FEATURE:
CONSERVATION

Recovery Planning for Endangered Species Act-listed Pacific Salmon: Using Science to Inform Goals and Strategies

ABSTRACT: Endangered and threatened populations of Pacific salmon (*Oncorhynchus* spp.) in the United States span major freshwater and marine ecosystems from southern California to northern Washington. Their wide-ranging habits and anadromous life history exposes them to a variety of risk factors and influences, including hydropower operations, ocean and freshwater harvest, habitat degradation, releases of hatchery-reared salmon, variable ocean productivity, toxic contaminants, density-dependent effects, and a suite of native and non-native predators and competitors. We review the range of analyses that form the scientific backbone of recovery plans being developed for Pacific salmon listed under the U.S. Endangered Species Act. This process involves: identifying the appropriate conservation units (demographically independent Evolutionarily Significant Units [ESUs] and their populations), developing viability criteria for Pacific salmon populations and overall ESUs, and using coarse-resolution habitat analyses and life-cycle modeling to identify likely consequences of alternative actions proposed to achieve recovery. Adopting this wide breadth of analyses represents a necessary strategy for recovering Pacific salmon and a model for conservation planning for other wide-ranging species.

Plan de recuperación para el salmón del Pacífico dentro del Acta de Especies Amenazadas: la ciencia como medio para informar metas y estrategias

RESUMEN: En los Estados Unidos, las poblaciones amenazadas y en peligro de extinción del salmón del Pacífico (*Oncorhynchus* spp.) pasan buena parte de su ciclo de vida tanto en ecosistemas de agua dulce como marinos desde el sur de California hasta el norte de Washington. Los hábitos e historia de vida propios de su condición anadrómica los expone a una variedad de influencias y factores de riesgo tales como operaciones asociadas a la obtención de energía hidráulica, pesca marina y dulceacuícola, degradación de hábitat, liberación de salmones cultivados, variaciones en la productividad oceánica, contaminantes tóxicos, efectos de denso-dependencia y una extensa gama de competidores y depredadores nativos y foráneos. Se hace una revisión de los enfoques medulares de los planes que se están desarrollando para la recuperación del salmón del Pacífico, enlistado en el Acta de Especies Amenazadas. Este proceso incluye: identificar apropiadamente las unidades de conservación (Unidades Evolutivas Significativas Demográficamente Independientes—ESU, por sus siglas en inglés- y sus poblaciones) desarrollar criterios de viabilidad para las poblaciones y ESUs de salmón y aplicar análisis de baja resolución de hábitat y modelación del ciclo de vida para identificar posibles consecuencias de las acciones alternativas que se proponen para lograr la recuperación. La adopción de esta extensa serie de análisis representa una estrategia necesaria para la recuperación del salmón del Pacífico y un paradigma para planear la conservación de especies de distribución y hábitos similares.

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INTRODUCTION

Depressed populations of fish species in general, and anadromous salmonids in particular, pose special challenges in terms of planning for their recovery and conservation. Their wide-ranging migration patterns and unique life histories take them across ecosystem and management boundaries in an increasingly fragmented world, which creates the need for analyses and strategies at similarly large scales. Recovery planning for any species must necessarily include scientific analyses of factors that limit, impair, or enhance recovery against a backdrop of management, policy, and societal realities. For Pacific salmon listed under the U.S. Endangered Species Act (ESA), the National Marine Fisheries Service (NMFS) is the federal agency that has been mandated to (1) identify the (groups of) populations whose status is threatened or endangered, and (2) to gather the scientific information that guides the policy decision process. However, clearly demarcating the boundary between the guidance and the decision can be a formidable task. In this article, we illustrate how science is being used to inform recovery planning for Pacific salmon in the western continental United States by presenting examples of scientific analyses that underpin recovery goals and strategies implemented by regional planning and local watershed groups. We believe that the suite of analytical tools and approaches that form the backbone of NMFS recovery planning for Pacific salmon provides a valuable model for efforts to recover and conserve other wide-ranging species.

THE CHALLENGE: THE PLIGHT OF PACIFIC SALMON

Seven species of anadromous Pacific salmon (*Oncorhynchus* spp.) occur in North America with geographic ranges occurring throughout the north Pacific from Russia, Japan, and Korea across to the west coast of the United States and Canada, from Alaska to southern California. Within the 6 species under its jurisdiction, NMFS/NOAA Fisheries has designated 52 evolutionarily significant units (ESUs; Waples 1991) of west coast Chinook salmon (*O. tshawytscha;* Myers et al. 1998), coho salmon (*O. kisutch;* Weitkamp et al. 1995), chum salmon (*O. keta;* Johnson et al. 1997), pink salmon (*O. gorbuscha;* Hard et al. 1996), sockeye salmon (*O. nerka;* Gustafson et al. 1997), and steelhead trout (*O. mykiss;* Busby et al. 1996). Half of the 52 ESUs are substantially reduced in abundance relative to historical levels (Good et al. 2005) and are listed as endangered or threatened under the ESA (Table 1). In addition, a large number of populations and some entire ESUs have been extirpated by the construction of impassable dams (NRC 1996, Gustafson et al. 2007). The genetic legacy of these populations and ESUs is largely lost, and most of these areas upstream of these dams continue to be inaccessible to anadromous salmonids. For the remaining extant populations, recent estimates of spawners generally range from < 1% to 76 % of historical abundance, and these estimates are considerably less when limited to natural-origin fish (Table 1). Recent extinction risk analyses estimate that 84% of the populations within ESA-listed Columbia River basin ESUs are not currently self-sustaining (McClure et al. 2003a). The scope of ESA listings is considerable, spanning almost every major freshwater ecosystem from the Sacramento River in California northward to the Canadian border (Schiewe and Kareiva 2000). Generally, ESU status is more imperiled in the southern regions and in the interiors of large watersheds such as the Sacramento-San Joaquin drainage and the Columbia River Basin (Good et al. 2005; Gustafson et al. 2007).

PACIFIC SALMON LIFE HISTORY

Pacific salmon are anadromous, migrating to the ocean as juveniles and back to freshwater as spawning adults. Consequently, they traverse environments and habitats in multiple ecosystems—open ocean, estuaries, rivers, and tributaries in coastal, montane, and desert habitats—and cover substantial geographical areas during their life cycle (reviewed in Groot and Margolis 1991). The freshwater phase of their life cycle, from eggs in the gravel to emergent fry and parr, occurs in lakes and streams up to thousands of kilometers from the sea. Considerable life history variation exists in the freshwater phase among and within species; Chinook salmon juve-

Table 1. Recovery planning domain, Endangered Species Act (ESA) listing status, and recent return levels of threatened (T) and endangered (E) Pacific salmon and steelhead evolutionarily significant units. Recent returns of total (wild and hatchery-origin) or natural-origin (wild) spawners are calculated as % of historic (ca. 1900) abundance estimates; ranges are from upper and lower estimates of historic abundance. Data were compiled by NMFS/NOAA fisheries for the Pacific Coast Salmon Research Fund (PCSRF 2005).

