

THE PACIFIC SALMON WARS: What Science Brings to the Challenge of Recovering Species

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■ **Abstract** Politicians, scientists, government agencies, and the public are all engaged in recovery planning for Pacific salmon. In order for science to fulfill its potential in the arena of salmon recovery planning, several shortcomings of the science and its application to decision-making must be rectified. The definition of conservation units using genetic and phylogenetic inference needs to be sharpened. Ecological analyses must get beyond casting blame for past declines in salmon numbers and examine mixed strategies of management that consider interactions between hatcheries, harvest, hydropower, and habitat factors as well as background natural stresses and invasive species. Glib acceptance of expert opinion and extrapolated or inferred data should be tempered. To deal with uncertainty, recovery teams should engage in scenario analyses in which a wide variety of assumptions are played out. Finally, there is a pressing need for analyses aimed at determining what circumstances and communication strategies give science an effective voice in decision-making.

INTRODUCTION

As increasing numbers of species become threatened with extinction, ecologists and evolutionary biologists continue to devise strategies to rebuild depleted populations. Although scientists sometimes forget this point, it is not their job to recommend a recovery strategy to policy-makers. Rather, the job of science is to make clear the biological targets that constitute recovery and the biological consequences of different suites of actions (or inaction) aimed at recovering threatened and endangered species. The actual recovery policy adopted by public agencies will inevitably balance biological consequences with social, political, and economic values. Biological science cannot and should not have any special place in determining how biological value is traded off against an economic or social concern.

However, science can and should be the preeminent voice in describing targets and anticipating the likely ecological consequences of alternative management actions. In other words, science cannot make policy, but it can illuminate the consequences of policy for threatened and endangered species. Unfortunately, science often fails to play this idealized role of making clear the consequences of alternatives. In turn, the failure of many high-profile conservation-planning decisions to adequately incorporate ecology and evolutionary biology is partly due to the inadequate light shed by science on the consequences of decisions. In this paper, we offer an illustration of how science—the collection of biological information and translation of that information into useful forms—can be used fruitfully to inform conservation planning for Pacific salmon. Our experience with salmon illustrates both the impediments to and opportunities for incorporating biological criteria into recovery decisions.

First, it is important to emphasize that Pacific salmon are of enormous economic, cultural, and social value, and the extinction of any Pacific salmon species would be viewed as a tragedy by the public (Smith 1979, Beckham 1977, Brown 1983, Cone 1995, Lichatowich 1999, Connelly 2001, Frank 2002). Part of the fascination with salmon can be traced to their remarkable anadromous life history. The spectacular journeys of spring-run chinook and sockeye in the Snake River Basin—traveling thousands of kilometers to the ocean and back to small headwater streams and lakes in Idaho—have captured the imagination of Native Americans for centuries. More recently, local disappearances and declines in salmon populations have become fodder for the campaign speeches of politicians, who promise that these species will not vanish on their watch. Fortunately, compared to the state of other highly visible species in decline, most species of Pacific salmon are at a relatively low risk of immediate extinction. Because Pacific salmon are still abundant in places, and are unlikely to be rapidly extirpated, we have a unique opportunity to use science thoughtfully to design recovery strategies that include multiple options instead of last ditch efforts that often typify endangered species management (Gore 1992, NRC 1995, Doremus 2000).

There have been many reviews of salmon ecology, evolutionary biology, and even salmon management (e.g., Cone & Ridlington 1996, NRC 1996, Lichatowich 1999, ISG 1999). Here we adopt a different tack. We examine the role science plays in shaping recovery planning and highlight where science can be useful, and where it has not been as effective. By focusing on the role of science in salmon recovery, we hope to provide warnings and lessons that may help in future attempts to recover species using the best available science.

Conservation planning for salmon in the western United States is especially high-profile because nearly everything people do in the Pacific Northwest affects salmon in some way. Consequently, the potential remedies for the salmon problem have huge implications for the ways people extract water, develop industrial, commercial and private properties, generate electricity, transport goods, harvest fish, and conduct their daily lives. A benefit of the high stakes of salmon recovery is that scientists have a willing audience: politicians and decision-makers are eager

for biological advice about how best to proceed in recovering salmon populations. Our charge as scientists is to respond to the intense pressure for biologically defensible answers in a way that clearly distinguishes scientific conclusions from policy choices. Recent crises in the public's confidence in biologists to contribute to policy decisions affecting high-profile species such as Canada lynx and grizzly bear (Mapes 2001, Boyle 2002, Dalton 2002, Mills 2002, *Seattle Times* 2002, Stokstad 2002, Strassel 2002, Weber 2002) illustrate the importance of our charge. Indeed, a recent controversial decision to cut off irrigation water to farmers in the Klamath River Basin to save listed coho salmon in Oregon and California prompted U. S. Secretary of Interior Gale Norton to request a National Academy of Sciences panel to review the scientific basis for the decision (Milstein 2002, NRC 2002). The heated policy debates surrounding the salmon recovery problem create an intensely challenging and exciting arena in which science is actively competing for influence.

