

Lost Watersheds: Barriers, Aquatic Habitat Connectivity, and Salmon Persistence in the Willamette and Lower Columbia River Basins

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Abstract.—Large portions of watersheds and streams are lost to anadromous fishes because of anthropogenic barriers to migration. The loss of these streams and rivers has shifted the distribution of accessible habitat, often reducing the diversity of accessible habitat and the quantity of high-quality habitat. We combined existing inventories of barriers to adult fish passage in the Willamette and Lower Columbia River basins and identified 1,491 anthropogenic barriers to fish passage blocking 14,931 km of streams. We quantified and compared the stream quality, land cover, and physical characteristics of lost versus currently accessible habitat by watershed, assessed the effect of barriers on the variability of accessible habitats, and investigated potential impacts of habitat reduction on endangered or threatened salmonid populations. The majority of the study watersheds have lost more than 40% of total fish stream habitat. Overall, 40% of the streams with spawning gradients suitable for steelhead (anadromous rainbow trout *Oncorhynchus mykiss*), 60% of streams with riparian habitat in good condition, and 30% of streams draining watersheds with all coniferous land cover are no longer accessible to anadromous fish. Across watersheds, hydrologic and topographic watershed characteristics were correlated with barrier location, barrier density, and the impacts of barriers on habitat. Population-based abundance scores for spring Chinook salmon *O. tshawytscha* were strongly correlated with the magnitude of habitat lost and the number of lowland fish passage barriers. The characteristics of barrier and habitat distribution presented in this paper indicate that barrier removal projects and mitigation for instream barriers should consider both the magnitude and quality of the lost habitat.

The Columbia River, the largest river basin in the Pacific Northwest, historically supported greater populations of Chinook salmon *Oncorhynchus tshawytscha* than any other river system in the world (Washington Department of Fisheries 1959). Many of these populations are currently listed as threatened or endangered under the Endangered Species Act. Loss of critical habitat as a result of anthropogenic barriers to migration, such as dams and culverts, is often cited as a cause of declines of Chinook salmon and steelhead (anadromous rainbow trout *O. mykiss*) (Northwest Power Planning Council 1986; Nehlsen et al. 1991). Dams and culverts can limit or restrict access to spawning and rearing habitat as well as modify instream habitat (Pess et al. 2003).

Resource managers have been aware of the detrimental impact of dams and other blocking structures on salmon populations since the 1300s (Montgomery 2003). Despite this awareness, dams and other instream structures were constructed across the Pacific Northwest in the mid-1900s, blocking a substantial fraction of salmonid habitat throughout the region (Craig and

Townsend 1946; Fulton 1970). Impassable dams are responsible for the loss of one-third of the historical Pacific salmon and steelhead habitat in the Columbia River basin, contributing to the extirpation of numerous salmon stocks (Northwest Power Planning Council 1986; Nehlsen et al. 1991; Spence et al. 1996). Large hydroelectric and flood-control dams have decreased the quantity and quality of main-stem riverine habitat; an estimated 87% of Chinook salmon main-stem spawning habitat has been inundated in the Columbia River alone (Dauble et al. 2003). Though large barriers are more widely recognized, small barriers (culverts, splash dams, diversion dams) are far more numerous and distributed more broadly across the landscape. Many of the estimated 10,000 culverts on fish-bearing streams on federal lands in Oregon negatively impact fish passage (OGNRO 2001).

Recent precipitous declines in Pacific salmon populations (Nehlsen et al. 1991; NMFS 2005) and the subsequent Endangered Species Act (ESA) listing of salmon stocks require managers to identify appropriate recovery activities at both regional and watershed scales. There have been many studies describing the impact of single or multiple large hydroelectric or flood control dams on salmon habitat (Raymond 1979; Sheer 1999; Dauble et al. 2003) but few comprehensive studies, such as that by McIntosh et

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al. (1994) that provide a regional perspective of the distribution and types of salmon habitat compromised or lost due to barriers. Barrier removal is a commonly recommended action to assist in restoring ESA-listed salmonids in the Pacific Northwest (Roni et al. 2002). An understanding of the distribution of barriers, size of area blocked, and barrier impact on stream habitat quality are important for prioritizing salmon-related stream restoration activities (Pess et al. 1998; Roni et al. 2002).

Barrier distribution influences the diversity and connectivity of accessible habitats and consequently, the viability of salmon populations (Montgomery and Buffington 1997; Montgomery et al. 1999; Burnett et al., in press). Changes in hydrologic flow regimes and limited access to certain physical habitat structures can reduce the suitability of a watershed for some salmonid life history phases (Beechie et al. 2006; Myers et al. 2006). Barriers can dramatically impact the fraction of the watershed accessible to migratory salmonids, potentially removing the ideal habitat. The lost habitat may have been particularly suitable for certain species and particular life stages. Natural landscape patterns such as geology, climate, riparian quality, and land use characteristics can be used as indicators of intrinsic habitat potential for salmon, even where migration is currently blocked (SWC 1998; Beamer et al. 2000; Pess et al. 2002; Steel et al. 2004; Burnett et al., in press).

The Willamette basin and Lower Columbia River region (WLC) is a large geographic area designated as a recovery domain by the National Marine Fisheries Service for management and recovery of threatened and endangered salmon species (Myers et al., in press). There are six salmon and steelhead evolutionarily significant units (ESUs) within the WLC recovery domain. Evolutionarily significant units are defined as distinct groups of salmon populations that can be listed under the Endangered Species Act (Waples 1991; 1995). Each ESU in the WLC recovery domain is composed of multiple populations of one of four species: Chinook salmon, steelhead, chum salmon *O. keta*, and coho salmon *O. kisutch*. Generally, steelhead and Chinook salmon use main-stem rivers and tributaries for migration, spawning, or rearing; spring-run Chinook salmon and winter-run steelhead spend more time rearing and spawning in smaller tributaries (Healey 1991). An understanding of the distribution and quality of currently accessible versus lost habitat (habitat upstream of barriers) in the WLC recovery domain is needed to provide realistic estimates of recovery goals and prioritized lists of actions such as barrier removals.

To understand the impact of barriers on population

status and develop effective recovery plans for salmon in the WLC, we need a regionwide analysis of lost habitat (upstream of anthropogenic barriers) versus accessible habitat (downstream of barriers). We can use this analysis to estimate the impact of the barriers on individual fish populations and ESUs. In this paper, we examine the magnitude and distribution of lost habitat due to migration barriers. We determine whether barriers have blocked particular types of habitat disproportionately, and we develop a simple model to predict salmon population performance from the quantity and distribution of barriers within a watershed.

Methods

Study area.—Our study area, the WLC recovery domain (47,046 km²), encompasses all Columbia River tributaries downstream from the Dalles Dam (308 river km from the mouth of the Columbia River), including the Willamette Basin (32,462 km²) (Figure 1). There are seventeen 4th-field hydrologic unit watersheds (Seaber et al. 1987) within this area, ranging in size from 1,057 to 5,590 km² (Figure 2). Six of these are high mountain watersheds with snow-dominated headlands that drain directly into the Willamette or Columbia rivers (MFW, MCK, NSA, CLK, LEW, UCW; see Figure 2 for locations and a key to the abbreviations used), and three have rain-dominated headlands that drain directly into the Willamette River (MOL, SSA, TUA) (NCDC 2005). Five watersheds are located primarily within the floodplain of the main-stem Willamette or Columbia rivers and straddle sections of these large main-stem rivers; these include small rain-dominated tributaries (LOW, MIW, UPW, CLA, LCL). The remaining watersheds include the main-stem Columbia River and associated larger tributaries that initiate in snow-dominated headlands (MID, SAN, LCW; Figures 1, 2). The study region includes Coast Range, Willamette Valley, Cascades, and Puget Lowland Level III Ecoregion zones (Omernik 1987).