Recovery planning domain	Evolutionarily significant unit (ESA listing status)	Recent total returns (% of historic)	Recent wild returns (% of historic)
Puget Sound[a]	Ozette Lake sockeye (T)	13.1–17.5	6.6–8.8
	Puget Sound Chinook (T)	5.9 –7.9	3.0–4.0
	Hood Canal summer-run chum (T)	35.0–45.0	10.5–13.5
Upper Willamette River/ Lower Columbia River	Lower Columbia River Chinook (T)	5.7–7.5	2.8–3.8
	Upper Willamette River Chinook (T)	19.6 - 25.1	3.9–5.0
	Lower Columbia River coho (T)		
	Columbia River chum (T)	0.4–0.5	0.4–0.5
	Lower Columbia River steelhead (T)	2.5–3.2	1.7–2.2
	Upper Willamette River steelhead (T)	3.3–4.3	2.5–3.2
Interior Columbia River	Snake River sockeye (E)	0.1–0.2[c]	–
	Snake River fall-run Chinook (T)	1.6–2.0	0.6–0.8
	Snake River spring/summer-run Chinook (T)	4.0–5.2	0.8–1.0
	Upper Columbia River spring-run Chinook (E)	11.8–14.9	5.9–7.4
	Middle Columbia River steelhead (T)	19.2–24.4	13.4–17.1
	Snake River basin steelhead (T)	45.8–65.0	6.9–9.1
	Upper Columbia River steelhead (T)	59.5–76.5	11.9–15.3
Oregon Coast	Oregon Coast coho (T[b])	7.1– 9.3	6.7–8.8
Southern Oregon/Northern California Coasts	S. Oregon/N. California Coasts coho (T)	4.1–5.4	4.1–5.4[d]
North-Central California Coast	California Coastal Chinook (T)	–	5.2–6.8[e]
	Central California Coast coho (E)	no data	no data
	Northern California steelhead (T)	–	1.5–1.9[f]
	Central California Coast steelhead (T)	no data	no data
California Central Valley	Sacramento River winter-run Chinook (E)	–	2.8–3.6[d]
	Central Valley spring-run Chinook (T)	–	21.0– 27.0[d]
	California Central Valley steelhead (T)	–	0.1–0.2[d, f]
Southern California Coast	South Central California Coast steelhead (T)	no data	no data
	Southern California steelhead (E)	no data	no data

a NMFS listed Puget Sound steelhead as threatened under the U.S. Endangered Species Act on 11 May 2007.
b Proposed threatened
c All progeny from captive broodstock
d Natural-origin/hatchery-origin ratio unknown
e Dam counts of wild fish on South Fork Eel River (1938–1975) as proxy for ESU
f Dam counts of total fish at Red Bluff Diversion Dam as proxy for ESU

niles, for example, may spend one or more years in freshwater before heading to sea (stream type) or may move to the ocean in their first year (ocean type; Healey 1991; Brannon et al. 2004a). Juveniles then undergo a physiological transformation (smoltification) and undertake a seaward migration. At sea, individuals can traverse thousands of kilometers during extensive oceanic migrations, while others spend their entire ocean residence on the continental shelf. After a few months to several years, adult salmon return to the river where they were born, where most spawn and die (semelparous) and the cycle begins again, although many steelhead trout are iteroparous and, if they survive, can spawn multiple times (Groot and Margolis 1991).

During their peregrinations, Pacific salmon experience a variety of physical, chemical, and biological conditions that can affect their survival and productivity (Stouder et al. 1997), many of which have contributed to their decline and influence their recovery. The orthodox explanation for the depressed nature of their present status has focused on core anthropogenic factors—commercial and recreational harvest, habitat degradation, hatchery fish production, and hydropower operations. Intense harvest certainly reduced some salmon populations beginning as early as the late nineteenth century (NRC 1996). Habitat degradation in the form of urbanization, agricultural development, reduced water quality and quantity, and increased road density are associated with reductions in population productivity, adult densities, and early life-stage production for Chinook and coho salmon over large geographic areas (Paulsen and Fisher 2001; Pess et al. 2002). Hatchery programs may impact wild populations by increasing harvest rates in mixed-stock fisheries and imposing potential negative genetic and ecological interactions (Williams et al. 1999; but see Brannon et al. 2004b). Hydropower operations have dramatically altered the riverine environment and directly and indirectly reduced survival of juvenile salmon during their seaward migration and subsequent return of adults spawning upriver of dams (Schaller et al. 1999; Levin and Tolimieri 2001). In addition, density-dependent effects (Zabel et al. 2006); variability in ocean productivity (Mantua et al. 1997; Welch et al. 2000); climatic cycles such as the Pacific Decadal Oscillation (Hare and Francis 1995); predation by fish (Friesen and Ward 1999), marine mammals (NMFS 1997), and birds (Roby et al. 2003; Good et al. 2007); and interactions with non-indigenous species (Fresh 1997) influence survival and productivity of Pacific salmon. All of these factors vary across the landscape, and their impacts at the species, ESU, and life history levels reflect variation in the use of freshwater, estuarine, and marine ecosystems over the life cycle (NRC 1996; Ruckelshaus et al. 2002b). Such characteristics and circumstances pose significant challenges for scientists conducting research in support of conservation planning for wide-ranging Pacific salmon.

THE STRATEGY: LARGE-SCALE RECOVERY PLANNING FOR ESA-LISTED PACIFIC SALMON

In the course of navigating many environments over their life cycle, Pacific salmon cross a number of management boundaries. The international, federal, state, tribal, and local agencies responsible for managing Pacific salmon have overlapping jurisdictions and mandates with respect to recovery of threatened and endangered Pacific salmon. For salmon populations whose natal rivers are in the United States, NMFS is charged with recovery of those that are listed under the Endangered Species Act and is responsible for developing recovery plans (the U.S. Fish and Wildlife Service has jurisdiction over generally non-anadromous cutthroat trout *O. clarki* and bull trout *Salvelinus confluentus*, species whose spawning and juvenile rearing distributions often overlap with those of anadromous Pacific salmon, as well as over rainbow trout, the resident form of *O. mykiss*). The strategy of the recovery planning process has thus been to confront the large-scale biological and management challenges by incorporating of relevant scientific information at similarly large scales and involving co-managers from other federal, state, tribal, and local government agencies and other stakeholders (Boersma et al. 2001).

Recovery plans outline delisting criteria which, when achieved, would allow the NMFS to delist the ESU. Delisting criteria are based in part on scientific guidance on population and ESU viability and the likely impacts of actions in associated habitat, hatchery, harvest, and hydropower sectors. Final determinations of delisting criteria involve additional policy judgments of the acceptable risk of extinction and certainty in the effectiveness of actions aimed at promoting recovery (McElhany et al. 2000; Ruckelshaus and Darm 2006). In contrast, the Department of Fisheries and Oceans Canada (DFO) mandates a non-governmental scientific group (Committee on the Status of Endangered Wildlife in Canada [COSEWIC]) to conduct biological assessments of risk for Pacific salmon that are separate from the socioeconomic consequences of listing as part of a two-step process to list species under the Species at Risk Act (SARA). While this system could conceivably lead to more species being considered for listing, the formal segregation can result in species on a biological status list not being on the SARA legal list and receiving legal protection (Irvine et al. 2005). Species listed under SARA also require "recovery strategies" and "action plans" that describe threats, population objectives, and research and management objectives and that outline measures to implement the recovery strategy, respectively (Irvine et al. 2005). In this article, we focus on the scientific guidance part of these efforts in the continental United States, by illustrating the ways that scientific analyses are informing recovery planning for Pacific salmon under the ESA.