Overview of Biological Declines and Legal Status

Seven species of anadromous Pacific salmonids in the genus *Oncorhynchus* occur in North America (*O. gorbuscha*—pink salmon, *O. keta*—chum salmon, *O. tshawytscha*—chinook salmon, *O. kisutch*—coho salmon, *O. nerka*—sockeye salmon, *O. mykiss*—steelhead, and *O. clarki clarki*—coastal cutthroat trout), with geographic ranges occurring throughout the north Pacific from Japan across to the west coast of the United States and Canada, from Alaska to southern California. Pacific salmonids generally follow a basic anadromous life history: they are born in freshwater streams, including such diverse locations as coastal lowlands and headwaters thousands of kilometers from the ocean. Juveniles grow in fresh water from several weeks up to two years, then migrate downstream to estuaries and oceans for one to six years before returning as adults to spawn in natal streams (Table 1, Groot & Margolis 1991). Five species of salmonids are obligately semelparous, and steelhead and coastal cutthroat trout can be iteroparous, making the fresh-to-saltwater migration two to three times before dying (Groot & Margolis 1991).

The myriad freshwater and saltwater habitats Pacific salmonids must traverse throughout their life cycle exposes them to a number of threats. Salmon declines have been blamed on many factors, including hydropower projects, harvest, reductions in freshwater habitat quantity and quality, predation by other fishes, birds and marine mammals, competition for rearing and spawning habitats, ocean conditions, and negative interactions between wild and hatchery-origin salmon. Combinations of such impacts have led to serious reductions in abundance, spatial distribution, and diversity of a number of Pacific salmon populations.

The National Marine Fisheries Service (NMFS) defines reproductively isolated groups of salmon with unique evolutionary legacies as Evolutionarily Significant Units (ESUs) under the Endangered Species Act (ESA) (NMFS 1991; Waples 1991, 1995). The NMFS has identified 51 ESUs within the 6 species of Pacific salmonids under its jurisdiction, and 26 of these currently are listed under the ESA

TABLE 1 Life history characteristics of Pacific salmon (modified from Pearcy 1992, Busby et al. 1996)

Species	Colloquial names	Ocean entry	Size at ocean entry (mm)	Freshwater residence	Marine residence	Age at maturity
Chinook salmon (<i>O. tshawytscha</i>)	King salmon; Tyee; Blackmouth; spring, summer, or fall chinook	May–Oct	40–110	0.5–2+ years	0.5–6 years	3–6 years
Coho salmon (<i>O. kisutch</i>)	Silver salmon	May–June	60–120	1 year	0.5–1.5 years	2–4 years; usually 3 years
Sockeye salmon (<i>O. nerka</i>)	Red salmon; Blueback	May–June	60–110	1–2 years	1–5 years	3–7 years; usually 3–4 years
Chum salmon (<i>O. keta</i>)	Dog salmon	March–June	30–40	1–3 months	2–4 years	2–7 years; usually 3–4 years
Pink salmon (<i>O. gorbuscha</i>)	Humpback salmon	May–June	30–40	1–3 weeks	1.6 years	2 years
Steelhead (<i>O. mykiss</i>)	Rainbow trout; redband trout; winter or summer steelhead	May–April	NA	2–7 years	0–4 years	2–7 years

TABLE 2 Conservation status of listed Evolutionarily Significant Units (ESUs) of Pacific salmonids*

Species	ESU	Listing status
Chinook salmon	Sacramento River winter-run	Endangered
	Upper Columbia River spring-run	Endangered
	Snake River fall-run	Threatened
	Snake River spring/summer-run	Threatened
	Puget Sound	Threatened
	Lower Columbia River	Threatened
	Upper Willamette River	Threatened
	Central Valley spring-run	Threatened
	California coastal	Threatened
Coho salmon	Central California	Threatened
	Southern Oregon/northern California coasts	Threatened
	Oregon coast	Threatened
Chum salmon	Hood Canal summer-run	Threatened
	Columbia River	Threatened
Sockeye salmon	Snake River	Endangered
	Ozette Lake	Threatened
Steelhead	Southern California	Endangered
	Upper Columbia River	Endangered
	South-central California coast	Threatened
	Central California coast	Threatened
	Snake River Basin	Threatened
	Lower Columbia River	Threatened
	California Central Valley	Threatened
	Upper Willamette	Threatened
Middle Columbia River	Threatened	

*The listing status of each ESU under the Endangered Species Act is specified—ESUs are listed separately as “species” under the Act as distinct population segments

(Table 2). The listed ESUs are considered to be distinct population segments under the ESA, and for legal purposes they are treated as separate species that must be recovered.

