.—Chinook salmon were historically found in all accessible areas of the Snake River downstream from Shoshone Falls and in all accessible areas of the Columbia River downstream from Windermere Lake, British Columbia (Evermann 1896; Parkhurst 1950; Fulton 1970; Howell et al. 1985a; NWPPC 1986) (Figures 12.5 and 12.6). Prior to overfishing and habitat alterations, migrating chinook salmon in the Columbia River formed a continuum from March to October with the largest part of the run likely consisting of summer chinook salmon (Thompson 1951). Like steelhead, chinook salmon formerly ascended the Snake River and spawned in reaches of Salmon Falls Creek, Nevada, more than 1,450 km from the ocean. An estimated 16,935 km of stream were accessible to chinook salmon in the Columbia River basin in the U.S. and Canada (NWPPC 1986).

Stream-type chinook salmon were the most widely distributed form, occupying about 46% of the subwatersheds and nine ERUs in the study area (Table 12.5). Ocean-type chinook salmon were much less widely distributed, occupying about 7% of the subwatersheds and six ERUs (Table 12.6).

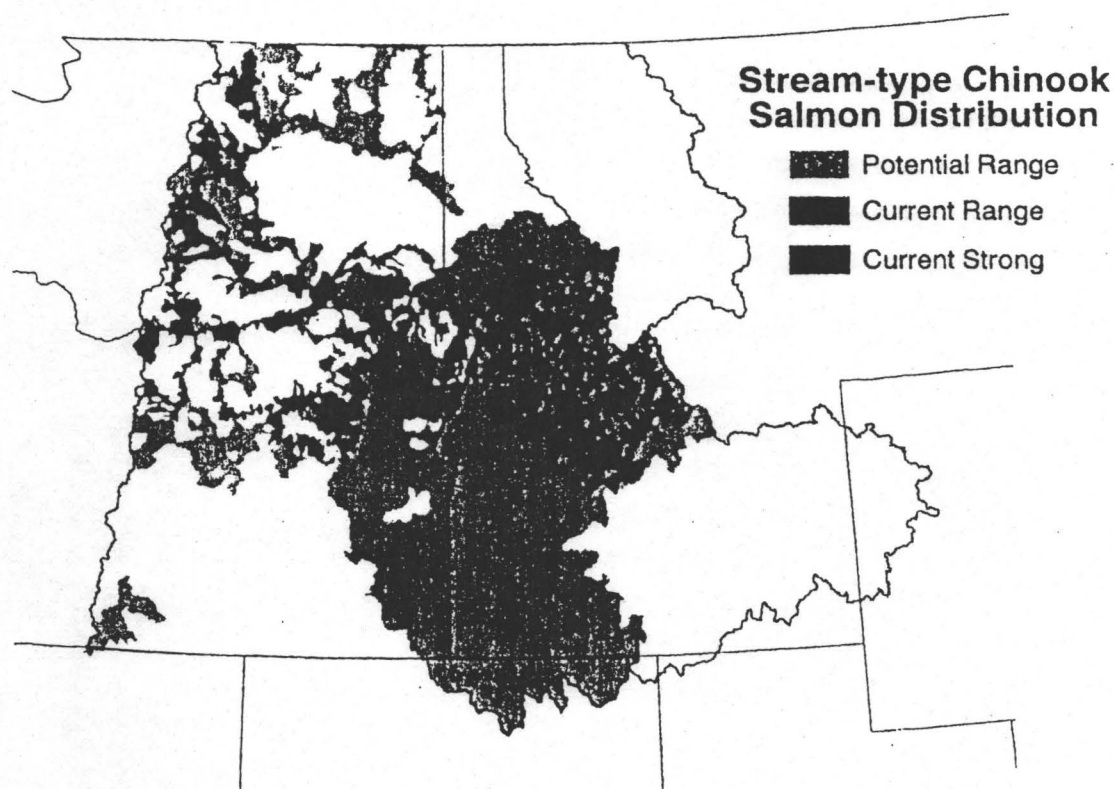


FIGURE 12.5 Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of stream-type chinook salmon within the interior Columbia River basin in the U.S. and portions of the Klamath River basin.