Recovery plans for threatened and endangered Pacific salmon within the continental United States are being developed in eight geographic regions or recovery planning domains, each of which has three to six ESA-listed salmon and steelhead ESUs (Figure 1). What constitutes recovery may vary among ESUs but will generally involve improvements in abundance, productivity, spatial distribution, and diversity of existing populations sufficient to recover their health and ensure their long-term sustainability. For each recovery-planning domain, an interdisciplinary Technical Recovery Team (TRT) is composed of technical experts in salmon biology, population dynamics, conservation biology, ecology, and conservation planning. These experts come from inside and outside of NMFS and are appointed by NMFS via a nomination process. The TRT is charged with developing biologically-based delisting criteria and providing technical guidance for recovery of all ESUs within its domain, specifically (1) identifying conservation units appropriate to the stated conservation goals (Ruckelshaus et al. 2002a), (2) defining viability criteria for salmonid populations and ESUs (McElhany et al. 2000), and (3) identifying likely consequences of alternative actions proposed for achieving recovery (e.g., Beechie et al. 2003a). Below, we provide examples of the breadth of analyses conducted by federal, state, and tribal scientists that form the scientific backbone for the recovery plans being developed for Pacific salmon.

ESTIMATING STATUS OF ESUS AND POPULATIONS

The first step in recovery planning is assessing the present status of the species. For Pacific salmon, assessments of the relative status of ESUs and the populations which comprise each of them are necessary to prioritize populations for recovery and conservation actions (Allendorf et al. 1997). As Pacific salmon spend part of their life cycle ranging throughout the north Pacific Ocean, identifying population units associated with their freshwater spawning areas is very important for conservation planning. For Pacific salmon, NMFS defined an independent population following Ricker's (1972) definition of a stock. In the context of viable salmonid populations, "not interbreeding to a substantial degree" means that two groups are considered independent populations if they are isolated to such an extent that exchanges of individuals (i.e., migration among populations) do not substantially affect their population dynamics or extinction risk over a 100-year time period (McElhany et al. 2000). For extant populations, one can examine extinction risks from intrinsic factors such as demographic, genetic, or local environmental stochasticity; defined populations can be used for modeling extinction risk and identifying recovery strategies at the appropriate scale (McElhany et al. 2000).

The TRTs have identified demographically independent populations for Pacific salmon ESUs based on a variety of geographical, ecological, genetic, and life history data. Within an ESU, the number of independent populations ranges from 1 to 30. For example, the Lower Columbia and Upper Willamette River TRT identified 17 historical winter-run steelhead populations based upon information on run-timing, passage barriers, and genetics (Figure 2). A similar process for population identification has been conducted for Chinook salmon, chum salmon, coho salmon, and steelhead ESUs in recovery team domains in the Lower Columbia and Upper Willamette rivers (Myers et al. 2006), Puget Sound (Ruckelshaus et al. 2006), the interior Columbia River basin (McClure et al. 2003b), the Oregon coast (Lawson et al. 2004), the southern Oregon/northern California coasts (Williams et al. 2006), north-central California coast (Bjorkstedt et al. 2005), the central valley of California (Lindley et al. 2004, 2006), and the south-central/southern California coast (Boughton et al. 2006).

DESIGNING VIABILITY CRITERIA

Population viability

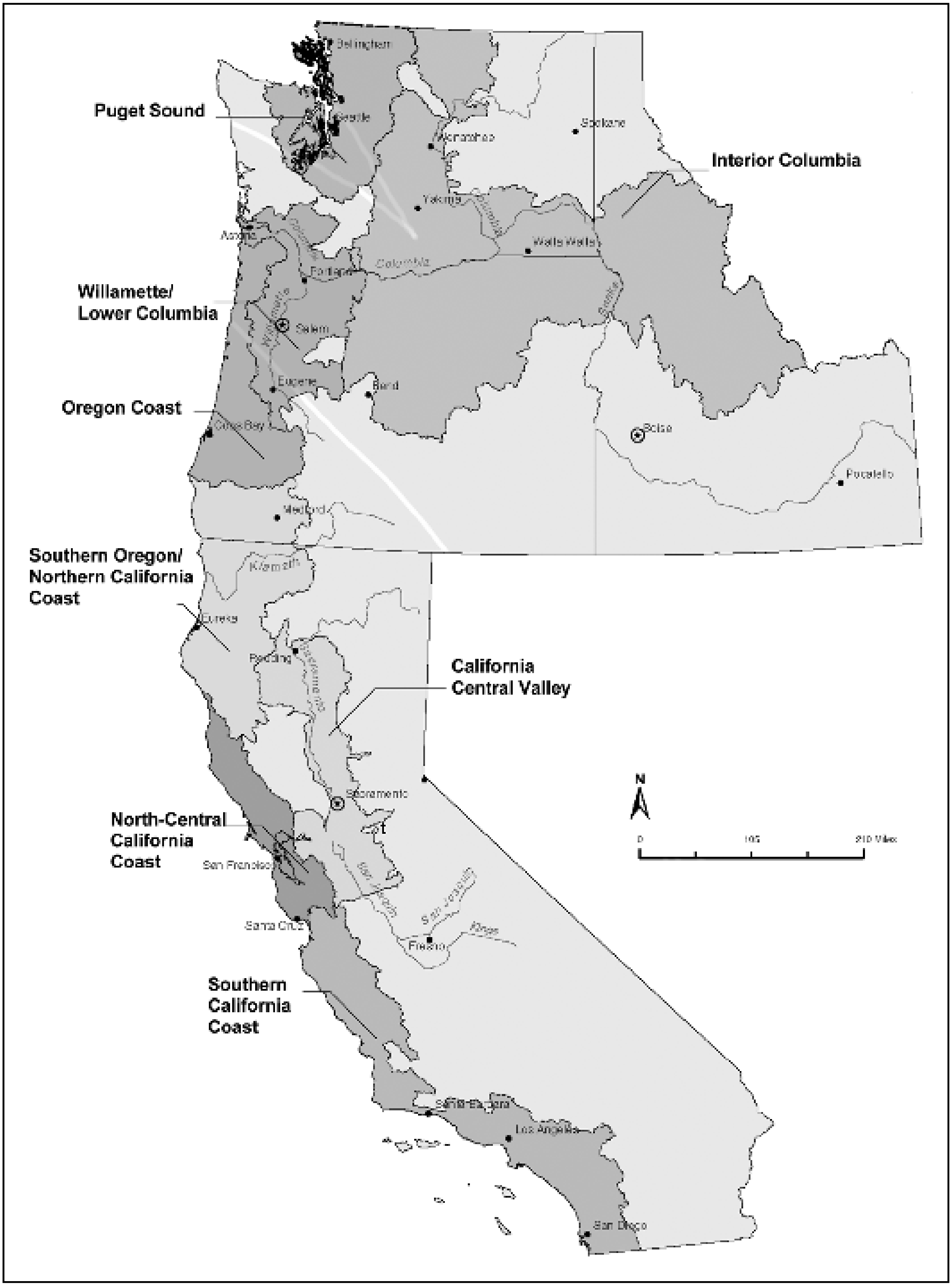
For Pacific salmon, criteria for viable salmonid populations (VSP) are based upon measures of population characteristics that reasonably predict extinction risk and reflect processes important to populations: (1) abundance, (2) productivity, (3) diversity, and (4) spatial structure (McElhany et al. 2000). Abundance is critical as small populations are generally at greater risk of extinction than large populations. Stage-specific or lifetime productivity (i.e., population growth rate) provides information on important demographic processes. Abundance and productivity data are used to assess the status of populations of threatened and endangered ESUs (Good et al. 2005). Genotypic and phenotypic diversity are important in that they allow species/ESUs to use a wide array of environments, respond to short-term changes in the environment, and survive long-term environmental change. Spatial structure reflects how abundance is distributed among available or potentially available habitats and how it can affect overall extinction risk and evolutionary processes that may alter a population's ability to respond to environmental change. For the purposes of estimating risk for Pacific salmon populations, NMFS considers a 95% probability of persistence in 100 years as their basic definition of viability. The TRTs also included a range of persistence probabilities (e.g., from 50–99%) in their population viability analyses to show how different levels of acceptable population risk change abundance and productivity requirements for populations (Ruckelshaus et al. 2002a; Cooney et al. 2005; McElhany et al. 2006).