Data sources.—We combined data on the locations of natural and anthropogenic barriers and associated information on current fish passage status and fish distribution from seven sources (Table 1) and from Steel and Sheer (2003). We included in our analyses only barriers that fully blocked fish movement year-round. Barriers were defined as impassable based on documented fish passage limitations for the particular barrier, the upstream end of known fish distribution, or documented barrier heights. We considered heights greater than 3–4.6 m as impassable, depending on data source certainty. This range is slightly higher than the maximum jumping height for steelhead as indicated in other studies (Aaserude 1984; Bjorn and Reiser 1991),

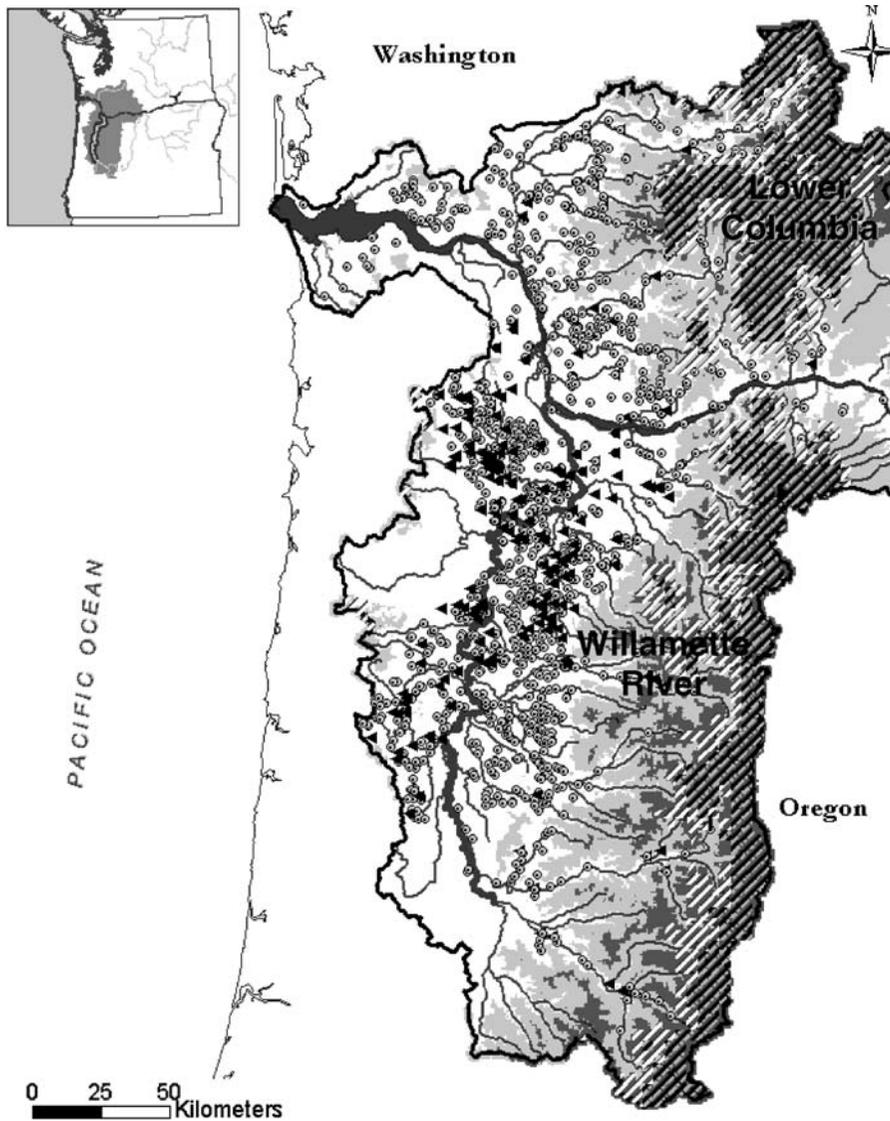


FIGURE 1.—Barrier-analysis study areas of watersheds in the Willamette River basin and the Lower Columbia River. Impassible anthropogenic barriers at the time of the analysis are indicated by triangles (dams and other structures) and circles (culverts). Background shading indicates elevation above mean sea level: 0–500 m (white), 500–1,000 m (gray), and more than 1,000 m (dark gray). Parallel bars show precipitation and runoff patterns; dark bars indicate areas with mean annual spring snowfall exceeding 3.3 m, light bars areas with mean annual spring snowfall less than 3.3 m (source: National Climatic Data Center 2005).

but was used as a conservative estimate of impassability in the absence of other corroborative information. Positional accuracy and quality of fish passage information varied among datasets. Barriers with positional inaccuracies (>500 m from the stream) and indeterminate passage data were removed from the analysis.

Stream habitat.—We estimated the amount of habitat accessible to anadromous salmonids above

each barrier based on a 1:24,000-scale hydrographic stream network with geomorphically designated stream reaches (Miller 2003), which was generated from a drainage-enforced digital elevation model (DEM). Reaches were dynamically designated by valley and channel morphology (resolved by the DEM), with reach lengths from 50 to 300 m. Lost streams were designated as those that were completely blocked by an

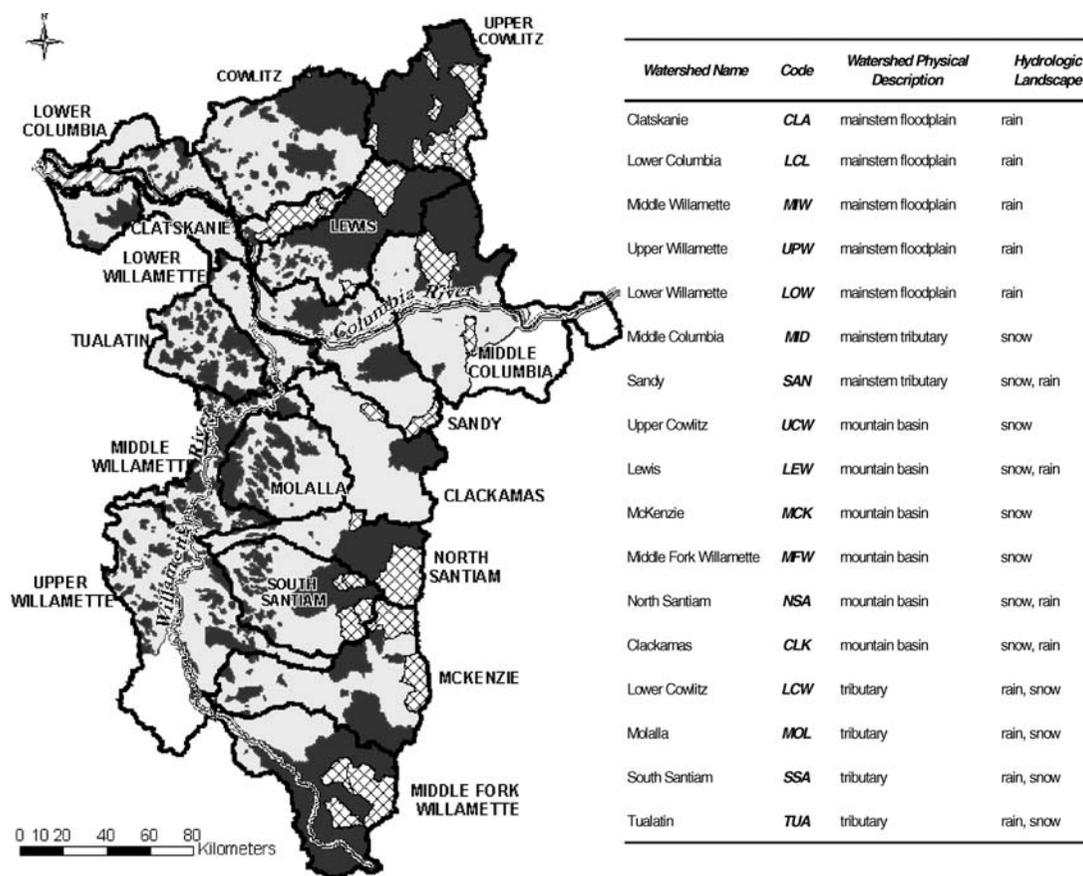


FIGURE 2.—Study watersheds and proportion of area blocked by anthropogenic barriers. Inset table includes a key to watershed code names, dominant precipitation, and stream hydrograph patterns. Black outlines are 4th-field watershed boundaries. Light gray areas are the portions of the watershed accessible to fish and dark gray areas the portions blocked by anthropogenic barriers. Crosshatching indicates areas upstream from natural barriers that were excluded from the analysis; white indicates areas that were excluded from the analysis owing to data limitations.

anthropogenic barrier, making them inaccessible to salmon. Streams upstream of impassible natural barriers, such as waterfalls, were excluded from the analysis.