The Snake River was considered the most important production area for ocean-type chinook salmon in the Columbia River basin (Fulton 1968).

Known Status and Distribution.—Stream-type chinook salmon were reported as present in about 21% and ocean-type chinook salmon in about 25% of the subwatersheds within the potential range (Tables 12.5 and 12.6). Strong populations were judged to be present in <1% of the potential range of stream-type chinook salmon and in 4% of the potential range of ocean-type chinook salmon. The distribution of stream-type chinook salmon was unknown or unclassified in 8% of the potential range (281 subwatersheds) and reported as present of unknown status in an additional 141 subwatersheds. The distribution of ocean-type chinook salmon was unknown or unclassified in 10% of the potential range (50 subwatersheds) and reported as present of unknown status in an additional 20 subwatersheds.

Predictive Models.—For stream-type chinook salmon, a total of 1,262 subwatersheds within the current range, with complete landscape information and known chinook status, were used to develop the predictive models. For ocean-type chinook salmon, 224 subwatersheds were used in the model. We excluded all subwatersheds in the potential range that were no longer accessible. The overall model predictive success rate was 83% for stream-type chinook salmon and 92% for ocean-type chinook salmon (Table 12.4). Variables including ERU, number of dams, hucorder, slope, elevation, and management cluster were useful in discriminating subwatersheds supporting chinook salmon (Table 12.4). Stream-type chinook salmon spawning and rearing areas were more likely to be found within certain ERUs in mid-size streams, above fewer mainstem dams, in steeper landscapes, and on Forest Service lands. Larger mainstem streams at lower elevations were more