Once an ESU is listed under the ESA, actions that might directly or indirectly negatively affect the species become restricted (Rohlf 1989). These so-called “take” prohibitions are designed to limit the deleterious effects of harvest, hydropower, and hatchery management practices, and of changes to habitat quantity and quality, on salmon populations. Recovery planning is complicated because, in addition to the ESA, the NMFS must also serve two other major legal mandates when making decisions about salmon. First, NMFS is charged with administering the Magnuson-Stevens Fishery Conservation and Management Act, as amended by the Sustainable Fisheries Act of 1996. This Act sets biological standards that

must be met in salmon populations subjected to commercial and tribal harvest and describes methods by which harvest levels should be allocated (Magnuson-Stevens Act 16 U.S.C. § 1801 et seq.). In addition, the U.S. government is a trustee for the salmon resource for a number of Native American tribes in the Pacific Northwest. This relationship was originally established through historical treaties signed in the mid-1850s and was reaffirmed in 1974 in the *United States v. Washington* case (the Boldt decision) and in 1983 in the *United States v. Oregon* case between the tribes and United States government. Consequently, the NMFS works closely with state and tribal comanagers to review harvest and hatchery management plans to ensure compliance with statutory requirements in the ESA, the Magnuson-Stevens Act, and tribal treaty rights. For thriving populations of salmon, tensions among these three primary legal standards are minimal. However, for threatened and endangered populations, where the pie to be divided is smaller, the debate becomes more heated (e.g., *Alesea Valley Alliance v. Evans* 2001, Federal Register 2002, Verhovek 2002, *Washington Trout v. Lohn et al.* 2001).

NMFS's Design of Recovery Planning for Pacific Salmonids

The NMFS has implemented a geographically based approach to developing recovery plans for the 26 listed ESUs under its jurisdiction. Eight recovery-planning domains have been identified, each encompassing 3–6 salmon ESUs that are listed as threatened or endangered under the ESA (Figure 1). For each geographic region, a Technical Recovery Team has been (or will be) established; the team's charge is to develop biologically based delisting criteria and provide technical guidance in determining which actions are necessary for recovery of all ESUs within the domain (NMFS 2000a).

Recovery teams face three major scientific challenges: identifying the units of conservation, establishing recovery goals, and recommending management actions that will abate existing threats and ultimately meet those recovery goals. Approaches to establishing recovery goals fall largely under the umbrella of "population viability analysis," which recently has been thoroughly reviewed (Lande 1993, Morris et al. 1999, Brook et al. 2000, Holmes 2001, Beissinger & McCullough 2002, Holmes & Fagan 2002), including a detailed synthesis of ideas regarding what represents viability for salmonids (McElhany et al. 2000). In contrast, the scientific challenges of defining appropriate conservation units and then completing a threats analysis on those units have not been reviewed elsewhere. By focusing on these scientific issues, we illustrate how guidance from basic science and clear communication from conservation practitioners can help advance conservation planning for species such as salmon.

IDENTIFYING UNITS FOR CONSERVATION

Salmon species are composed of multiple lineages marked by varying levels of evolutionary divergence. This variation can be seen in neutral genetic markers (e.g., Utter et al. 1989, Wood et al. 1994, Nielsen et al. 1997, Ford 1998,