Habitat length summaries do not include lateral area or length contribution from side channels, islands, and sloughs. Lateral habitat lost from channelization or diking is not represented, though the main-stem Willamette River and other large rivers in the study (>50-m width) historically had substantial amounts of lateral habitat (Minear 1994; Benner and Sedell 1997).

For all stream reaches we determined channel gradient, Strahler's stream order (Strahler 1952), valley width, mean annual precipitation, depth, elevation, and upstream drainage area as calculated from the DEM (Miller 2003). Channel width was derived from these parameters using a bankfull-width regression model developed for the WLC (Steel and Sheer 2003). We

binned stream width into size categories that generally correspond to distinctions in salmonid life history use (Beechie et al. 2001, in press). Categories are as follows: small tributaries (0–5 m), large tributaries (5–10 m), small main-stem rivers (10–25 m), and large main-stem rivers (>25 m). We estimated elevation by overlaying stream reaches on a classified 10-m DEM and calculated elevations for midpoints of each stream reach.

Spawning gradient preference ranges were delineated for Chinook salmon and steelhead. Preference ranges are defined as follows: Chinook salmon, 0–7% gradient (general) and 1–2% gradient (prime physical range); steelhead, 0–12% gradient (general) and 1–5% gradient (prime physical range) (WDFW 2000; Steel and Sheer 2003). Gradients greater than 20% (adult steelhead) and 16% (adult Chinook salmon) function as natural physical limits to Chinook salmon

TABLE 1.—Geographical information systems data layers used in the barrier analysis. All data layers were provided by federal and state agencies or academic institutions, and represent spatial subsets of original source data.

Data layer (scale)	Description	Source
1. Willamette Basin culverts (1:24,000)	Culvert locations and passage information	Oregon Department of Fish and Wildlife, unpublished data
2. Natural and artificial barriers (1:100,000)	Western Oregon dams and natural barriers to fish	StreamNet Oregon Department of Fish and Wildlife, unpublished data
3. Bonneville Power Administration hydroelectric dams (scale >1:100,000)	Dams and possible hydroelectric development site database	Bonneville Power Administration, unpublished data
4. Interior Columbia Ecosystem Management Project (ICBEMP) artificial barriers (scale > 1:100,000)	Dams with >10 acre-feet storage capacity	ICBEMP and U.S. Army Corps of Engineers, unpublished data, Quigley et al. (2001)
5. Gresswell and Bateman barriers (unknown scale)	Natural and anthropogenic barriers to fish passage, western Oregon	R. Gresswell and D. Bateman, Oregon State University, unpublished data
6. Mt. Hood National Forest (unknown scale)	Anthropogenic and natural barriers	U.S. Forest Service, unpublished data
7. Washington State barriers (1:24,000)	Barrier data for southwest Washington	Washington Department of Fish and Wildlife, unpublished data
8. Digital Elevation Model (DEM) watershed boundaries(1:24,000)	Multiple DEMs mosaicked and used to delineate barrier watershed boundaries	U.S. Geological Survey 10-m digital elevation model (DEM)
9. Hydrologic network (1:24,000)	Hydrologic stream network including habitat variables and stream accessibility	Miller (2003); Steel and Sheer (2003)

and steelhead in Pacific Northwest streams (WDFW 2000). Species-specific summaries in this analysis do not include streams above these natural limits.

Landscape characteristics.—To characterize lost versus accessible physical habitat, we delineated individual subwatersheds upstream of each anthropogenic barrier and substantial natural migration barriers (waterfalls). We used the delineated areas upstream of substantial natural migration barriers to define natural exclusion zones; summary data in these areas were excluded from the analysis. The term “lost subwatershed” in this paper refers to hydrologically delineated areas initiating at the downstream anthropogenic barrier, terminating at the first natural barrier, and excluding tributaries with gradients greater than the natural species’ limits described above. Watershed summary statistics were based on lost subwatersheds and accessible habitat within each 4th-field watershed (REO 2002). In some cases, total watershed area is larger than the analysis area (sum of the lost and accessible subwatersheds). The difference between these is the proportion of natural exclusion areas located in the watershed.

We estimated dominant land cover and the quality of riparian function for the study area using classified satellite imagery of coniferous and deciduous crown cover and land use from the Interagency Vegetation Mapping Project (IVMP; BLM 2001). Estimates of riparian quality were derived using methods modified from Lunetta et al. (1997). Lunetta et al. (1997) derived seral-stage land-cover classes from 1988 Landsat 5 Thematic Mapper (TM) data, estimated seral-stage

proportions by stream segments, and characterized riparian habitat quality based on this information. We used a similar approach, translating canopy cover and tree-size information in the 2001 IVMP imagery into similar seral-stage categories (Lunetta et al. 1997; Table 2) and overlaying the stream network with the vegetation imagery (ESRI 2004). We then summarized riparian condition rankings (i.e. good, fair, or poor) for all streams. Note that the riparian analysis has a modified stream length because the streams were converted to pixels (GRID data structure) to do the geographical information systems (GIS) analysis, resulting in slight differences in total stream length. Length is still accurate relative to riparian extent. Land use (i.e., area in urban, agricultural, or forested land cover) was summarized using the 12 general land-use classes in the IVMP data.

Salmon population performance indices.—We used scores for salmon abundance and productivity estimated by the Willamette Lower Columbia Technical Recovery Team (WLC-TRT) as a metric of salmon population performance for each watershed (McElhany et al. 2003). The WLC-TRT is a panel of scientists convened to provide guidance on recovery planning. We chose to use these estimated scores, rather than estimates of population growth rate (λ) alone, because of variability in quality, temporal extent, and spatial extent of data used to calculate λ (McElhany et al. 2000, 2003). The WLC-TRT reviewed all available data on salmon populations including trap counts, redd counts, spawner surveys, recruits per spawner estimates, and population viability estimates. Based on

TABLE 2.—Conversion values for translating remotely sensed classified vegetation imagery to riparian condition factor (after Lunetta et al. 1997). Seral stage refers to the seral stage described by Lunetta et al. (1997). Forest type and conifer cover indicate specific thresholds from the Interagency Vegetation Mapping Project—classified satellite imagery to approximate the seral stage vegetation indices used in this analysis (BLM 2001).

Factor	Riparian condition				
	Good		Fair		Poor
Seral stage	Late	Mid	Early	Other (vegetated)	Nonforest
Conifer cover	>70%	>70%	10–70%	<10%	<10%
Forest type	>50% trees with DBH > 20 in ^a	<50% trees with DBH > 20 in ^a	<75% of land cover deciduous forest, remainder coniferous forest	>70% of land cover deciduous forest	>70% of land cover nonforest (agriculture, urban, barren)

^a DBH = diameter at breast height; 1 in = 2.54 cm.

these data, they assigned a score estimating abundance and productivity for each population. Population performance scores were given on a scale of 0–4, with 0 being extinct or nearly so, and 4 being less than a 10% chance of extinction in the next 100 years (McElhany et al. 2003).

Statistical methods.—We compared lost versus accessible habitat for all but one watershed. No comparisons were done for the Upper Cowlitz (UCW) watershed, because it is located entirely upstream of an impassible dam. We summarized lost and accessible stream segments with respect to elevation, stream order, and bankfull width. We also calculated the fraction of accessible habitat for each watershed. This is defined as the fraction of salmon-accessible stream kilometers currently on the landscape as a proportion of the amount of historically salmon-accessible stream kilometers in the watershed. We used simple linear regression to compare the fraction of lost habitat with the number of barriers in a watershed.