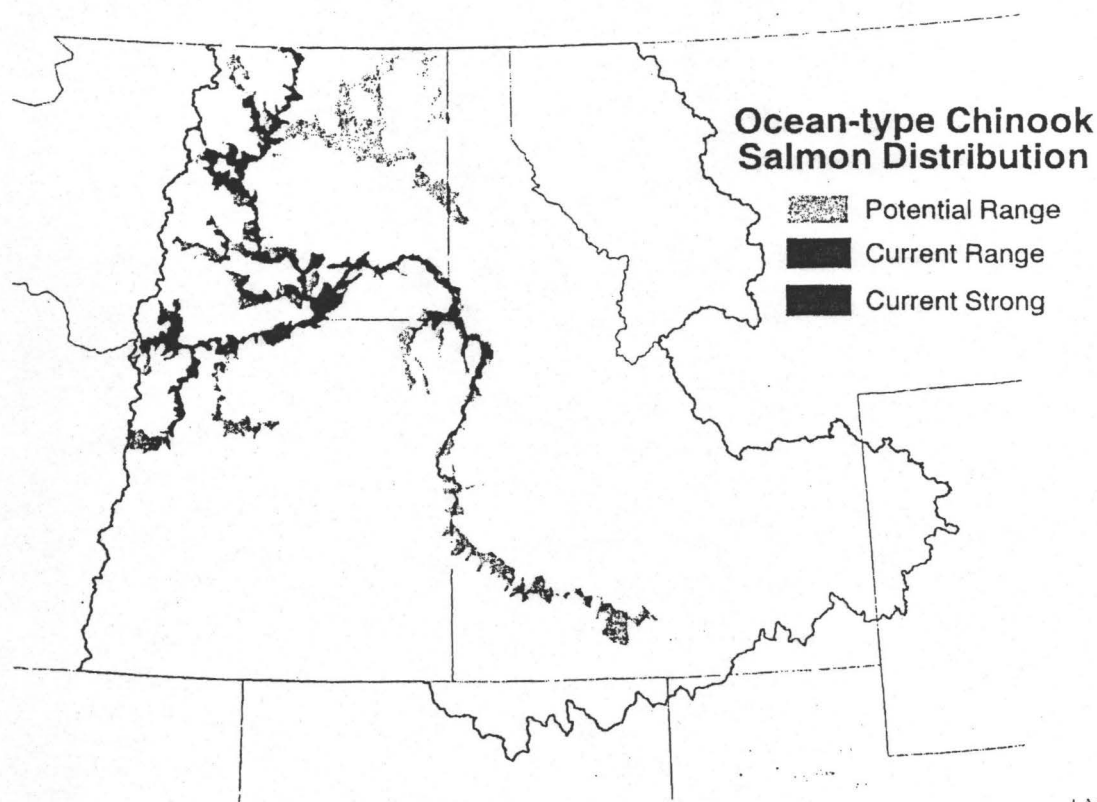


FIGURE 12.6 Map of the potential historical range, the known and predicted current range, and known and predicted strong populations of ocean-type chinook salmon within the interior Columbia River basin in the U.S. and portions of the Klamath River basin.

likely to represent migratory corridors. In contrast, the distribution of ocean-type chinook salmon spawning areas were associated with mainstem segments of the Columbia and Snake rivers.

Current Status and Distribution.—Chinook salmon populations have been extirpated in large portions of their potential range. Current known and predicted distributions of stream-type and ocean-type chinook salmon include 28% and 29%, respectively, of the potential range (Tables 12.5; 12.6). Stream-type chinook salmon are no longer present in the Upper Klamath, Lower Clark Fork, and Owyhee Uplands ERUs; and they have been extirpated from portions of their potential range in other ERUs (Figure 12.5). Ocean-type chinook salmon remain in all ERUs in the potential range but are extirpated from more than 70% of the potential subwatersheds (Figure 12.6).

Most chinook salmon populations are depressed and have been influenced by non-indigenous forms. We estimated that about 20% of the potential range still supports spawning and rearing areas for stream-type chinook salmon and 1.2% of those subwatersheds (0.2% of the potential range) were classified as supporting strong populations (Table 12.5; Figure 12.5). The North Fork of the John Day River contains the only strong population of stream-type chinook salmon. About 17% of the potential range still supports spawning and rearing areas for ocean-type chinook salmon and 26% of those subwatersheds (4.5% of the potential range) were classified as supporting strong populations (Table 12.6; Figure 12.6). The Northern Cascades, especially the Hanford reach of the Columbia River, and the Columbia Plateau ERUs support the remaining core of strong ocean-type chinook salmon populations. Like steelhead, many remaining chinook salmon populations have been influenced by hatchery-reared fish. Wild populations unaltered by hatchery stocks are rare

TABLE 12.5

Summary of the potential historical range and known (as reported by biologists) and predicted classifications of current range and status (number of subwatersheds) for stream-type chinook salmon. The numbers predicted are based on the classification trees and are shown in parentheses. Known status is the remainder of known and predicted minus predicted. Eight subwatersheds classified as unknown had incomplete information and were omitted from analysis. Transient refers to transient in migration corridors. Wild indigenous subwatersheds were those judged to be unaltered by hatchery programs.

Ecological Reporting Unit	Total sub- watersheds	Potential historical range	Current known range	Current known and predicted range	Known and predicted status				Wild indigenous
					Where present			Absent	
					Strong	Depressed	Transient		
Northern Cascades	340	219	89	123 (34)	0	104 (33)	19 (1)	94 (20)	0
Southern Cascades	141	51	18	26 (8)	0	21 (8)	5 (0)	25 (0)	0
Upper Klamath	175	35	0	0	0	0	0	35 (0)	0
Columbia Plateau	1,089	465	114	129 (15)	0	39 (5)	90 (10)	331 (46)	0
Blue Mountains	695	504	192	208 (16)	8 (0)	152 (14)	48 (2)	295 (22)	68
Northern Glaciated Mountains	955	172	7	7 (0)	0	1 (0)	6 (0)	165 (5)	0
Lower Clark Fork	415	98	0	0	0	0	0	98 (0)	0
Owyhee Uplands	956	866	0	0	0	0	0	866 (0)	0
Central Idaho Mountains	1,232	1,051	314	465 (151)	0	351 (138)	114 (13)	586 (97)	60
Entire Assessment Area	7,498*	3,461	734	958 (224)	8 (0)	668 (198)	282 (26)	2,495 (190)	128

*This total includes 4 ERUs with no potential range.