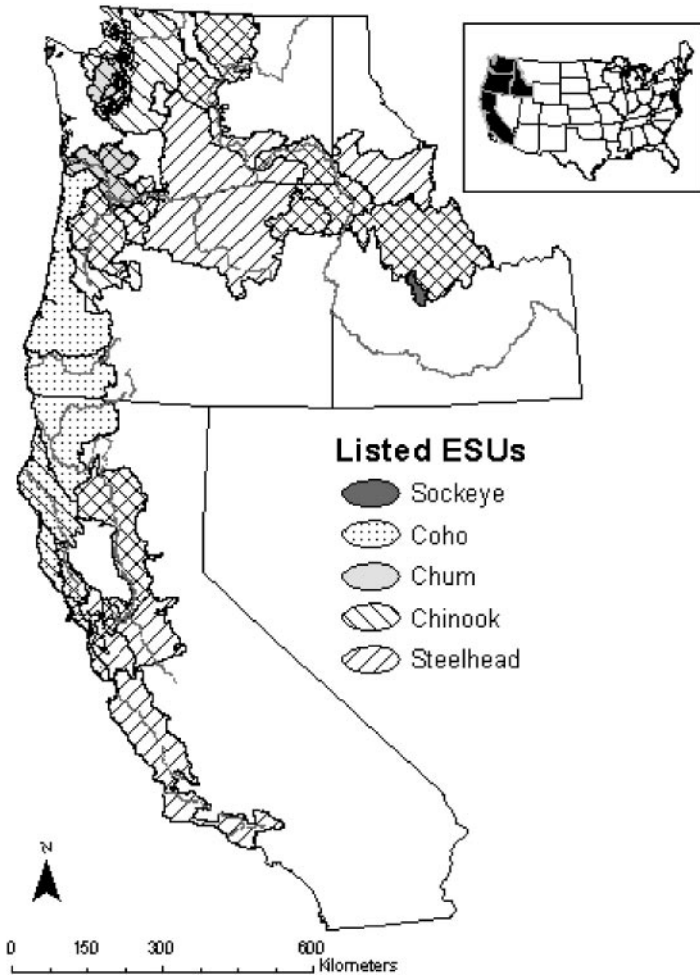


Figure 1 Map showing the geographic distribution of listed ESUs of Pacific salmonids.

McCusker et al. 2000, Smith et al. 2001), and also in the wide range of life history strategies employed within each species (Table 1; Groot & Margolis 1991, Taylor 1991, Waples et al. 2001). A demographically based viability analysis that simply counts fish—without regard to genetic or life history variants—could result in missed opportunities for future evolvability of a population. Yet, the reality is that not every salmon lineage can be saved; thus one of the first critical questions conservation planners must address is: What are the biologically significant units for conservation of the species?

There is a rich history to the question of how to identify and prioritize conservation units, and ongoing debates surrounding this issue for imperiled species

continue in the biological literature (see discussion below). Advances in molecular genetic and statistical tools have led to impressive algorithms for discriminating among groups within species—in some cases, to the level of distinguishing between individuals. Nevertheless, resolution of distinct genetic lineages within a species of conservation concern does not help to identify which hierarchical level of organization is the appropriate one to save (Waples 1995). In this section, we offer a brief history of the debate about appropriate means for identifying conservation units and how they have been delineated for Pacific salmon under legal constraints of the ESA. We then highlight important omissions in formulating definitions of conservation units and how those definitions are applied in practice. We argue that incorporating a phylogenetic perspective into identification of conservation units will greatly improve assessment of their relevance for the conservation of imperiled species.

The Conservation Unit Debate: What is the Best Way to Identify Relevant Clusters of Diversity?

Delineating conservation unit boundaries and major evolutionary lineages within species has been the focus of considerable research over the past 15 years. Ryder (1986) introduced the concept of Evolutionarily Significant Units to categorize evolutionary diversity within rare mammal species. Waples (1991, 1995) later adopted the ESU concept as a way to identify stocks of Pacific salmon that could receive formal protection as “distinct population segments” under the ESA. Given their propensity to home to natal streams, salmon are naturally subdivided into a hierarchy of genetically distinct groups that tend to show local adaptation to varying selective environments (reviewed in Taylor 1991). Therefore, the biological framework used by NMFS to define an ESU includes: (a) substantial reproductive isolation and (b) assurance that the designated population or group of populations contains an important component of the evolutionary legacy of the species, which in application means that salmon ESUs show major divergence from one another (Waples 1991).

Although the ESU criteria for salmon are clear, approaches underlying ESU designations are not universally agreed upon in the broader conservation community (reviewed in Fraser & Bernatchez 2001). Recent controversy stems from disagreement about the relative importance of using neutral molecular data as opposed to ecological adaptations to delineate groups (Crandall et al. 2000). Moritz (1994) argued that ESUs should be distinct phylogenetic lineages and that the criterion to delineate such lineages should be reciprocal monophyly based on DNA sequence data. Strict reliance on neutral marker data to the exclusion of local adaptations can be troublesome (Barlow 1995, Crandall et al. 2000). Yet, the value of determining phylogenetic relationships among evolutionary lineages and integrating this information with knowledge of local adaptations remains underappreciated (Mayden & Wood 1995).

Recovering species must have continued opportunities to evolve. Waples (1995) envisioned this need by describing the evolutionary legacy of Pacific salmon as “a

reservoir of genetic variability upon which future evolutionary potential depends.” Yet most ESU designations, including those in Pacific salmon, are based largely on static views of evolution divergence. We seldom have a clear understanding of the multiple mechanisms by which patterns of evolutionary divergence (or convergence) could have occurred. In order to evaluate the significance of divergent lineages to species persistence, and when necessary to establish priorities among ESUs, the potential processes that gave rise to patterns of divergence must be understood. There are at least two problems with viewing reproductive isolation and evolutionary divergence as two independent criteria that offer unambiguous indications of conservation unit boundaries.