Simpson’s diversity index (*D*; Begon et al. 1996) was calculated for each 4th-field watershed as $1 - (n/N)^2$, where *n* is the number of reaches of a particular stream type (e.g., streams of a particular width [four classes], elevation class [nine classes], and stream order [seven classes]), and *N* is the total number of reaches in all stream types. Diversity indices were summarized by reach counts. Reach counts decreased in floodplain zones, due to the dependence of reach-length breaks on geomorphic variability. Paired *t*-tests ($\alpha = 0.05$) were used to test for significant differences in habitat attributes and diversity between lost and accessible habitat across all watersheds.

We used simple linear regression models to relate salmon population performance scores to patterns of barrier distribution. Models could only be developed for situations in which watershed boundaries corresponded to species demographic population boundaries, as defined by the WLC-TRT (Myers et al. 2006).

This only occurred for nine spring Chinook salmon populations in eight watersheds (LCL, LEW, LCW, MFW, NSA, SSA, MOL, CLK). Performance scores were square-root transformed to improve normality. We used the resulting model to predict population performance scores for spring Chinook salmon for all watersheds. Using the barrier distribution metrics that were strongly correlated with population performance in the model, we delineated three barrier impact groups. We classified watersheds by type of barrier impact. Analysis of variance (ANOVA) was used to compare habitat attributes across groups of watersheds.

Results

Barrier Distribution

We identified 1,491 anthropogenic barriers to fish passage in the study area, which blocked 14,931 km of stream (Table 3). Anthropogenic barriers were concentrated primarily near roads, in lower elevations near tributary outlets, and within the floodplain of the Willamette River basin (Figure 1). Lost streams were more highly concentrated in elevations greater than 500 m above mean sea level (AMSL), while accessible streams were more highly concentrated in low relief valley bottoms, floodplains of main-stem rivers, and in elevations less than 500 m AMSL. Barriers within the floodplain of the Willamette and Columbia rivers were typically located near floodplain edges, usually at elevations less than 100 m (Figure 1; Table 4). Surprisingly, we found no correlation between the total number of barriers in a watershed and the fraction of the naturally accessible area that is lost to anadromous salmonids ($r = -0.067$).

Disconnected Aquatic Habitat

The amount of lost stream habitat varies substantially across watersheds (Figures 2, 3; Table 3). Only 58% of the original stream habitat in the WLC remains accessible to salmonids (Table 3). Seven watersheds

TABLE 3.—Study watershed size, stream length blocked, and species-specific (gradient preference in percent gradient) habitat. A key to watershed names is given in Figure 2. Percentage values are proportions of total stream length lost per watershed by species preference range. Length (km) of accessible stream reaches or subwatersheds (km²) are indicated by A, lost reaches or subwatersheds by L. Lost and accessible areas do not always sum to total watershed size, since natural exclusion areas were not included in this sum. The UCW watershed has no accessible areas.

Water-shed	Watershed size (km ²)			Stream length (km)			Chinook salmon (general, 0–7%)			Chinook salmon (prime, 1–2%)			Steelhead (general, 0–12%)			Steelhead (prime, 1–5%)		
	Total	L	A	L	A	%	A	L	%	A	L	%	A	L	%	A	L	%
MID	5,590	4,501	1,080	1,483	1,205	55	398	728	65	65	139	68	641	981	61	63	116	65
SAN	2,786	2,174	601	931	1,271	42	685	478	41	120	85	42	909	594	40	84	49	37
LEW	2,761	761	1,655	1,213	627	66	373	584	61	63	90	59	479	995	68	37	89	71
CLA	2,179	1,961	216	285	1,937	13	997	98	9	138	11	7	1,405	219	13	114	13	11
UCW	2,658	1,814	0	629	0	100	0	431	100	0	73	100	0	506	100	0	36	100
LCW	3,795	2,293	1,489	1,446	2,173	40	1,339	859	39	201	140	41	1,754	1,158	40	113	90	44
LCL	1,334	1,116	218	272	1,583	15	807	91	10	130	16	11	1,130	202	15	90	14	14
MFW	3,540	943	2,079	1,136	757	60	520	640	55	84	107	56	678	830	55	26	58	69
UPW	4,848	4,137	702	1,619	2,507	39	1,943	1,034	35	209	152	42	2,185	784	26	99	96	49
MCK	3,468	2,510	947	672	899	43	532	392	42	66	55	45	656	373	36	36	39	52
NSA	1,980	769	739	523	400	57	319	289	48	28	38	58	343	251	42	13	30	69
SSA	2,697	1,743	773	834	1,198	41	775	436	36	118	70	37	900	535	37	51	44	46
MIW	1,843	1,152	687	1,188	1,189	50	995	835	46	118	149	56	1,073	886	45	50	87	63
MOL	2,266	1,633	618	838	1,164	42	862	650	43	151	116	43	947	756	44	63	52	45
TUA	1,837	1,176	662	1,258	1,398	47	977	661	40	117	96	45	1,131	830	42	72	69	49
CLK	2,439	2,085	352	368	1,215	23	464	25	5	97	3	3	534	72	12	76	34	31
LOW	1,058	947	117	234	1,127	17	723	148	17	98	30	23	833	170	17	47	14	23

have lost more than 1,000 km of stream length; 11 watersheds have lost more than 40% of the naturally accessible stream reaches. The greatest proportion of lost streams (by length) occurs in watersheds with large flood-control or hydroelectric dams (MID, LEW, NSA, UCW and MFW; Table 3; Figure 2). Mountain basins in the Columbia River drainage (LEW, COW, UCW) have lost, on average, 70% of midsize streams and large tributaries (5–25 m channel width). Willamette

watersheds ($n = 9$) have lost, on average, 50% of smaller 1st- and 2nd-order tributaries. Floodplain watersheds of the Columbia and Willamette rivers maintain a high degree ($\geq 70\%$) of tributary accessibility (CLA, LCL, LOW, CLK).

Landscape Characteristics

Habitat characteristics differed between lost and accessible areas (Table 5; Figure 4). Intact coniferous

TABLE 4.—Barrier distribution and diversity metrics for study watersheds. A key to watershed names is given in Figure 2. Values are the proportions of total length (km) or area (km²). Accessible stream reaches or subwatersheds are indicated by A, lost stream reaches or subwatersheds by L.

Watershed	Barrier count elevation (m)		Stream order			Channel width			Elevation		
	<250	>250	All	A	L	All	A	L	All	A	L
MID	8	36	0.27	0.25	0.29	0.80	0.75	0.87	0.20	0.22	0.21
SAN	50	27	0.29	0.28	0.31	0.63	0.61	0.67	0.39	0.42	0.34
LEW	65	30	0.25	0.29	0.23	0.54	0.60	0.50	0.29	0.56	0.20
CLA	66	7	0.29	0.29	0.30	0.70	0.69	0.78	0.60	0.61	0.51
UCW	0	44	0.20	NA	0.20	0.47	NA	0.47	0.59	0.00	0.61
LCW	88	51	0.29	0.30	0.27	0.67	0.68	0.65	0.46	0.58	0.36
LCL	9	4	0.32	0.32	0.32	0.72	0.73	0.69	0.66	0.72	0.46
MFW	6	16	0.22	0.24	0.21	0.61	0.64	0.57	0.26	0.29	0.27
UPW	186	1	0.33	0.32	0.37	0.67	0.64	0.77	0.74	0.74	0.72
MCK	23	14	0.25	0.26	0.23	0.62	0.63	0.61	0.34	0.38	0.27
NSA	15	14	0.26	0.29	0.21	0.57	0.63	0.48	0.31	0.43	0.26
SSA	78	3	0.28	0.28	0.27	0.67	0.65	0.71	0.40	0.41	0.40
MIW	175	1	0.37	0.36	0.39	0.69	0.64	0.75	0.93	0.95	0.91
MOL	178	22	0.33	0.29	0.40	0.58	0.55	0.64	0.52	0.46	0.63
TUA	232	3	0.33	0.31	0.34	0.74	0.70	0.78	0.77	0.72	0.84
CLK	5	9	0.31	0.30	0.35	0.73	0.73	0.75	0.20	0.22	0.50
LOW	25	0	0.33	0.33	0.35	0.86	0.85	0.93	0.87	0.92	0.67