TABLE 12.6

Summary of the potential historical range and known (as reported by biologists) and predicted classifications of current range and status (number of subwatersheds) for ocean-type chinook salmon. The numbers predicted are based on the classification trees and are shown in parentheses. Known status is the remainder of known and predicted minus predicted. Five subwatersheds classified as unknown had incomplete information and were omitted from analysis. Transient refers to transient in migration corridors. Wild indigenous subwatersheds were those judged to be unaltered by hatchery programs.

Ecological Reporting Unit	Total sub-watersheds	Potential historical range	Current known range	Current known and predicted range	Known and predicted status				
					Where present				Wild indigenous
					Strong	Depressed	Transient	Absent	
Northern Cascades	340	79	25	39 (14)	13 (1)	21 (9)	5 (4)	39 (11)	0
Southern Cascades	141	31	9	9 (0)	0	0	9 (0)	22 (3)	0
Columbia Plateau	1,089	147	51	57 (6)	12 (3)	14 (3)	31 (0)	86 (21)	11
Blue Mountains	695	99	38	41 (3)	0	27 (2)	14 (1)	58 (7)	16
Northern Glaciated Mountains	955	149	15	15 (0)	0	9 (0)	6 (0)	134 (0)	0
Owyhee Uplands	956	48	0	0	0	0	0	48 (0)	0
Entire Assessment Area	7,498*	553	138	161 (23)	25 (4)	71 (14)	65 (5)	387 (42)	27

*This total includes 7 ERUs with no potential range.

and present in 4% of the potential range and 15% of the current range for stream-type chinook salmon and 5% of the potential range and 17% of the current range for ocean-type chinook salmon (Figure 12.4). With the exception of strong populations in the Hanford reach, the only subwatersheds classified as strong were those sustaining wild stocks. About 50% of stream-type chinook salmon strong populations were found in designated wilderness or National Park Service lands and 88% were found on Forest Service or BLM lands. No strong populations of ocean-type chinook salmon were found in wilderness and 20% were found on Forest Service or BLM lands.

DISCUSSION

CURRENT STATUS AND DISTRIBUTION

The status and distribution of chinook salmon and steelhead within the study area is very different than it was historically; we estimated that stream-type and ocean-type chinook salmon have been extirpated from more than 70% of their potential range and steelhead from 54% of their potential range. About 12,452 km of streams in the potential range in the Columbia River basin in the U.S. and Canada are no longer accessible to anadromous fish (NWPPC 1986). Construction of numerous dams without passage facilities, such as Swan Falls in 1906, Grand Coulee in 1941, and the Hells Canyon complex in 1967, blocked fish access (IDFG 1992). Where accessible habitats remain, most wild chinook salmon and steelhead are declining. Populations in 99% of remaining spawning and rearing areas for stream-type chinook salmon, 76% of those for ocean-type chinook salmon, and 98% of those for steelhead were classified as depressed. Because our potential ranges remain speculative and because the resolution of our potential and current range data was not sufficient to map upper and lower distributional boundaries within subwatersheds, we cannot quantify extirpations at finer scales. Quantification of extirpations are further complicated by the likelihood that the distribution of steelhead and both chinook salmon forms was naturally restricted by physical characteristics of streams (for example, see Burner 1951; Platts 1974; Mullan et al. 1992). Spawning areas for ocean-type chinook salmon in Idaho, for example, appear to have been restricted to mainstem reaches where at least 960 temperature units accumulate from about November 15 to a late April-early May emergence (B. Connor, U.S. Fish and Wildlife Service, personal communication).