ESU viability

Viability criteria for Pacific salmon ESUs rely on determining how many and which populations need to be at a particular status for the ESU as a whole to have an acceptably low extinction risk. In general, an assessment of an ESU as being viable will be more likely if it contains multiple populations (metapopulations), some of which meet viability criteria. Viability of the ESU is also more likely if: populations are geographically widespread but some are close enough together to facilitate connectivity, populations do not all share common catastrophic risks, and populations display diverse life-histories and phenotypes (McElhany et al. 2000). Establishing conservation priorities among populations within an ESU may involve difficult decisions about which life history traits should have primacy in the prioritization process, and, in extreme cases, deciding whether some populations play redundant roles in ESU viability (Ruckelshaus et al. 2004).

Demographic models alone do not capture the likely buffering effects of life history and genetic diversity among populations on ESU persistence. Thus, ESU-level diversity concerns have been incorporated by stratifying ESUs into historical diversity groups that need protection. One way to estimate major diversity groups that have been lost due to population extinction is to relate salmon diversity to environmental characteristics. For example, life history traits of Puget Sound Chinook salmon are correlated with hydrologic regime; "stream-type" fish, which spend one or more years as juveniles in freshwater and perform extensive offshore oceanic migrations, are associated with a snowmelt-dominated hydrograph (Beechie et al. 2006a; Figure 3). Spawning areas with this hydrograph pattern are confined to upper reaches of main river basins, where mean elevation is high and most winter precipitation is stored as snow until spring. However, as dams block access to many historical high-elevation spawning grounds, extant stream-type populations are currently restricted to a small area of northeastern Puget Sound. The conservation-planning implications of this are two-fold. First, these remaining stream-type populations are now recognized in the recovery planning process as hav-

Figure 1. Recovery planning domains for Pacific salmon ESUs in Washington, Oregon, Idaho, and California.

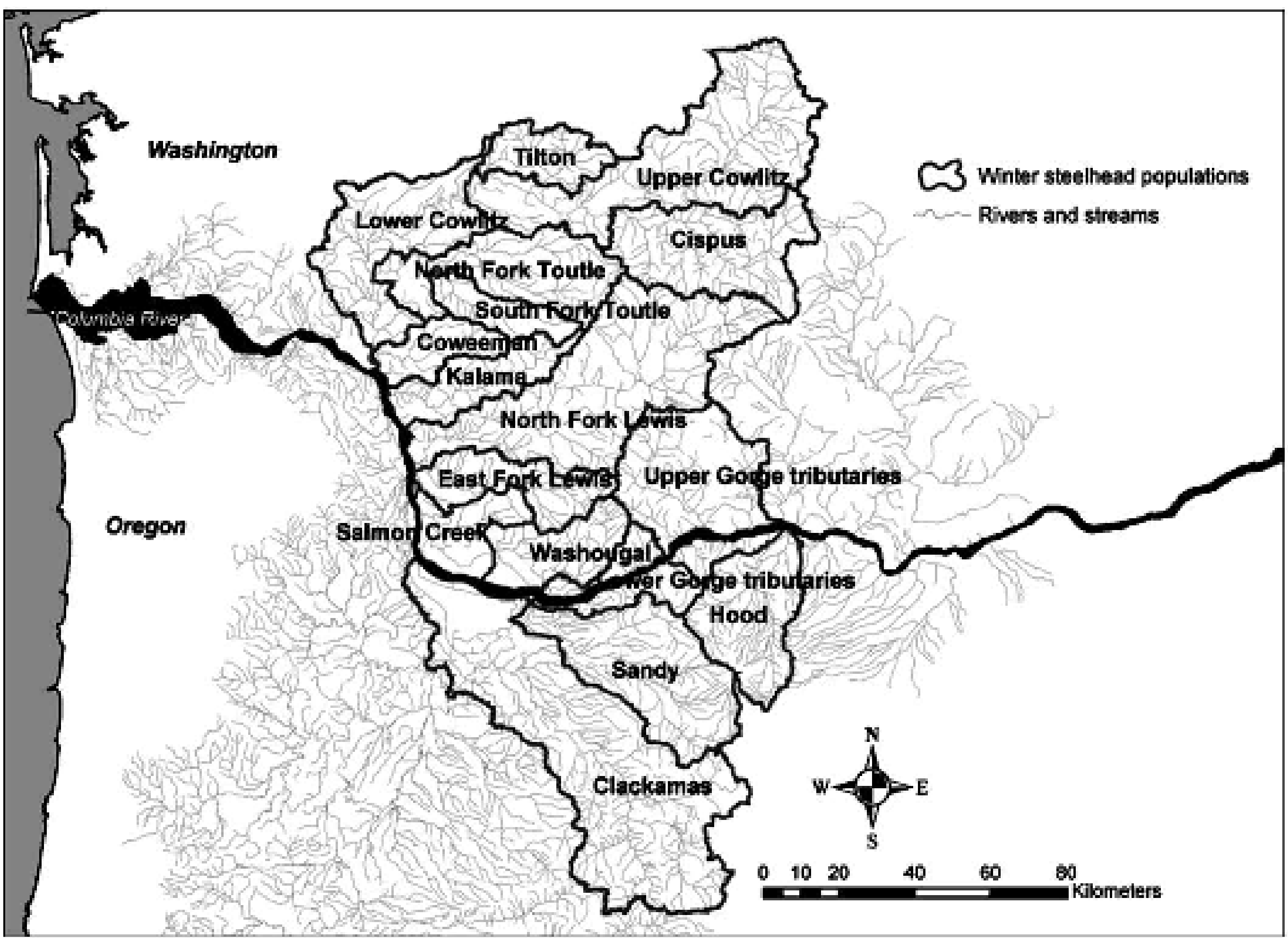


ing considerable conservation value and being at relatively high risk owing to their proximity to each other. Second, restoring stream-type populations to other snowmelt rivers in which they historically occurred is a desirable conservation goal. Such a goal appears to be feasible, as ocean-type populations likely retain a genetic composition that allows rapid re-emergence of the stream-type form (Waples et al. 2004), and Chinook salmon life history traits can diverge rapidly in transplanted populations (Unwin et al. 2000). Still, efforts to re-establish Chinook salmon populations where they have previously been extirpated are relatively recent, and some caution must be maintained relative to the potential for success of such projects.

Incorporating the spatial structure of populations is also important to designing ESU viability criteria. In particular, the collection of extant, healthy populations within an ESU ought to be spatially arranged to buffer against catastrophic losses (> 50% mortality in one year; Reed et al. 2003) due to natural disasters or anthropogenic events. Formal consideration of catastrophic losses has led to innovative recovery strategies for the southern sea otter and the short-tailed albatross (Ralls et al. 1996; USFWS 2005). The potential impacts of catastrophic events can be incorporated into the recovery planning process by assessing catastrophic risk levels among populations and spreading risks spatially among populations and life history types.