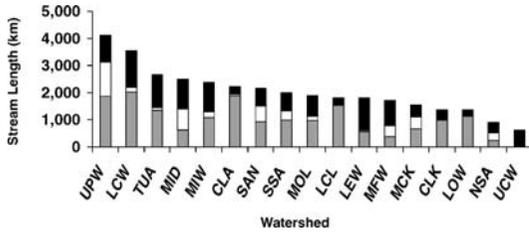


FIGURE 3.— Proportion of stream kilometers blocked by dams or culverts for each watershed. Watershed code names are given in Figure 2. Black indicates lost stream kilometers (<20% gradient), gray accessible habitat, and white partially blocked streams (streams with variable access to fish). Watersheds are ordered by total stream length.

forests are concentrated primarily in higher-elevation areas (>500 m AMSL) where streams have been lost, and development is concentrated in the floodplains and at lower elevations where streams tend to remain accessible (<100 m AMSL). The majority of watersheds are dominated by coniferous land cover ($n = 9$, $\geq 50\%$ total km^2), with the exception of the floodplain watersheds, which contain mostly agriculture, deciduous, or mixed forest (Figure 4a; Table 5). The largest loss, 40–60%, of accessible coniferous forest (conifer-dominant watersheds) occurs in MFW, LEW, and NSA.

Two watersheds (MFW, LEW) have lost more than 50% of the watershed area in coniferous forest (Table

5). We found a small but significant difference in the fraction of lost (1%) versus accessible deciduous forest area (16%; $P = 0.016$). For all watersheds, on average, anthropogenic barriers blocked 30% of wetland areas. The average area in agricultural use differed significantly between accessible (345 km^2) and lost watersheds (110 km^2 ; $P = 0.026$). The area of urban land use (on average) was significantly larger (22 km^2) in accessible than in lost areas (4 km^2 ; $P = 0.009$).

We found that across all watersheds, 61% of the accessible stream riparian condition is good or fair, while 66% of the lost stream riparian is good or fair (Table 5). In forested, mountain watersheds of the Willamette and Columbia rivers, there is more good habitat in inaccessible (lost) stream reaches than in accessible reaches. For floodplain watersheds, the relationship is opposite: there is more good riparian habitat in the accessible stream reaches than in inaccessible (lost) reaches. (Table 5) Modified habitat conditions (nonforested conditions) are generally more common with the lost streams than the currently accessible streams in UPW, MIW, MOL, and TUA.

Habitat Diversity

Median Simpson’s diversity index scores for all watersheds combined are 0.71 (stream order), 0.33 (stream size), and 0.54 (elevation) (Table 4). Habitat diversity varies substantially across watersheds (Figure

TABLE 5.—Land use and riparian habitat in accessible (A) and lost (L) subwatersheds. A key to watershed names is given in Figure 2. Percentage values are the proportions of total area (km^2) measured per watershed. Results for deciduous and coniferous forests include both area and percentage values. Multiple land use categories are represented in “other”, including urban, residential, transitional, shrub, and wetland land cover.

Watershed	Riparian quality ratio		Deciduous forest (km^2)			Coniferous forest (km^2)			Mixed forest (%)		Agricultural (%)		Other (%)		Land use metrics	
	AGAP ^a	LGLP ^b	A	L	Total %	A	L	Total %	A	L	A	L	A	L	Conifer ^c	Riparian ^d
MID	4.99	6.86	209	50	4.8	2,167	813	55.8	1.5	0.4	14.4	0.6	22	3	Mod	Equal
SAN	2.05	3.05	303	67	13.9	1,100	365	55.3	5.3	1.7	7	2	18	3	Low	Equal
LEW	1.24	4.88	174	112	12.3	312	1,133	62	4	2.8	3.6	0.8	5	14	High	High
CLA	1.27	2.37	484	45	24.7	799	120	42.9	13.9	1.6	5.9	0	4.1	0.3	Low	Equal
UCW		3.84	0	86	5	0	1,335	76.8	0	3.1	0	1.2	0	10		
LCW	1.03	1.29	347	262	17	926	649	43.9	9.4	5.1	4.4	1.8	19	12	Mod	Equal
LCL	1.65	9.14	294	36	26	483	126	47.8	14.2	2.3	2.7	0	3	1	Low	High
MFW	7.92	10.84	29	27	1.9	690	1,744	82.1	2.8	3.1	2.4	0.4	2	5	High	Equal
UPW	0.74	0.50	124	27	3.2	1,205	250	30.5	9.2	1.7	40.3	6.2	38	4	Low	Low
MCK	6.36	14.95	58	14	2.1	1,918	822	82.4	3.9	1.1	2.2	0.2	16	5	Mod	Equal
NSA	1.81	6.29	38	10	3.2	441	596	70.1	3.6	1.9	11.4	2.1	3	2	Mod	High
SSA	2.47	2.31	67	20	3.5	1,087	489	63.2	6.3	2.6	11.7	4	6	4	Mod	Equal
MIW	0.25	0.15	45	27	4	144	52	10.9	4.9	3.3	38	26.5	5	2	Low	Low
MOL	1.51	0.30	72	7	3.5	775	77	37.9	7.3	1.8	23.2	20	7	3	Low	Low
TUA	0.77	0.59	121	63	10.1	337	155	27	7	3.3	23.7	16.1	8	5	Low	Low
CLK	5.99	10.26	112	3	4.7	1,485	286	73.2	4.9	0.4	7.7	0.2	7	2	Low	Equal
LOW	0.50	0.98	144	19	16.2	161	38	19.7	6.3	1	14.8	0.9	10	1	Low	High

^a Ratio of accessible good habitat to accessible poor habitat.

^b Ratio of lost good habitat to lost poor habitat.

^c Amount of conifer cover upstream of barriers relative to that downstream.

^d Proportion of good-quality riparian habitat upstream of barriers relative to that downstream. The fractions of good and poor riparian habitat within the lost and accessible streams were calculated from the lengths of the lost and accessible streams, respectively.