Extinctions and declining populations have resulted in lower diversity and total abundance of chinook salmon and steelhead. Cumulative habitat changes that eliminate or isolate segments of populations may increase both demographic and environmental stochasticity (thereby increasing the risk of extinction of remaining populations) because of reduced population structure or distribution (Rieman et al. 1993). Local extinction and subsequent refounding may be a natural and perhaps common element in the dynamics of many species (Rieman and McIntyre 1995; Schlosser and Angermeier 1995). Large scale processes such as climatic variation associated with fluctuating ocean conditions, drought and flood patterns, and local storm frequency and intensity may influence abundance and distributions in shorter time scales. The recent declines in Columbia River salmon and steelhead, for example, have likely been influenced by ocean conditions (Lichatowich and Mobrand 1995) and a period of extended drought (Anderson 2000). Although environmental variability is a factor and may be the proximate cause of decline or extinction in some cases, the effects of human-caused disturbance appear to be far more important to the declines in abundance of chinook salmon and steelhead.

FACTORS INFLUENCING STATUS

The association between status of chinook salmon and steelhead and disturbance variables (*dampass*, *mngclus*) in our models suggests these species have responded negatively to environmental disruption (Table 12.4). Because the models were designed to develop a complete database and not

test hypotheses, there are several possible reasons for the lack of strong influence of these and other disturbance variables (such as *roaddn*) in discriminating anadromous fish status (e.g., Table 12.2). First, the status of anadromous fish is influenced by environmental factors within both the freshwater environment and in areas outside the study area. Our disturbance variables may not adequately reflect factors such as passage mortality, harvest, and ocean survival that occur outside the subwatersheds. Second, the model did not differentiate between wild and natural fish and did not address the influence of introduced stocks. In some heavily disturbed areas, remnant numbers of fish may be present only because of annual hatchery supplementation so disturbance may not be a good predictor of fish presence. Third, too few strong populations were represented in the model to relate their presence to disturbance. The number of subwatersheds where strong populations were known to be present included 8, 21, and 23 for stream-type chinook salmon, ocean-type chinook salmon, and steelhead, respectively. For these reasons, although the model included disturbance variables, it does not provide an adequate prediction of risk associated with different management scenarios. Salmon and steelhead declines can be associated with a variety of human-caused factors that include habitat disruption linked to land management; watershed development for hydropower and irrigation; competition, hybridization, and predation linked to the introduction of non-native species or stocks of fish; and harvest.

Freshwater Habitat Degradation.—Work at finer scales has confirmed that degradation of freshwater habitats is a consistent and pervasive problem facing the productivity and persistence of aquatic animals in the study area and throughout much of the western U.S. (Williams et al. 1989; Nehlsen et al. 1991). Numerous studies describe the negative effects of land-use activities on habitat conditions, and link habitat conditions to survival and productivity of anadromous fish (Meehan 1991; Murphy 1995; NRC 1996). More than 95% of the healthy native stocks of anadromous fish identified by Huntington et al. (1996) were judged to be threatened by habitat degradation. Nehlsen et al. (1991) identified habitat loss or degradation as a major problem for 90% of the 195 at-risk salmon and steelhead stocks they identified. Alterations of anadromous fish habitat can be attributed to mining (Meehan 1991), timber harvest (Meehan 1991), agriculture (NWPPC 1986), industrial development, and urbanization (NWPPC 1986).

Hydropower Development.—Construction and operation of mainstem dams on the Columbia and Snake rivers is considered to be the major cause of recent declines of anadromous fish (CBFWA 1990). Hydroelectric development changed Columbia and Snake river migration routes from mostly free-flowing in 1938 to a series of dams and impoundments by 1975. Reservoirs reduce flows in most years by about 50% during smolt migration (Raymond 1979). Anadromous fish must navigate as many as nine mainstem dams. At each dam, adults are delayed during upstream migrations. Smolts may be killed by turbines; become disoriented or injured, making them more susceptible to predation; or become delayed in impoundments behind dams (IDFG et al. 1990). Smolt-to-adult return rates declined from more than 4% in 1968 to less than 1.5% from 1970–1974. In 1973 and 1977, low flows resulted in 95% of migrating smolts never reaching the ocean (Raymond 1979). Losses of mid- and upper-Columbia ocean-type chinook salmon were estimated to be about 5% per dam for adults and 18 to 23% per dam for juveniles (Chapman et al. 1994b). The influence of passage mortality is illustrated by Huntington et al. (1996), who concluded that, although much of the Pacific Northwest's best remaining spawning and rearing habitat is in central Idaho, no healthy stocks of anadromous fish were found there.