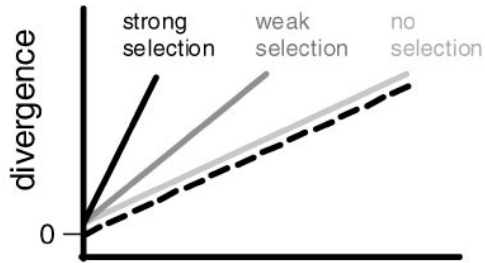
First, different evolutionary processes produce different rates of divergence between lineages for neutral markers (used to measure reproductive isolation) and adaptations. Applications of ESU concepts ignore these different processes, instead focusing on the degree of divergence at a single time. For example, rapid evolutionary shifts caused by selection can outpace neutral marker divergence and lineage sorting by orders of magnitude (Figure 2A). In some cases, evolution is so swift that distinct populations can be almost genetically indistinguishable at neutral alleles while showing significant adaptive divergence (Pascual et al. 2001). Salmon introduced to novel environments offer striking evidence for this phenomenon. Evolutionary radiations of chinook salmon in New Zealand (Quinn et al. 2001, Kinnison et al. 2002) and steelhead introduced to Argentina (Pascual et al. 2001) both show rapid life history divergence but very little neutral marker divergence. More troubling are cases where gene flow is high (Waples 1998), but selection is strong enough for populations to evolve local adaptations (Figure 2B; e.g., Tallman & Healy 1991, 1994). Such populations, although not reproductively isolated, constitute important evolutionary components of the biological species, but probably warrant no unique protection. Finally, populations can show high levels of reproductive isolation (measured by neutral markers) but show very little or no phenotypic divergence. Stabilizing selection or convergent evolution between geographically isolated populations could both lead to this pattern (Figure 2C; e.g., Teel et al. 2000, Craig & Foote 2001). Clearly, different evolutionary processes can lead to very different relationships between neutral markers and adaptive traits. In short, degree of divergence in traits per se is not a simple indicator of evolutionarily significant diversity that should be protected in a conservation plan.

Second, reproductive isolation and evolutionary divergence are not always independent events, and isolation does not always precede adaptive differentiation. In fact, in many cases natural selection itself causes reproductive isolation. This occurs when natural selection operates on traits that limit opportunities for groups of individuals to mate, or limits reproductive success of hybrids. This process, dubbed ecological speciation (Schluter 1998, Johannesson 2001), could be quite common in Pacific salmon, where selection on traits such as run timing or homing ability can result in spatial or temporal isolation among breeding groups. Recent evidence in sockeye salmon suggests that even subtle differences such as local morphological adaptation to spawning habitats can lead to early stages of reproductive isolation (Hendry 2000). If we are viewing life history lineages in the early stages

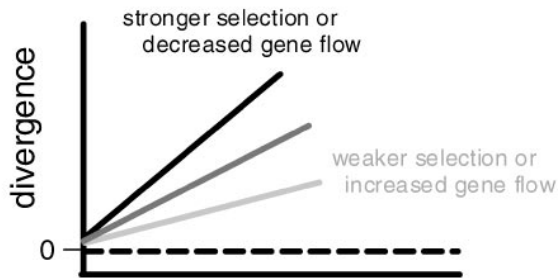
Characters Used to Define ESUs

- phenotype / adaptation
 - - - neutral markers

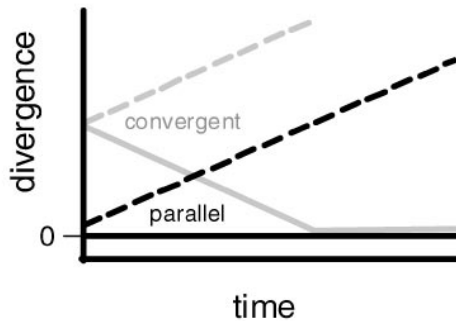
A) Process: Rapid Evolution



B) Process: Adaptive Evolution Despite Gene Flow



C) Process: Convergent or Parallel Evolution



of ecological speciation, then there may be no genetic barriers to reproduction, and genetic differentiation could still be modest, yet the diverging lineages could be important from a conservation perspective because they represent evolution's answer to the most recent environmental challenges.

Finally, it is also important to recognize that reliance solely upon variability at neutral molecular markers as a way to assess evolutionary potential may fall short of what will actually be required to maintain a species. Bowen (1999) makes a strong case for consideration of additional criteria to identify potential sources of future evolutionary diversity, including spatial or temporal isolation, behavioral variation (Barlow 1995), unique niche use, morphological divergence, and preserving lineages with a recent history of evolutionary diversification. None of these ideas has been implemented in any species' recovery plan (Boersma et al. 2001).