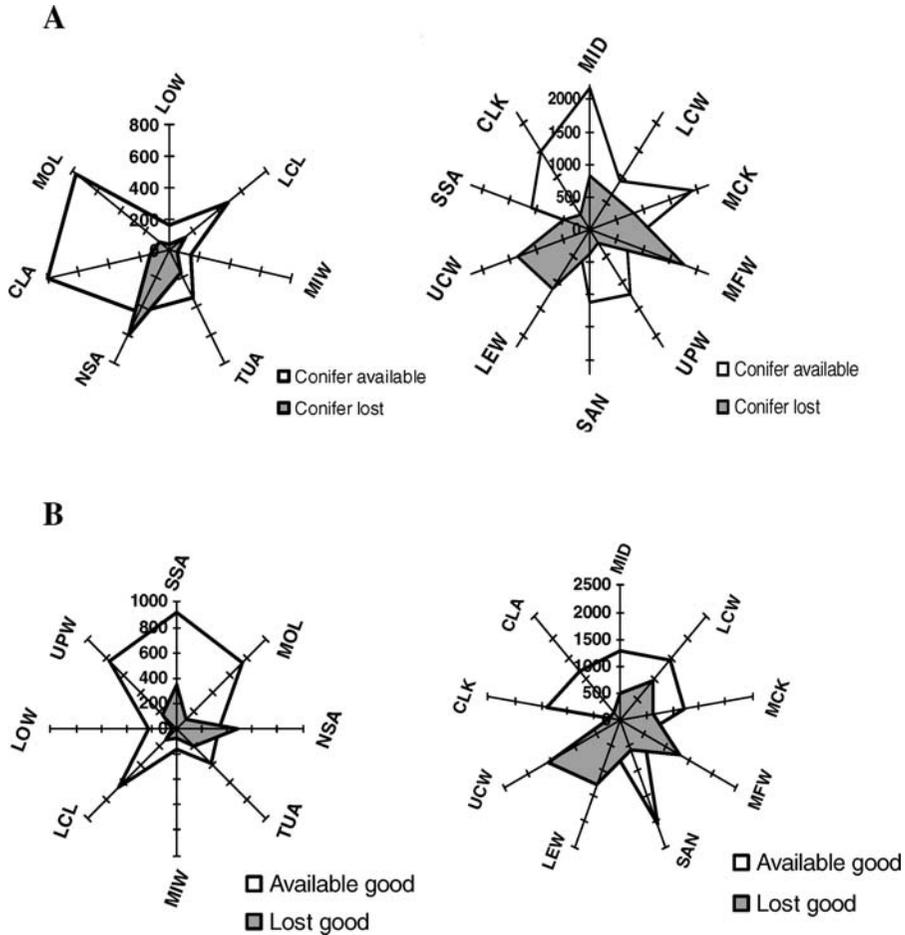


FIGURE 4.—Plots of the amount of (A) coniferous land cover (km²) and (B) good riparian function (km) for all watersheds. Each axis represents a single watershed. Watersheds were split into two radiographs to improve visual representation; the graphs on the left are of watersheds with lower values for area or stream length. The white area of panel (A) represents the amount of coniferous land cover in the accessible parts of the watershed; the shaded area represents total coniferous land cover in lost subwatersheds. The white area of panel (B) represents the amount of good riparian habitat in the accessible parts of the watershed; the shaded area represents the amount of good riparian habitat in lost subwatersheds.

5). Diversity was slightly higher than the overall diversity score for channel width and stream order for MID, SAN, CLK, MOL, TUA, MIW, and LOW. We found no significant difference across all watersheds between lost and accessible habitat for these two variables. Elevation, on average, did not show a trend of consistent diversity differences. Over all watersheds, approximately 80% of the stream length above 750 m AMSL is lost, while only 30% of the habitat below 250 m is lost.

Impacts of Barrier Distribution on Salmonids

A significant amount of preferred habitat streams (defined by gradient thresholds) is lost for both Chinook salmon (8,380 km) and steelhead (10,142

km) (Figure 6; Table 3). The WLC has lost 1,369 km (43%) of the prime gradient habitat for Chinook salmon, and 930 km (47%) of the prime gradient habitat for steelhead. More than half of the prime Chinook salmon or steelhead spawning habitat is lost for six of the watersheds (MID, MIW, LEW, MFW, NSA; Figure 6; Table 3).

The most informative and statistically significant model to predict population performance scores using barrier indices was a regression between the number of barriers in low-elevation areas (<500 m AMSL) and the fraction of historically accessible area that is currently accessible ($r^2 = 0.80, P = 0.008$; Table 6; Figure 7). These two metrics were used to create three impact groups to characterize the impact of barriers by

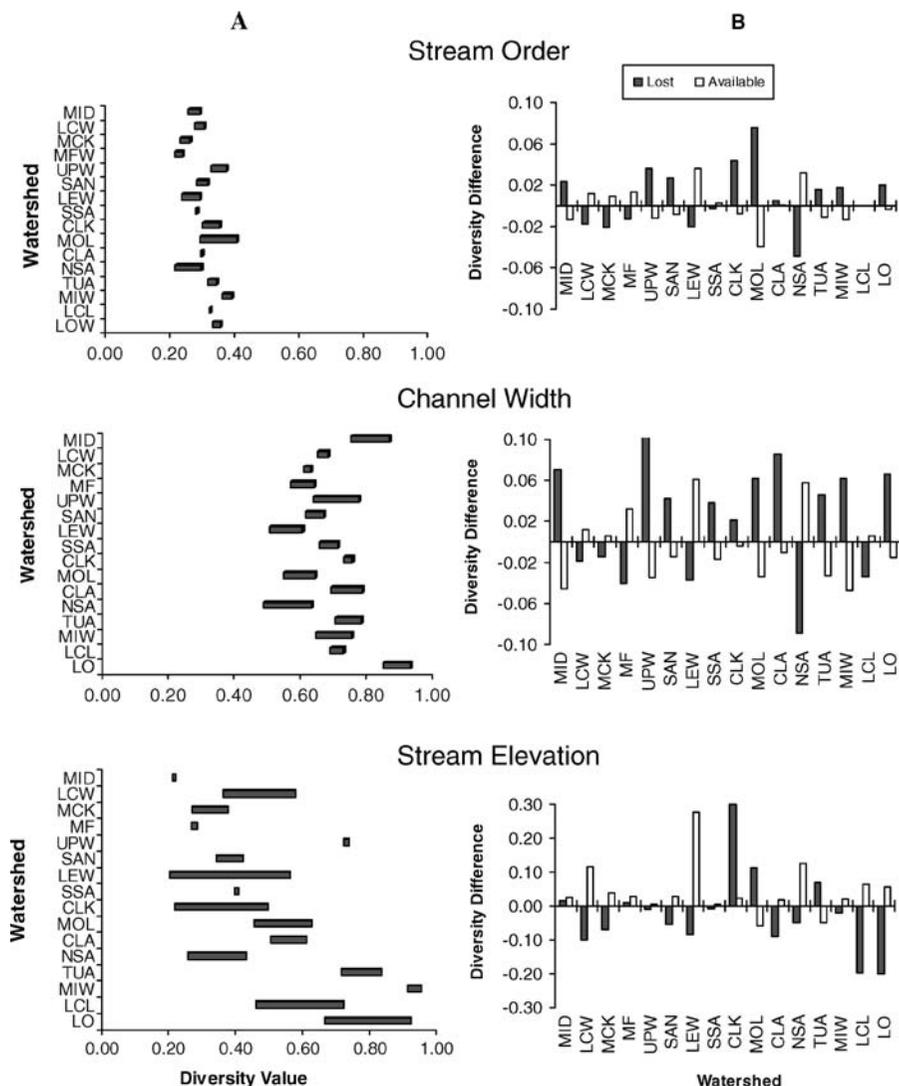


FIGURE 5.— Simpson’s diversity indices for stream order, channel width, and stream elevation. The graphs in column (A) show the ranges of the diversity values for accessible and lost habitat combined. Those in column (B) show the differences between the diversity value for an entire watershed and the values for the lost and accessible portions alone. Values greater than zero (the baseline) indicate features that are more diverse than the baseline, and conversely for values less than zero. Watershed code names are given in Figure 2.

watershed. We defined a “large-area impact group” as watersheds with less than 60% of their historical stream kilometers, the “downstream-impact group” as having a large number of barriers (>100) at elevations less than 500 m AMSL, and the “moderate-impact group” as watersheds with more than 60% of historical habitat remaining and less than 100 barriers at low elevations (Figures 7, 8; Table 6). We found significant differences in the fraction of currently accessible prime gradient steelhead ($P = 0.002$) and Chinook salmon (P

$= 0.016$) habitat across the three barrier impact watershed groups.

The moderate-area impact group had the largest remaining fraction of prime-gradient habitat (0.58 for steelhead and 0.67 for Chinook salmon; Table 3; Figure 6). The downstream-impact group had an intermediate fraction of accessible habitat (0.50 for steelhead and 0.55 for Chinook salmon). In the large-area group watersheds, there was, on average, only a small amount of the prime gradient habitat accessible (0.26 for steelhead and 0.36 for Chinook salmon).