Introduced Species.—Predation, competition, and genetic introgression from introduced species or stocks has influenced the status of anadromous salmonids. More than 55 introduced fishes occur within the current range of salmon and steelhead. In many reaches of the Snake and Columbia rivers, introduced species outnumber indigenous fish (Li et al. 1987). Hobbs and Huenneke (1992) suggested that non-natives may pose a greater risk to native species where habitat has been disturbed. Dams have created habitat that is suitable for a variety of native and non-native predators and potential competitors (e.g., Beamesderfer and Rieman 1991).

With few exceptions, most watersheds supporting chinook salmon and steelhead are also likely to be influenced by hatchery stocks. Existing populations are comprised of four types: wild, natural (non-indigenous progeny spawning naturally), hatchery, and mixes of natural and hatchery fish. Most existing chinook salmon and steelhead production is supported by hatchery and natural fish as a result of large-scale hatchery mitigation programs. By the late 1960s hatchery production surpassed natural production in the Columbia River basin (NWPPC 1986). Meanwhile, production of wild anadromous fish in the Columbia River basin has declined by about 95% from historical levels (Huntington et al. 1996). Hatcheries may affect salmon and steelhead populations through genetic introgression and loss of fitness, creation of mixed-stock fisheries, competition for food and space, and disease organisms (Reisenbichler 1977). Studies of the interaction between wild and hatchery fish illustrate that survival of progeny from hatchery or hybrid (wild $\times$ hatchery) parentage is less than for progeny of wild fish pairings (Reisenbichler and McIntyre 1977; Chilcote et al. 1986). Rainbow trout have been introduced throughout the current steelhead range (Lee et al. 1997) and have the potential to hybridize with steelhead (Chapman et al. 1994b). Byrne et al. (1992) suggested that supplementation of native stocks with hatchery fish have typically resulted in replacement, not enhancement of native fish. Most (107/121) of the healthy anadromous salmonid stocks identified by Huntington et al. (1996) either have had no fish culture activities in the home watershed or have been exposed to little risk from stock transfers or interaction with hatchery fish. Adult collection and egg-taking may also be detrimental to individual populations (Chapman et al. 1994b). Introductions of large numbers of hatchery-reared parr may cause localized decreases in the density of juveniles (Pollard and Bjornn 1973; McMichaels et al. 2000) and induce early migration of wild fish (Hillman and Mullan 1989). 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-type and ocean-type chinook salmon unaltered by hatchery releases to be present in 10, 4, and 5% of the potential range, respectively.

Harvest.—Salmon and steelhead stocks have historically provided harvest opportunities for tribal, commercial, and sport fisheries. Harvest has contributed to the decline of spring and summer chinook salmon in the study area since the late 1800s (Fulton 1970) and to the decline of fall chinook salmon after 1920 (Lichatowich and Mobrand 1995). Historical ocean and river harvest rates exceeded 80% (Ricker 1959). Thompson (1951) reported that by 1919, as a result of excessive harvest, the characteristics of the Columbia River chinook salmon run had changed. Formerly large portions of the run were reduced making smaller portions of the run more important to the fishery. The once nearly continuous run of salmon became segregated into more discrete groups. Lichatowich and Mobrand (1995) divided the fishery into four phases: initial development (1866–1888), sustained production (1889–1922), resource decline (1923–1958), and maintenance at a depressed level (post-1958). Wild populations have declined as numbers of hatchery steelhead have increased, creating harvest management problems. Hatchery fish that are surplus to egg-taking needs can be harvested while declining runs of wild fish cannot. In response, sport and commercial harvest of most wild adult salmon and steelhead has been closed (NWPPC 1986; IDFG 1992; Chapman et al. 1994b), harvest of wild juvenile steelhead has been restricted (IDFG 1992), and tribal fisheries are regulated (NWPPC 1986; Chapman et al. 1994b). Although the harvest of wild stocks has been reduced, wild salmon and steelhead are killed during tribal fisheries, commercial salmon fisheries in the Columbia River and coastal marine waters, and in high seas driftnet fisheries (Cooper and Johnson 1992; Chapman et al. 1994b).