The relative risks from catastrophic events were summarized for populations of Puget Sound Chinook salmon by combining available spatial information on various events (e.g., landslides) with salmon spawning, rearing, and migratory habitat (Figure 4). Combined assessments for eight natural and anthropogenic catastrophic risks were spatially correlated; that is, overall risk scores were more similar within geographic regions than among geographic regions. More importantly, analyses tested spatial arrangements of populations recommended by the Puget Sound TRT for ESU viability. Risk scores for population combinations selected according to recommendations (≥ 2 viable populations from each of 5 geographic regions, including "early-run" and "late-run" Chinook life histories where possible) were lower on average than combinations of 10 populations selected at random (Good et al. in press). The strategy of spreading the risk implicit in the TRT recommendations simultaneously minimized risk of catastrophic loss and maximized representation of the less common "early-run" life history type. Similar assessments of natural and anthropogenic catastrophic risks for ESUs

Figure 2. Demographically independent populations of the Lower Columbia River steelhead evolutionarily significant unit (ESU) within the Willamette/Lower Columbia rivers recovery domain (from Myers et al. 2006). The 17 historical winter populations were delineated based on geography, migration fidelity, genetic attributes, life history patterns and morphological characteristics, population dynamics, and environmental and habitat characteristics.

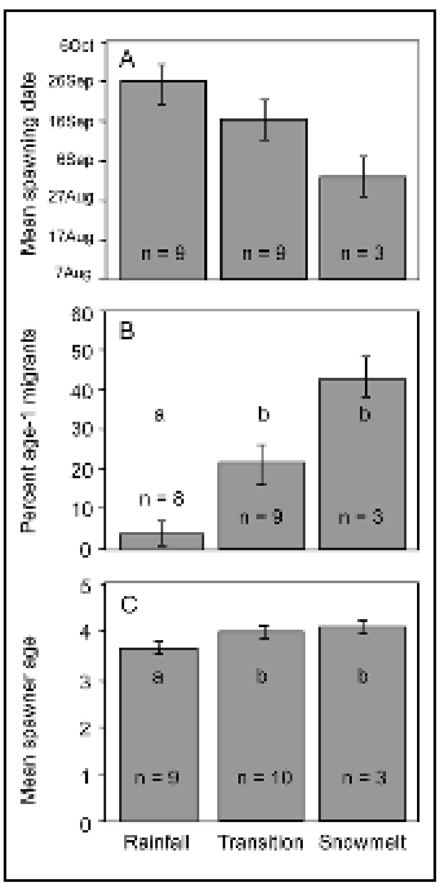


in the Willamette and lower Columbia rivers (Good and Fabbri 2003) were used to determine the number and identity of population/life history combinations necessary to spread risk and promote ESU-level viability (McElhany et al. 2003). Such approaches formalize the incorporation of spatial structure and diversity into recovery planning for Pacific salmon.

Identifying consequences of recovery actions

Wide-ranging species such as Pacific salmon pose a particular challenge to identifying recovery actions. There are many places in their life cycle where threats occur, and identifying the stage(s) where an improvement in survival can be most effective at increasing population viability can be difficult. Two main analytical approaches to this dilemma have been employed for Pacific salmon: broad-scale threats analyses and life-cycle modeling. Analyses of the relative magnitude and distribution of threats to Pacific salmon throughout their entire geographic range can be illuminated using statistical models (Hoekstra et al. in press). Analyses performed at a regional scale to identify where habitat-forming processes (e.g., sediment supply rates, riparian growth, stream temperature and flow regimes) are impaired provide information over large geographic areas that guide the scale and location of recovery actions (Beechie and Bolton 1999; Beechie et al. 2003a). Life cycle models inform prioritization of actions, helping to identify which parts of the life cycle are most affected by limiting factors (e.g., habitat impairment). Both types of analyses can be conducted at coarse scales to focus on geographic areas and types of habitat problems that warrant further analysis or at smaller spatial scales (e.g., within populations or watersheds), where more detailed data can identify and prioritize site-specific restoration actions (Steel et al. 2003).

Figure 3. Mean (+1 SE) life history phenotypes of Chinook salmon populations spawning in rivers with rainfall-dominated, snowmelt-dominated, or transitional hydrograph patterns:
A—Mean date of spawning.
B—Percent of smolts age 1+.
C—Mean age of spawners.
Where the main effect of hydrograph type was significant at $\alpha = 0.05$, different letters indicate significant pairwise differences between groups based on Tukey tests for multiple comparisons (adapted from Beechie et al. 2006a). Sample sizes are given within bars.



Broad-scale habitat analyses

In the interior Columbia River basin, where seven salmon and steelhead ESUs are listed as threatened or endangered, broad-scale analyses of habitat-forming processes have shown patterns of change in process rates (e.g., supply of sediment, stream discharge) or their controlling factors (e.g., riparian conditions; McClure et al. 2004). Process rate patterns, which are mainly a function of topography, soil type, vegetation cover, and land uses, illustrate the relative degree of human impact on processes. This process-based approach, by recognizing natural spatial variation in processes that form and sustain aquatic ecosystems (i.e., that the historical template of Pacific salmon habitat is not uniform throughout their range), explicitly identifies causes of habitat change. The analyses illustrate where specific land uses have altered habitat-forming processes across the landscape and where and what types of restoration actions are needed for sustainable recovery of salmon habitats. Site-specific actions are identified through field inventories (e.g., restoring riparian function along a single reach; Beechie et al. 2003b); however, the broad-scale analyses help to target these field inventories to areas where specific types of habitat degradation are most likely to have occurred and identify areas with significant opportunities for habitat improvement (Figure 5). Currently, recovery plans for interior Columbia basin ESUs are being developed considering both local information for site-specific actions, and broad-scale analyses to develop ESU-scale recovery scenarios.

Understanding where Pacific salmon occurred historically across the landscape, but have become extinct, is also useful for prioritizing potential restoration projects. Broad-scale analyses of the intrinsic potential of salmon habitat have been conducted for adult spawning and juvenile rearing for interior Columbia River basin and Puget Sound ESUs. The analyses rely on field-based information that associates landscape characteristics such as stream gradient, width, and land cover with spawner or juvenile density; the relationships are then extrapolated to stream reaches that have not been surveyed for salmon and steelhead or that are currently inaccessible (Cooney and Holzer 2004) and used to identify and prioritize habitat areas for conservation actions. For example, in the upper Yakima River basin, nearly 500 stream km (56% of the historically accessible streams) are accessible to anadromous fishes, but access to areas with habitat most suitable for steelhead spawning is almost entirely blocked, leaving only relatively low-suitability mainstem areas available for spawning and rearing. In Puget Sound watersheds, broad-scale assessments of stream channel characteristics revealed landscape-scale changes from anthropogenic barriers and changes in riparian condition (Davies et al. 2007), changes which have reduced the adult spawning and juvenile rearing potential in most watersheds supporting Puget Sound Chinook salmon. Intrinsic potential analyses highlight how important it is for Pacific salmon to have access to areas of naturally high suitability (McClure et al. 2004). These analyses have helped conservation planners set protection and restoration goals, develop recovery strategies to address impairments to population-level spatial structure and diversity in the interior Columbia River basin (e.g., Oregon Mid-Columbia steelhead draft recovery plan; www.dfw.state.or.us/fish/esa/mid-columbia), and evaluate land-use restoration and protection scenarios in Puget Sound watersheds (Bartz et al. 2006; Scheuerell et al. 2006).