In sum, we need to take care that our views of ESUs are not unduly typological, and instead accommodate the variety of processes that could generate superficially similar patterns. All genetically distinct populations do not warrant equal protection; it depends on the mix of adaptation, gene flow, uniqueness, or irreplaceability of the units. Part of the problem with applying ESU concepts in recovery planning grows out of what has become the standard interpretation of the ESA. The conventional view is that the primary intent of the ESA is to eliminate immediate extinction risks to biological species, or to distinct population segments within species (Federal Register 1996). Hence, recovery-planning efforts typically focus primarily on estimating short-term extinction risks and discussing ways to reduce those risks. However, conservation scientists recognize that one broader goal of conservation is to preserve the biological processes of life (Bowen 1999). For Pacific salmon, this means that it is first necessary to identify the phylogenetic

Figure 2 Expected patterns of divergence for neutral markers and adaptive traits over time between hypothetical lineages for three evolutionary processes. (A) depicts the case where there is no gene flow among lineages and diversifying selection is operating. Here, divergence at neutral markers increases linearly as a function of time; divergence for adaptive traits also increases as a function of time, with the rate dependent on the strength of diversifying selection. (B) depicts the case where gene flow is operating, but diversifying selection is strong enough to overcome the effects of gene flow. Here, lineages again show no differences at neutral markers, but show varying rates of divergence for adaptations, depending on the strength of selection and levels of gene flow. (C) depicts the case where there is no gene flow, but lineages experience identical selective pressures. Here, divergence at neutral markers increases linearly as a function of time, but adaptations converge or remain at common phenotypes, for convergent and parallel evolutionary processes, respectively. For simplicity, all models assume that there is adequate genetic variation for evolutionary adaptations to occur, and that neutral markers do not become saturated over time.

history and current evolutionary trajectories of salmon lineages in order to define the biological heritage we are charged to protect.

Identifying Conservation Units That are Commensurate with Conservation Goals

The ultimate goal of recovery planning is to foster natural persistence of imperiled species or conservation units. The difficulty in identifying relevant units arises from the fact that species continue to evolve, so it is not obvious whether it is better to conserve existing diversity or save units with maximum potential to adapt to changing environments. For example, if our underlying conservation goal is to preserve historical diversity, then a recently evolved lineage with closely related sister groups may have lower priority for protection than more distant evolutionarily distinct groups. Alternatively, if the goal is to foster future evolutionary radiation, then it may make more sense to protect rapidly diversifying lineages (despite their recent common ancestry) as opposed to lineages that are older but more evolutionarily inert.

Typically, data are not available to establish quantitative links between historical diversity or evolutionary potential and species viability. Instead, assertions about the importance of conserving a representative sample of historical diversity or a species' evolutionary potential are bolstered mainly by theoretical arguments (Lynch & Lande 1993, Lande & Shannon 1996, Storfer 1996). In practice, Pacific salmon ESUs have been defined by reproductive isolation based on allozyme frequency data or morphological, life history, or habitat characteristics (Myers et al. 1998; Busby et al. 1994, 1996; Weitkamp et al. 1995; Hard et al. 1996; Gustafson et al. 1997). As mentioned above, listed ESUs all are protected under the ESA, so recovery efforts must be made to ensure the persistence of any Pacific salmon ESU threatened with extinction, irrespective of its contribution to the long-term persistence of the species.

The difficult choices about which units of Pacific salmon to conserve therefore occur within ESUs, at the level of populations. For salmon ESUs, populations are defined based on their degree of relative demographic independence so that viability can be evaluated using single-population viability analysis (McElhany et al. 2000). The conservation goal underlying identification of independent populations is to determine how many and which viable populations are necessary for persistence of the ESU (Ruckelshaus et al. 2002). Work conducted to date suggests that the number of demographically independent populations per ESU ranges from 3 to 30, and life history and genetic diversity vary greatly among populations within an ESU (Ford et al. 2001, PS TRT 2001, Myers et al. 2002). Determining which populations must be saved for ESU persistence involves identifying critical components of ESU diversity that must be protected. We believe that estimating the population diversity necessary for ESU persistence will benefit from a phylogenetic perspective on the significance of the diversity we observe within salmon ESUs—a topic we address in the next section.

Incorporating Evolutionary Pattern and Process into Identifying Relevant Units for Conservation

Given political, economic, and even biological constraints, conservation planners are often forced to establish conservation priorities among evolutionary lineages. This necessity translates into difficult decisions about which traits should have primacy in establishing conservation priorities, or in extreme cases, deciding which groups are expendable. Conservation units—like most taxonomic designations—are best viewed as convenient ways of identifying and organizing phenotypic or genetic differences among diverging lineages. Advances in intraspecific phylogeography provide a historical framework to examine current patterns of evolutionary divergence in rare species and ESUs within species (Templeton 1998, Edwards & Beerli 2000, Avise 2001). Yet, in salmon recovery planning, very little attention has been paid to phylogeographic patterns and the underlying processes that give rise to distinct evolutionary lineages (see Bowen 1998, 1999; Moritz 2002).