EMPHASIS AREAS

With the exception of the Central Idaho Mountains and perhaps the Northern Cascades ERUs, most of the areas supporting naturally reproducing salmon and steelhead exist as patches of scattered watersheds. Many are not well connected or are restricted to much smaller areas than was the case

historically. Many are associated with high-elevation, steep, and more erosive landscapes. These may be more extreme or variable environments contributing to higher variability in the associated populations, and higher sensitivity to watershed disturbances. Risks could be aggravated with further development. While we may be able to reestablish some populations in portions of the range, reopening large tracts of the former range to anadromous salmonids is unlikely in the short term. Identification and conservation of the most important populations and habitats will likely be critical to broad-scale persistence of these fish species.

Refugia or emphasis areas providing high quality habitat and populations of special significance are cornerstones of most species conservation strategies (Lee et al. 1997). Emphasis areas can be defined as watersheds and habitats that support remaining areas of high intrinsic value for aquatic species. These include areas supporting strong populations for one or multiple species, areas of high genetic integrity, areas located on the fringe of a species range, areas that support listed species, and areas with excellent habitat but too few fish. Within the study area, concern for the persistence of native anadromous fish has led to several efforts to identify emphasis areas. These include the concept of "key watersheds" (Reeves and Sedell 1992; FEMAT 1993), Section 7 and High Priority Watersheds in the Snake River basin (Lee et al. 1997), and PACFISH watersheds (U.S.D.A. Forest Service and U.S.D.I. Bureau of Land Management 1995).

We focused on identifying emphasis areas of two types: subwatersheds with designated strong populations and those retaining naturally reproducing populations of salmon and steelhead, including genetically intact populations. We used consistent rules to spatially locate these populations. As a result of the diverse life history and extensive migrations of salmon and steelhead, factors outside spawning and rearing areas influenced the distribution of strong populations. Consequently, strong populations were rare or absent even in relatively undisturbed habitats in the Central Idaho Mountains ERU. Because salmon and steelhead have very few strongholds, subwatersheds supporting naturally reproducing populations and populations with high genetic integrity may represent the only areas available from which to anchor a conservation strategy.

Although much of the native ecosystem has been altered, emphasis areas remain for rebuilding and maintaining functional native aquatic systems. Watersheds that support strong populations likely represent a fortuitous balance of habitat quality, climatic and geologic constraint, and geographic location, which effectively minimizes cumulative threats to these species (Lee et al. 1997). The most productive, abundant, and diverse populations are likely to be most resilient. Thus, they are more likely to serve as sources for the support of weak or at-risk populations, refounding of locally extinct populations, or repopulating habitats made available through restoration (Schlosser and Angermeier 1995). Because native gene complexes likely offer the best resources for refounding extinct populations in similar environments, conservation of locally adapted and marginal populations will also be critical (Scudder 1989). Populations that historically were distributed over broad geographic areas have likely evolved under relatively distinct environments with little gene flow across the species range (Lesica and Allendorf 1995). Conservation of the genetic diversity in these species then implies sustaining populations over the broad geographic area (Allendorf and Leary 1988; Leary et al. 1993).

Federal land management will be crucial to the establishment of emphasis areas. Both steelhead (70%) and stream-type chinook salmon (88%) have most of their strong populations on federal land. The recovery of depressed populations will also depend on management of federal lands because 61% and 77% of depressed stream-type chinook salmon and steelhead populations, respectively, occupy federal land. Only ocean-type chinook salmon are less influenced by federal land management since they tend to occupy larger mainstem systems which are more influenced by private lands.