Life-cycle modeling

The potential significance of specific recovery actions to populations can be evaluated by exploring the potential effects of the recovery actions in a life-cycle context. This is particularly important for populations and ESUs that are experiencing impacts other than habitat degradation. Such analyses can evaluate the relative importance of varying recovery actions at the scale of ESUs, or they may more closely examine the effect of specific recovery strategies at the scale of populations. In the simplest cases, considering overall population productivity allows the effect of a change in survival at one life stage to be evaluated in the context of overall viability. Detailed life cycle modeling can estimate the effects under more stringent conditions or identify portions of the life cycle where improvements to Pacific salmon survival or population capacity might have the greatest impact on population status.

One of the primary uses of life-cycle modeling is to assess the effect of estimated survival improvements at a single life stage in the context of overall population productivity (or growth rate, λ), which is essential to assessing population viability and predicting extinction risk. Calculating population growth rate in an annualized manner provides a standard metric for comparison between conservation units such as species or ESUs and for comparing likely outcomes of various management strategies. The methods used to derive λ have been developed for data sets with high sampling error and age-structure cycles (Holmes 2001), extensively tested using simulations for threatened/endangered populations and low-risk stocks (Holmes 2004), and cross-validated with time series data (Holmes and Fagan 2002).

At the scale of ESUs, this general methodology has been used to compare how various recovery actions will likely improve the status of listed Pacific salmon in the Columbia River (McClure et al. 2003a). The modeling analyses suggested that improvements to the federal Columbia River hydropower system aimed at increasing migration survival for juvenile and adult fish would not, for most ESUs, increase population growth rate enough to reverse current declines. Similarly reducing current harvest rates alone was also insufficient alone to reverse declines for most ESUs. Importantly, for some ESUs, harvest rates have already been reduced dramatically (e.g., to 2–8% for Snake River spring/summer Chinook salmon); thus, eliminating current harvest provides relatively small improvements. In contrast, for a few ESUs subject to both ocean and in-river harvest, such as the Upper Willamette Chinook salmon ESU and the Snake River fall Chinook salmon ESU, elimination of harvest could substantially reduce declines.

Similar life-cycle modeling has explored the impact of avian predators in the Columbia River. Predation on outmigrating juveniles of Pacific salmon by Caspian terns (*Sterna caspia*) nesting in the Columbia River estuary was significant enough that reducing or eliminating predation from the largest tern colony in the Pacific Northwest had the potential to increase population growth rate of threatened and endangered steelhead ESUs in the Columbia River basin (Good et al. 2007). These analyses were considered in the course of drafting an environmental impact statement charged with managing the level of Caspian tern predation on Pacific salmon in the Columbia River basin.

These analyses point to the need for a multi-faceted approach to recovery-planning particular to each ESU. This approach would incorporate improvements from a variety of sectors rather than relying on a single action or type of action considered generally applicable to recovering all threatened ESUs. This approach would also require consideration of survival and/or productivity across all life stages, although efforts may be constrained by limited data on connections between population growth rate and potential management actions across the landscape.

For individual populations or ESUs, such models have been employed to explore the demographic effects of reducing mortality at different life stages for Snake River spring/summer Chinook salmon. Density-independent, deterministic matrix modeling has suggested that significant increases in survival during in-river migration of either adults or juveniles were not likely to reverse the decline of that ESU toward extinction (Kareiva et al. 2000). Instead, this analysis, as well as that of Wilson (2003) suggested that modest reductions in first-year mortality or estuarine mortality had the potential to reverse current population declines. This approach does have limits, as it treats all habitats as if they have experienced the same degree of degradation and assumes that all habitats are equally restorable. More recent efforts at stochastic matrix modeling include density-dependence in the early freshwater life stage (Zabel et al. 2006). This and similar models evaluated whether increases in freshwater survival required under the Federal Columbia River Power System Biological Opinion (NMFS 2004) were consistent with realistic freshwater survival rates (McClure et al. 2004). In all cases, information gaps challenge modeling efforts in conservation planning, but advances in modeling should improve on their heuristic value by achieving more biological realism.

Also at the scale of individual populations, models that simultaneously incorporate multiple factors—habitat attributes, hatchery operations, and harvest management—have also been developed for Pacific salmon conservation planning. The SHIRAZ model relies on a set of user-defined relationships among habitat attributes, fish productivity, and carrying capacity to evaluate population performance across space and time (Scheuerell et al. 2006). This model was applied to two populations of the threatened Puget Sound Chinook salmon ESU in the Snohomish River basin in Washington. By incorporating hatchery and harvest management data, the analyses translated proposed actions (land-use restoration and protection) throughout the river basin into projected improvements in Chinook salmon abundance, productivity, spatial structure, and life history diversity (Bartz et al. 2006; Scheuerell et al. 2006). This model framework was instrumental in helping a multi-stakeholder recovery planning group in the Snohomish Basin craft and compare conservation alternatives for its Chinook salmon recovery plan. Subsequent analyses on the success of alternative restoration strategies suggest that the approach adopted by the watershed will help somewhat in mitigating against negative impacts of future climate changes. These results were also used to bolster the adoption of the recovery strategy by the watershed council (Battin et al. 2007).

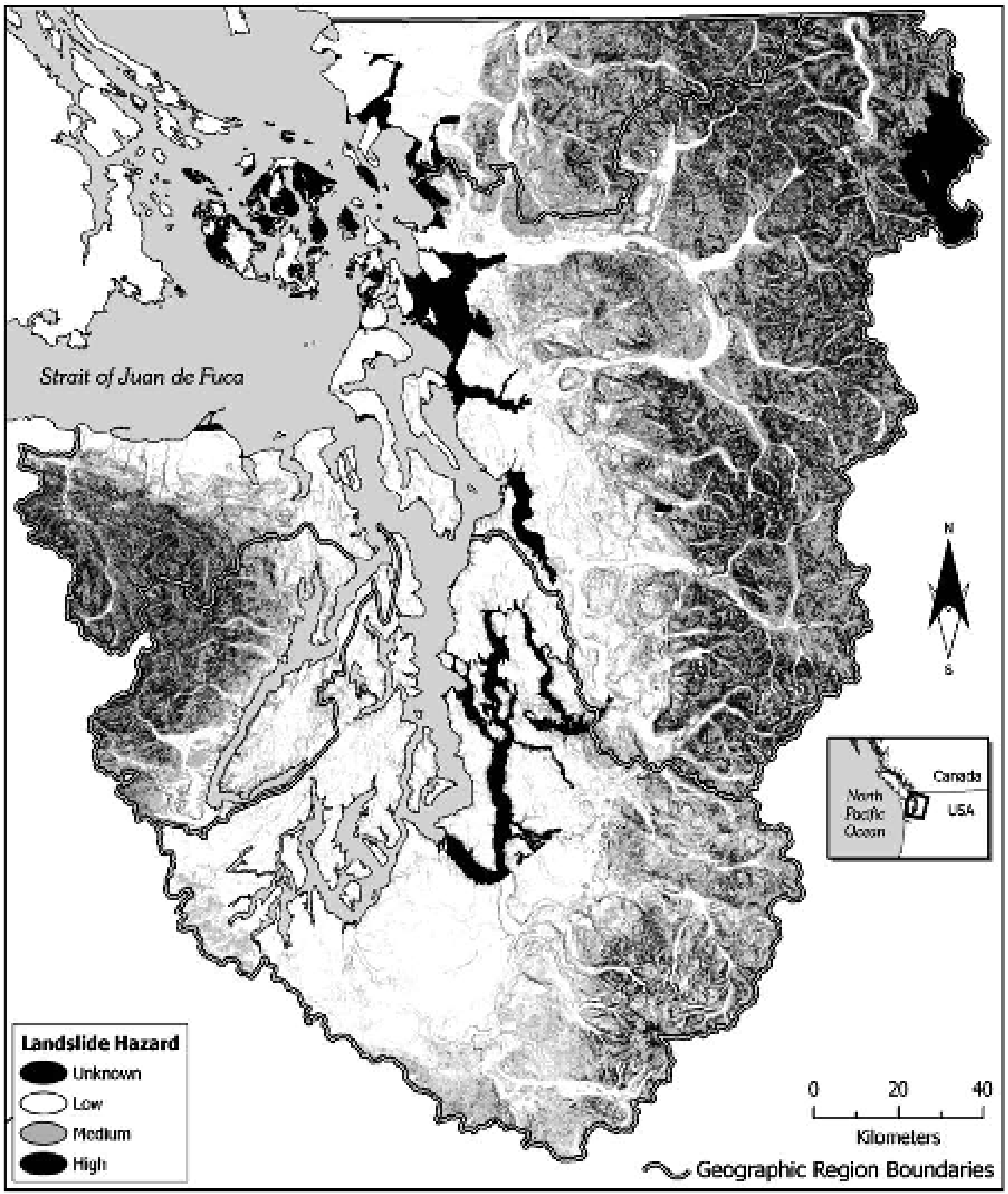
Each of these analyses involves considerable uncertainty in both model form and model parameters. This uncertainty has been addressed in two ways: (1) use of sensitivity analyses that assess how altered model form might influence model results, and (2) use of analyses that evaluate how parameter uncertainty alters model results. In the first approach, Greene and Beechie (2004) showed that choosing among models incorporating density-independent mortality, density-dependent mortality, and density-dependent movement between habitats can alter conclusions about which components of the salmon life cycle are limiting. That is, one model form predicted that spawning habitat constrains salmon recovery, a second model form suggested that in-river rearing habitats were the bottleneck, and the third model suggested that a combination of river and estuarine rearing habitats were most important to restore. While the third model form was deemed most realistic and guided managers toward restoring rearing habitats, the model comparisons also instilled caution and suggested that bet-hedging strategies be used.