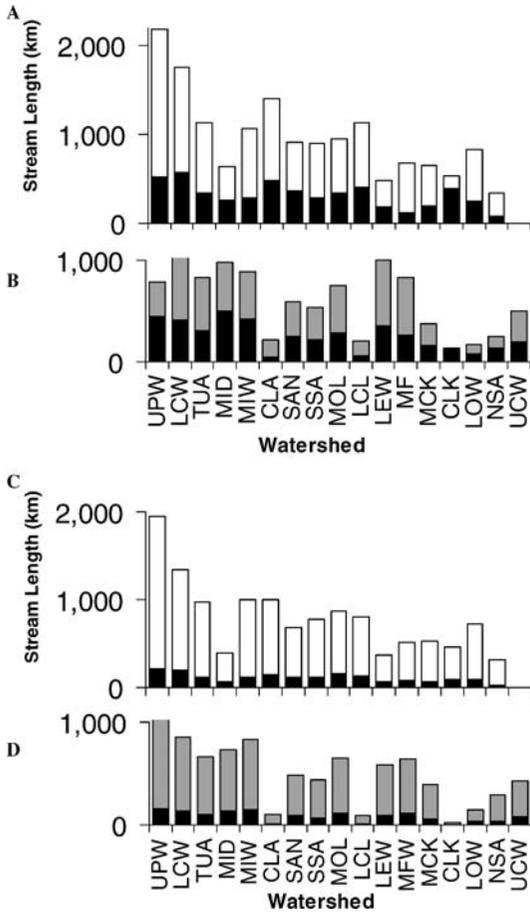


FIGURE 6.—Inaccessible and accessible stream kilometers with spawning gradients preferred by steelhead and Chinook salmon. Panels (A) and (C) pertain to accessible habitat for steelhead and Chinook salmon, respectively. The white portions of the bars in these graphs indicate the number of kilometers that meet general habitat criteria in currently accessible streams; the black portions indicate the extent of prime habitat. Panels (B) and (D) pertain to lost habitat for these two species. Watersheds are sorted by total stream length. Watershed code names are given in Figure 2.

Highest losses of good riparian habitat (≥ 400 km, $\geq 20\%$ total watershed stream length) have occurred in watersheds in the large-area impact group (plus MCK). The percent of the area in agricultural land use varies significantly between barrier impact groups (moderate-impact group = 9.9%, downstream-impact group = 36.3%, and high-area impact group = 13.5%; $P = 0.006$; Table 5). The three designated barrier impact groups show marginally significant differences in the diversity of accessible habitats with respect to stream order ($P = 0.072$), stream size ($P = 0.082$), and

elevation ($P = 0.088$) (Table 4). In all cases, the large-area group has the lowest diversity in accessible streams ($D_{\text{stream order}} = 0.20$, $D_{\text{size}} = 0.47$, $D_{\text{elevation}} = 0.32$). The downstream-impact group ($D_{\text{stream order}} = 0.32$, $D_{\text{size}} = 0.64$, $D_{\text{elevation}} = 0.69$) and moderate-impact group ($D_{\text{stream order}} = 0.29$, $D_{\text{size}} = 0.70$, $D_{\text{elevation}} = 0.49$) show no significant differences in these diversity indices between lost and accessible streams (Table 4).

Discussion

Barriers in the WLC domain have caused a 42% (14,931 km) loss of accessible stream habitat; this loss is not distributed evenly across the landscape. The distribution of barriers is highly correlated with population status of ESA-listed salmon populations. We categorized two types of barrier impact within a watershed: (1) upstream barriers that block large amounts of higher-elevation streams and (2) large numbers of low-elevation barriers that block a high proportion of floodplain tributaries. We identified several watersheds for which barriers have reduced access to large quantities of the highest-quality habitat. Because we did not include barriers presenting only a seasonal migration blockage, barriers with positional inaccuracies, and barriers with indeterminate passage data, our results represent a conservative estimate of lost habitat and of the impacts of anthropogenic barriers on salmonids.

Disproportionate Loss of High-Quality Habitat

The differences between lost and accessible streams suggest that high-quality habitat has been disproportionately lost in many watersheds. The remaining accessible streams tend to drain subwatersheds with younger forests, less coniferous forest (to contribute large wood to the stream and provide shade), and greater amounts of urban and agricultural development than lost subwatersheds. Accessible streams have less canopy cover than the lost streams. Natural topographic and hydrographic variation, patterns of land use development, ownership, and forestry practices, coupled with the distribution of barriers have created these differences across the landscapes. Because older coniferous forests produce woody debris that increases habitat complexity and pool density and riparian cover provides shade, large woody debris recruitment, and bank stability, accessible streams likely have poorer instream conditions than those that have been lost (FEMAT 1993; SWC 1998). Deciduous and mixed forests are naturally more dominant in the disturbance-prone low-elevation floodplains of larger streams within the study area (Minear 1994), and accessibility

TABLE 6.—Key barrier distribution variables and population status predictions from population performance regression. A key to watershed names is given in Figure 2. Accessible fraction is the fraction of historically accessible stream kilometers that is currently accessible. Elevation <500 m is a count of barriers less than 500 m above mean sea level. Predicted score is the viability score predicted by the population performance regression model. The barrier impact group was assigned according to the accessible fraction and number of barriers below 500 m. Low barriers indicates whether the watershed meets the low-barriers criteria (more than 100 barriers at elevations <500 m), and fraction indicates whether the watershed meets the accessible-fraction criterion (<60% historical habitat remaining).

Watershed	Accessible fraction	Elevation <500 m	Predicted score	Barrier impact group	Low barriers	Fraction
MID	0.806	17	2.018	Moderate	No	No
SAN	0.783	74	1.305	Moderate	No	No
LEW	0.315	83	0.100	Large area	No	Yes
CLA	0.901	72	1.818	Moderate	No	No
UCW	0.000	14	0.006	Large area	No	Yes
LCW	0.606	133	0.356	Downstream	Yes	No
LCL	0.837	13	2.215	Moderate	No	No
MFW	0.312	19	0.337	Large area	No	Yes
UPW	0.855	187	0.621	Downstream	Yes	No
MCK	0.726	30	1.514	Moderate	No	No
NSA	0.510	29	0.760	Large area	No	Yes
SSA	0.693	80	0.930	Moderate	No	No
MIW	0.626	176	0.202	Downstream	Yes	No
MOL	0.726	199	0.270	Downstream	Yes	No
TUA	0.640	235	0.050	Downstream	Yes	No
CLK	0.855	8	2.374	Moderate	No	No
LOW	0.890	25	2.335	Moderate	No	No

to this type of riparian habitat has not been significantly reduced by barrier placement.

Reductions in Habitat Connectivity

Physical features such as channel morphology and gradient are related to salmon distribution (Montgomery and Buffington 1997; Montgomery et al. 1999; Steel and Sheer 2003; Burnett et al. in press), life history diversity, and habitat connectivity. Salmon require connectivity between the diverse habitats that are suitable for different life history stages (Roni et al. 2002; Pess et al. 2003). Barriers clearly reduce the connectivity of streams, and may therefore influence the spatial structure and abundance of fish populations, and potentially, life history variation. Prime spawning habitat for Chinook salmon has been reduced by at least one third in the Lewis, Middle Fork Willamette, and South Santiam river watersheds. Spring Chinook salmon have been reduced or extirpated in sections of these watersheds (Myers et al. 2006). Both the Lewis and Middle Fork Willamette have lost at least 60% or more of their accessible streams to barriers (large dams), and the majority of intact, good-quality riparian habitat in these watersheds is located upstream of these dams (>70%).

The loss of habitat connectivity may also impact juvenile salmonids; spring-run Chinook salmon and coho salmon sometimes move upstream to rear in areas with high-quality rearing habitat that contain ample food and cover (Healey 1991; Sandercock 1991).

Disconnected streams can limit dispersal to these areas or concentrate juveniles into homogenous habitats, thereby impacting the productivity and carrying capacity of the stream (Beechie et al. 1994; Pess et al. 2003). The population performance scores include measures of juvenile abundance, and the populations with the highest risk scores (≤ 0.5) had all lost at least 400 km of general Chinook salmon habitat each (TUA, MIW, MFW, LCW, LEW, UCW).