A phylogenetic perspective could be used to assess the relative importance of salmon adaptations by revealing the order in which characters have evolved through time (Avise 1989). For example, Quinn et al. (2000) argue that timing of migration is a key life history trait in salmon because it provides a means by which populations become temporally isolated, thereby facilitating further divergence in secondary adaptations. Similar arguments could be made regarding the effects of natal homing on spatial isolation among breeding groups. By mapping the evolution of migratory timing to a phylogeny, we can formally test whether these adaptive traits consistently precede the evolution of secondary adaptations. Such information would help clarify the relative importance of conserving particular traits or populations containing such traits.

Phylogenies can also be used to identify the rarity of adaptations. For example, a recent reconstruction of relationships among rainbow trout populations in British Columbia showed a repeated evolutionary shift from anadromy to a freshwater life cycle and repeated evolutionary divergence in adult migration timing (McCusker et al. 2000). This pattern of independent evolution across multiple lineages suggests that on an evolutionary timescale, variation for both of these traits appears to be quite easy to recover. By comparison, sockeye salmon also show repeated evolution from anadromy to freshwater life cycles, but adult migration timing appears to be canalized on a very local scale (Wood 1995). Hence, in sockeye salmon, care should be taken to preserve populations containing adaptations associated with run timing because these traits may be difficult or impossible to recover once lost.

In practice, conducting analyses to illuminate the history of evolutionary processes occurring within salmon ESUs (i.e., processes generating diversity among populations) is difficult because of the ubiquitous presence of hatchery fish in most ESUs. Transfers of hatchery fish between streams within ESUs, and even from streams outside the geographic boundaries of an ESU, have been commonplace since the early to mid 1900s (e.g., Myers et al. 1998). Hatchery fish usually

constitute an unknown fraction of the parents of any generation, so ascribing evolutionary mechanisms to observed genetic relationships or potential adaptive differences among stocks is very difficult.

Despite the difficulty in reconstructing patterns of and processes generating historical diversity among populations, recovery teams recognize the importance of describing major diversity groups within ESUs so that a representation of historical diversity can be included among those populations given highest priority for conservation efforts. In areas where patterns of extant diversity are not seriously tainted by the presence of hatchery fish, the approaches outlined in the previous section are a promising means of more clearly identifying those populations harboring significant sources of historical diversity or future evolutionary potential. Unfortunately, in order to characterize historical patterns of diversity among populations, recovery teams in most cases will be forced to use proxy information, such as historical diversity of habitat types or life history information from historical fisheries. Decisions about which populations should have highest priority for protection of diversity can then be based on what fraction of historical diversity across the ESU is deemed necessary for recovery. To the extent such characterizations of diversity can include a closer look at its likely evolutionary sources, we will improve our choices about which groups of salmon to protect.

THE ORTHODOX EXPLANATION FOR SALMON DECLINES: HARVEST, HABITAT, HATCHERIES, AND HYDROPOWER

Pacific salmon have been extirpated from nearly 40% of their historical habitat in the Pacific Northwest, and of the remaining salmon populations, almost one half are thought to be at risk of extinction (Nehlsen et al. 1991, Levin & Schiewe 2001). Recent quantitative estimates of extinction risk for 87 populations of 13 listed ESUs of chinook, chum, and steelhead suggest that 84% of the populations currently are not viable (as judged by persistence over 100 years or high risk of decline) (McClure et al. 2002; NMFS's recovery teams, unpublished data). However, contrary to the dismal views conjured up by these risk calculations, salmon are capable of generating remarkable rates of population growth and have successfully invaded many non-native ecosystems (Pascual et al. 2001, Quinn et al. 2001). Consequently, only modest changes in mortality may reverse salmon declines.

The key question for recovery then is, "What actions should we take to reverse population declines?" Unfortunately this question has too often been replaced by the question, "What caused the historic decline of salmon?" These two questions might seem similar, but they actually set up the scientific problem in very different ways. For example, it is clear that excessive harvest drove some salmon populations to low levels in the mid-twentieth century (NRC 1996). In response to these declines, harvest was reduced to low levels in several ESUs; some ESUs responded positively to harvest reductions—others did not (PSC 2001a,b). Therefore,

further reductions in harvest are not likely to lead to recovery in all cases. In short, a factor could have caused a decline historically, but not be an effective place to look for recovery now.

This is a case of scientists posing a question (what historic factors caused the decline of salmon?) that does not shed as much direct light as one would hope on the consequences of decisions regarding alternative management actions that might be taken now to reverse salmon declines. History is important, but even more important is understanding the likely consequences of today's alternative actions. Hence, as we examine the risk factors in the next few pages, we focus on what might be done today to reduce these risks, as opposed to focusing on the history of ecological degradation and resource mismanagement that has gotten us to the current situation.

A Historical Depiction of the Salmon Crisis: The Single-Factor Approach

Salmon biologists have long held that four major human-induced factors have been responsible for salmon declines: (a) habitat degradation; (b) hydroelectric dams and other impoundments; (c) harvest practices; and (d) the proliferation of fish hatcheries. These factors (colloquially called the four H's) have been the primary focus of salmon recovery research and there is, indeed, considerable evidence that each can have direct negative impacts on salmon population status—sometimes dramatically so.