Any changes in the environment that increase survival and productivity of remaining chinook salmon and steelhead, including improvements in rearing habitats, harvest, predation, and main stem passage, will improve chances for persistence (Emlen 1995; NRC 1996). Under current migrant survival conditions, many stocks are at serious risk. The differences between those that

persist and those that are extirpated depends on chance events combined with stock survival and productivity, which are largely influenced by freshwater habitat quality, quantity, and accessibility. Without substantial improvement in migrant survival, securing and restoring the quality of freshwater habitats may make the critical difference in persistence for many of the remaining populations. In the short term, conservation and rehabilitation of habitats available to remaining populations will be key. In the long term, main stem passage conditions must be improved, followed by conservation and restoration of broader habitat networks to support the full expression of life histories and species (Lichatowich and Moberg 1995; NRC 1996). Rehabilitation of depressed populations cannot rely on habitat improvement alone, but requires a concerted effort to address causes of mortality in all life stages including freshwater spawning, rearing, and overwintering, juvenile migration, ocean survival, and adult migration.

IMPLICATIONS FOR SUSTAINABLE FISHERIES

To conserve fisheries resources and ensure sustainability, agencies will need a multilevel understanding of spatial variation in the demographic attributes of fish populations (Schlosser and Angermeier 1995). This understanding can help to identify, protect, and restore key habitats and the ecosystem processes generating them. In the case of Pacific salmon, Healey and Prince (1995) report that genotypic variation maps mainly on the population scale whereas phenotypic variation maps strongly on the ecosystem and landscape scales. This suggests that local populations may have a much larger effect on phenotypic diversity than on overall genotypic diversity. The authors suggest that, because phenotypic diversity is a consequence of the genotype interacting with a particular environment, it is critical to preserve unique habitats and ensure their accessibility to Pacific salmon. The critical conservation unit, therefore, is the population within its habitat.

Conservation of salmon and steelhead populations will require the maintenance or rehabilitation of a network of well-connected, high-quality habitats that support the full expression of potential life histories and dispersal mechanisms, and the genotypic and phenotypic diversity necessary for long-term persistence and adaptation in a variable environment (Lichatowich and Moberg 1995; Healey and Prince 1995). Protection of stronghold emphasis areas will not be sufficient. Such reserves will never be large enough or sufficiently distributed to maintain biological diversity (Franklin 1993). Watershed restoration and the development of more ecologically compatible land-use policies are required to ensure the long-term productivity of many systems (Thurrow et al. 1997).

Protection and maintenance of system integrity and functioning will require innovative approaches. Simple solutions such as setting aside small, scattered watersheds probably will not be adequate for the persistence of even current distributions and diversity. The problems are too complex and too pervasive. However, there are several actions which could be taken to maintain or restore the integrity of larger aquatic ecosystems: first, definition and conservation of emphasis areas; second, reconnection and expansion of the mosaic of habitats for widely distributed species to enhance the integrity of larger systems. For wide-ranging fishes such as salmon and steelhead, this includes conservation and restoration of migratory corridors, as well as spawning and rearing areas. Third, an approach is necessary to provide for multiple species or complete communities (Gresswell et al. 1994; Frissell et al. 1995). Conservation and restoration of important habitats should provide for associated species (e.g., cutthroat trout and bull trout) and will sustain important processes that influence structure and function within these systems.

Restoration and management of watersheds on federal lands is critical but will not be sufficient. River corridors surrounded largely by private lands are a particularly important part of the habitat networks. Much of the overlap in species distributions occurs in the larger river corridors because many of the species range widely. Anadromous species use the entire system of rivers as migratory corridors and for overwintering and short-term rearing. The connections and habitat provided by larger river systems are thus critical to the maintenance of anadromous populations. Although much of the highest-quality habitat for anadromous fish probably remains in the Central Idaho Mountains

ERU, no strong populations persist there, due largely to passage mortality in migration corridors. These corridors provide a critical link maintaining the complex life histories of other species as well.

All remaining populations and habitats within the Central Idaho Mountains, Blue Mountains, Northern Cascades, Columbia Plateau, Northern Glaciated Mountains, and Southern Cascades ERUs are critical to the persistence of chinook salmon and steelhead within the study area. Protection of those core areas critical to stock persistence and restoration of a broader matrix of productive habitats will be necessary for full expression of phenotypic and genotypic diversity and establishment of sustainable fisheries.

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