Reductions in Habitat Diversity

Barriers have contributed to a disproportionate loss of certain habitat types, such as higher-elevation habitats. Habitats at higher elevations in the WLC typically require longer migrations, have the highest annual flows in spring (snow-dominant hydrograph), consist of 1st or 2nd order streams, and are typically conifer-dominated. Winter steelhead or spring Chinook salmon are particularly well suited to these habitats because their migration timing (late winter–early spring) allows them to pass natural barriers during high flows. Beechie et al. (2006) found that in Puget Sound, stream-type spring-run Chinook salmon have been extirpated from this type of habitat, primarily as a result of anthropogenic barriers. All watersheds in the high area barrier impact group and a few in the moderate-impact group are mountain drainage basins that have lost a large proportion of snow-dominated channels, or channels characterized by snowmelt-driven high spring flows. Watersheds in the down-

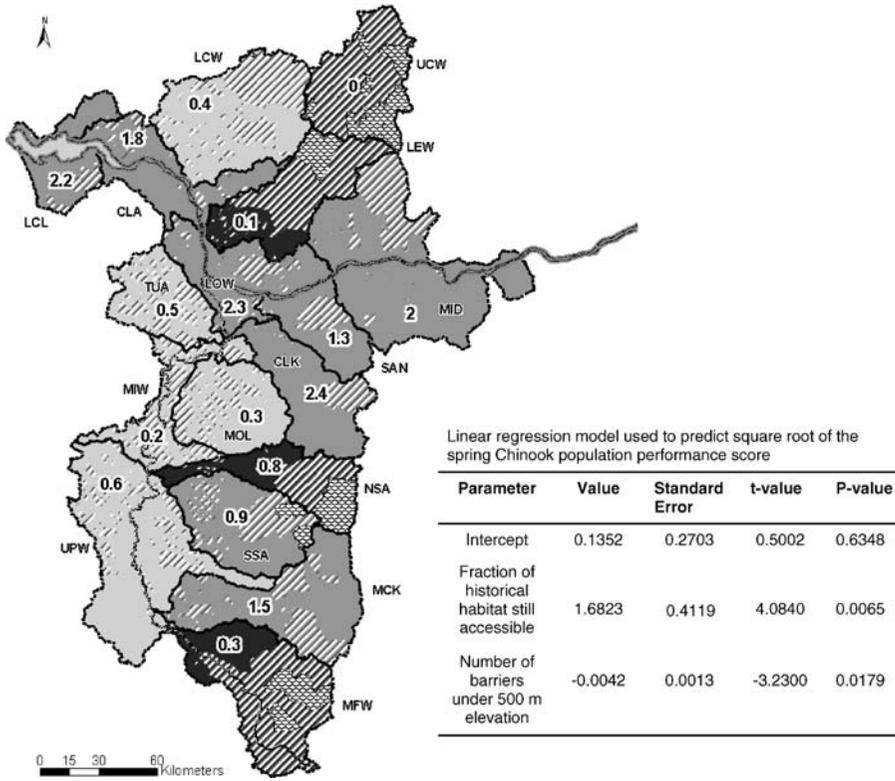


FIGURE 7.—Watershed classification based on linear regression model parameters. The table shows the parameters of the model that best predicted the square root of the spring Chinook salmon population performance score ($P = 0.008$). Each watershed is labeled with the score predicted by the model (see Table 6). Shading represents groupings based on estimated viability and barrier impact variables as follows: light gray = downstream impact, dark gray = moderate impact, and black = large-area impact. Crosshatching indicates natural exclusion zones and diagonal lines blocked areas. Though not apparent from the shading, Upper Cowlitz watershed (UCW) is entirely blocked; it is classified as a large-area barrier impact watershed.

stream-impact group have rain-dominated channels and headlands, with highest annual flows occurring in the winter. Reductions in different types of hydrologic habitat may explain losses of historical population traits and may impact future life history diversity and population viability (Beechie et al. 2006).

Correlations between Barrier Distribution and Salmon Population Viability

We identified strong correlations between spring Chinook salmon population performance levels and barrier distribution. The quantity of lost habitat and the number of small lowland barriers were important in predicting population declines, as reflected in viability scores. We might expect that barriers have a larger impact on steelhead populations because of their tendency to use steeper gradient ranges. We found that a larger proportion of prime steelhead spawning habitat has been lost to barriers than is the case with prime Chinook salmon spawning habitat. Barriers

likely have different effects on other species such as coho or chum salmon, because of differences in run-timing, distribution and life history patterns. For example, barriers that remove small high-gradient streams from a river network may have a disproportionate impact on potential spawning patches for spring-run Chinook salmon. Conversely, barriers that remove large low-gradient streams and unconfined channels from a river network may have a disproportionate impact on chum salmon (adult spawning), fall-run Chinook salmon (spawning and juvenile rearing) and overwintering juvenile coho salmon (rearing habitat), based on life history preferences (Salo 1991; Sandercock 1991; Healey 1991). Our analysis did not consider losses of lateral habitat, which may have even greater impacts on species that use large floodplain rivers for rearing and spawning.

We conclude that anthropogenic barriers have had a tremendous impact on the landscape of the Pacific Northwest and that these impacts can be strongly

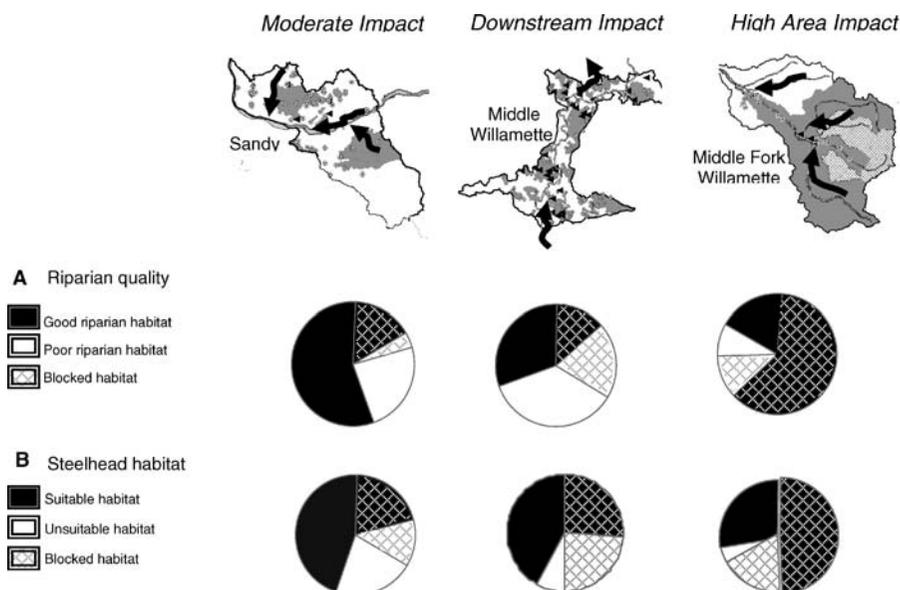


FIGURE 8.—Summary charts of habitat variables for barrier impact watershed groups. The values in the charts summarize (A) riparian condition and (B) steelhead habitat suitability for moderate-impact, downstream-impact, and large-area-impact groups. A representative watershed map for each group depicting the spatial pattern of barriers and lost areas is included above each pie chart; blocked areas are in gray, and arrows indicate flow direction and downstream orientation.

correlated with salmon population status. Simple metrics such as the number of barriers or the kilometers of lost streams may not suffice to understand the impact of barriers on aquatic ecosystems. Barriers tend to disproportionately block high-quality upland streams draining intact coniferous watersheds with prime spawning gradients for Chinook salmon and steelhead and lowland tributaries essential for spawning and rearing of many salmonid species. Habitat remaining for anadromous fishes tends to be less diverse, has a lower proportion of prime spawning gradients for steelhead and Chinook salmon, and has a higher proportion of urban and agricultural development. Understanding the impact of barrier distribution on salmon and on aquatic systems can aid in developing customized watershed management and salmon recovery plans.

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