The second approach to evaluating uncertainty uses a Monte Carlo approach to illustrate the combined effect of multiple parameter uncertainties on model results. For example, Beechie et al. (2006**a**) showed that incorporating parameter uncertainty into predictions of present-day spawning habitat capacity for Puget Sound Chinook populations produces estimates that range over four orders of magnitude. Nevertheless, there was virtually no overlap of distributions of spawner capacity estimates with current spawner population sizes, suggesting that spawning habitat is not a likely constraint on recovery of these populations. Such models help understand the feasibility of specific restoration options suggested by sensitivity analyses, and can help narrow the range of options that managers must consider in recovery planning.

CONCLUSIONS

Scientific analyses for Pacific salmon populations continue in the TRTs throughout the Pacific Northwest. These teams are completing initial tasks, such as population identification and risk analysis, and recommendation of viability targets for threatened and endangered ESUs in their domains. The TRTs have moved on to analyses of the cumulative effects of multiple factors over large spatial scales, employing metapopulation models where possible, and fostering the use of large-scale experimentation to manipulate or

Figure 4. (A) Landslide hazard in the watersheds of Puget Sound and (B) quartile ranks of the relative risk (% of population area under high and

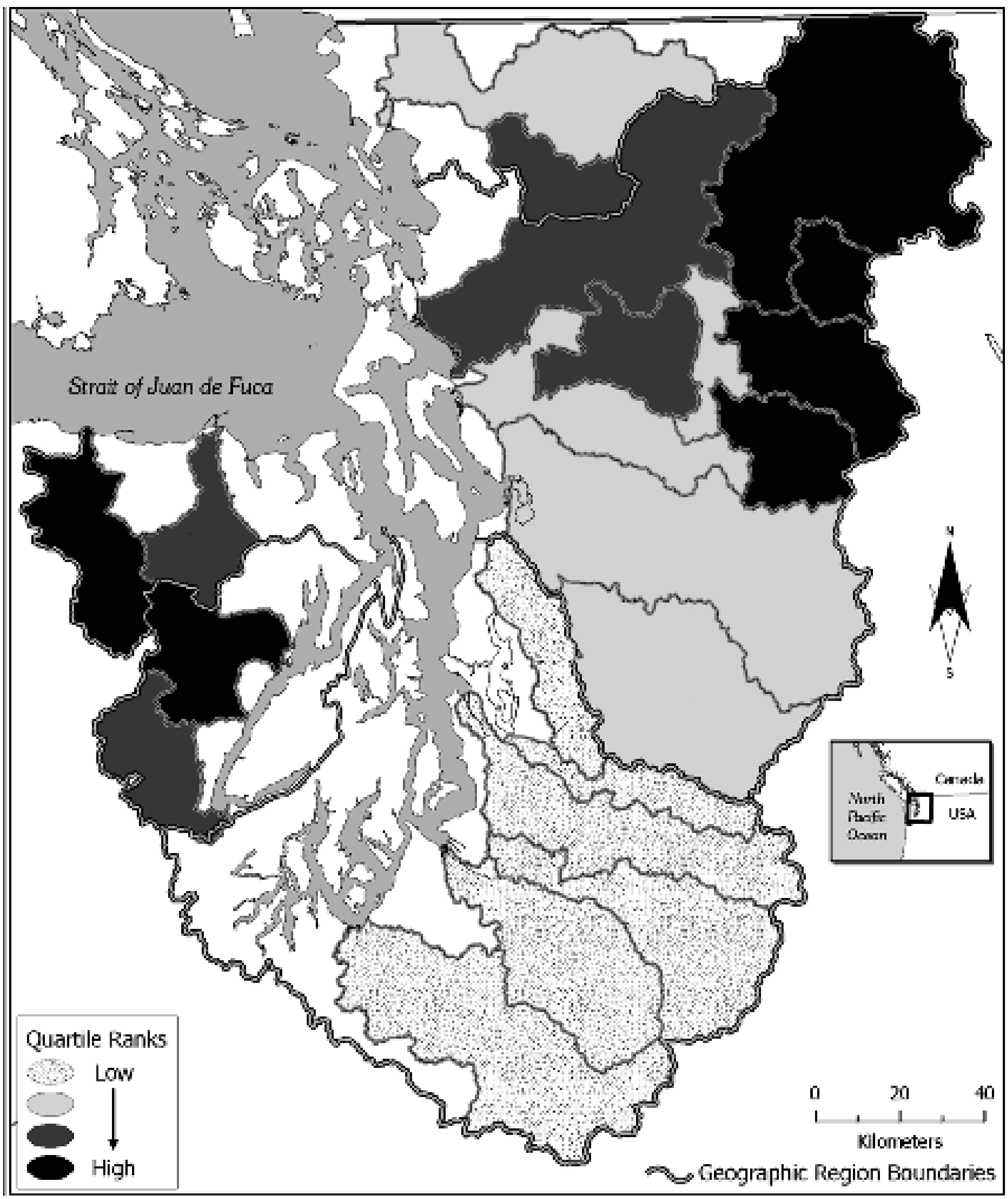


take advantage of natural variation in ecological factors in the impact of hatchery fish, in harvest effects, and in the influence of non-indigenous species. Scenario analyses have shown promise in addressing global issues (Bennett et al. 2003) and are also being investigated as a way to make predictions about alternative sets of actions whose combined effects will suffice to recover the listed Pacific salmon ESUs (Steel et al. 2003; Battin et al. 2007). Simulation models have been used to explore different assumptions about the environment and their influence on Pacific salmon (ISAB 2001), and scenarios for salmon recovery consider variability in oceanic and freshwater conditions and technical solutions to severe anthropogenic factors with deleterious effects (e.g., changes in hatchery management, changes in dam engineering and management, stream restoration actions, and selective harvest) and environmental variability. In the future, scenario analyses could help inform decision makers by explicitly illuminating trade-offs between economics and ecology or social values and biology.

The general challenges of conservation planning for Pacific salmon are twofold: (1) to identify and cope with the suite of biological/environmental factors that vary across the landscape and (2) to navigate the management boundaries and mandates of resource agencies charged with conserving these icons of the Pacific Northwest. The recovery planning approach being enacted for ESA-listed Pacific salmon endeavors to illuminate the consequences of alternative management strategies, in the face of both ecological and political uncertainties, by (1) incorporating analyses of landscape-scale processes with the effects of local recovery actions throughout the life cycle, and (2) incorporating federal, state, tribal agencies, and local government and watershed groups in both the technical and policy stages of recovery planning.

These strategies have been outlined by the Shared Strategy of Puget Sound in their Puget Sound salmon recovery plan (Shared Strategy 2007). This groundbreaking collaborative effort to protect and restore salmon runs across Puget Sound engaged local citizens, tribes, technical experts and policy makers in recovery planning endorsed by the people living and working in the watersheds of Puget Sound. The Shared Strategy group (1) identified what should be in a recovery plan and assessed how current efforts can support the plan, (2) set recovery targets and ranges for each watershed, (3) identified actions needed at the watershed level to meet targets, (4) determined if identified actions add up to recovery (and if

medium hazard probability) among the 22 populations of the Puget Sound Chinook salmon evolutionarily significant unit (ESU) (Good et al. in press).



not, identified needed adjustments), and (5) finalized the plan, actions and commitments necessary for successful implementation. The recovery plan developed by Shared Strategy was officially adopted by NMFS/NOAA Fisheries in January of 2007. Similar efforts will ultimately result in recovery plans for more than two dozen endangered and threatened Pacific salmon in the Pacific Northwest and may be a model for recovery planning for other wide-ranging taxa. Our effectiveness at developing and implementing these plans ultimately will be reflected in the status of the region's salmon for many decades into the future.

ACKNOWLEDGMENTS

We thank the members of the regional Technical Recovery Teams (Puget Sound, Willamette-Lower Columbia, Interior Columbia Basin, Oregon/Northern California Coast, North-Central California Coast, South-Central California Coast, and California Central Valley). We are indebted to J. Hard, M. Scheuerell, and A. Steel for helpful comments on the manuscript, which was spawned by a 2003 Society for Conservation Biology symposium, entitled "Conservation Planning for Wide-ranging Species."

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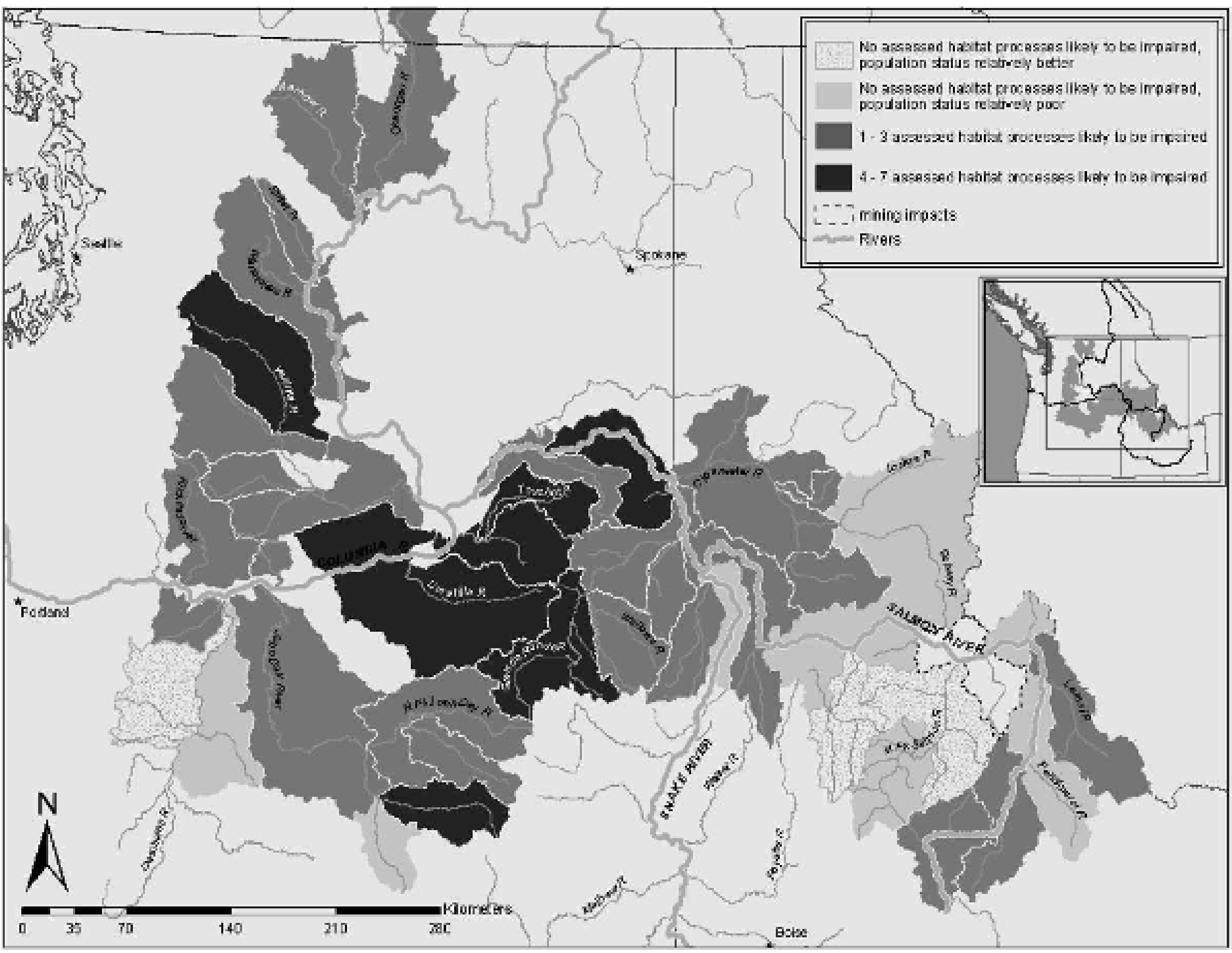
Figure 5. Steelhead populations in the interior Columbia River basin recovery domain categorized by likelihood of impairment to one or more habitat conditions: instream flow, diversion entrainment, riparian condition, floodplain condition, water quality (toxics), mass wasting, and fine sedimentation. Darker colors indicate more factors are likely impaired. Impairment was defined as the relative change from historic conditions in each factor; populations within the top 30% of this range were considered impaired (MM, unpublished data). Population status was determined by evaluating current abundance, long-term and short-term trends in abundance, and current vs. likely historical distributions (in space and across ecoregional boundaries). All but one of the populations (NF John Day) showed some impairment in at least one of these traits. Those that are noted as being in relatively better condition showed impairment only in abundance or trend; those in relatively poor condition were impaired in abundance, trend and some aspect of distribution.



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