Habitat Degradation and Loss

With exponential human population growth, increases in timber harvest, intensive grazing, and urban development, habitat degradation is obviously a major factor underlying salmon declines (NRC 1996). Documentation of the threats posed by habitat loss and degradation generally has come in two forms: Large-scale, multi-factor correlative studies and smaller-scale explorations of the effects of a few habitat features on particular life stages of salmon. Results from broad-scale correlative studies suggest that human-influenced landscape features affecting salmon vary geographically. Human-induced characteristics such as percent of urbanized or agricultural lands, poor water quality, and 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 (Bradford & Irvine 2000, Paulsen & Fisher 2001, Pess et al. 2002, Regetz 2002, Feist et al. 2002). At the other end of the geographic spectrum, there is a plethora of local-scale studies demonstrating the effects of stream habitat characteristics on salmon density and life history characteristics. Effects of such features as large woody debris in streams, water temperature and water flow, stream channel morphology, proportions of pools, riffles, and glides within streams, and nutrient budgets all can affect early life stages of salmon and their total population productivity (reviewed by Beechie et al. 2002).

Results from neither the large- nor small-scale studies alone are adequate to guide recovery planning in freshwater habitats. The large-scale crude classes of habitat variables give little guidance regarding what specific actions might be taken to rectify problems, and results from small-scale studies typically are not framed within the whole life cycle of salmon populations. Because of these realities, it has proven very difficult to identify robust relationships between habitat variables that can be managed or restored and salmon population dynamics (Collings et al. 1972, Regetz 2002). No one questions the importance of habitat to salmon; but no one has unequivocal recipes for how to alter habitat in a way that encourages the recovery of depleted salmon populations.

Management of habitat for salmon recovery reflects the difficulty articulated above—it largely has proceeded along two philosophically divergent tacks: (a) fix in-stream habitat characteristics so that they resemble those required by salmon, or (b) fix the landscape processes within watersheds so that in-stream habitat functions naturally, thus supporting all species in the ecosystem. The first approach has been criticized because of its focus on the symptoms, rather than the causes of habitat dysfunction (Frissell & Nawa 1992, Beechie et al. 1996, Beechie & Bolton 1999). A favorite example is in cases where thousands of dollars are spent in dumping high quality spawning gravels into a stream, only to have them be washed out of the system within a matter of months because the processes governing gravel recruitment have not been adequately repaired. Furthermore, rarely have either of the approaches to habitat management attempted to quantify fish population responses—the general assumption of habitat management is, “if you build it, they will come.” A few good studies have shown how impossibly long lists of projects designed to fix processes or habitat features in a watershed can be prioritized with explicit comparison of the effects of alternative projects on fish population vital rates (e.g., Reeves et al. 1989, 1991; Beechie et al. 1994).

Hydroelectric Dams and Impoundments

Dams clearly harm anadromous salmon through their effects on the amount, timing, and characteristics of water flows and by blocking access to previously available habitat (Raymond 1988, Williams & Tuttle 1992, Bednarek 2001). The effects of hydropower development on salmon are vividly illustrated in the Columbia River Basin in the Pacific Northwest. For example, the construction of the Hell’s Canyon dam resulted in the loss of 90% of the historic spawning habitat of fall-run chinook in the Snake River Basin (a major tributary of the Columbia River) in Idaho, landing this ESU squarely on the Endangered Species list (McClure et al. 2001). Even passable dams can be devastating to salmon—they convert rivers into reservoirs, change aquatic communities (Bednarek 2001), and also present passage challenges to down- and upstream migrants. For example, survival of juvenile chinook in the Columbia River during their seaward migration dramatically declined as hydropower projects were constructed along their migration corridor through

the 1960s–1970s (Williams et al. 2001). This reduction in survival was associated with subsequent declines in adults returning to spawn (Schaller et al. 1999, Levin & Tolimieri 2001).

Much has been done to reduce the impacts of dams that completely block access to historical habitats. Logistically and financially demanding interventions such as truck and haul projects and creation of artificial spawning habitats have recreated whole salmon runs in areas completely isolated from the sea (WDFW & WWTIT 1993, Gustafson et al. 1997). Without constant human assistance, these populations would perish. The success of engineering solutions is even more striking in situations where hydropower projects provide for fish passage and upriver habitats are plentiful. Most noteworthy are the mitigation measures designed to reduce passage mortality in the Columbia Basin hydropower system after 1975—including fish-passage facilities, predator control, barging fish around dams, and flow augmentation. Taken together, these expensive efforts (costing billions of dollars) have increased the survival of spring/summer chinook salmon migrants to levels similar to those experienced before the hydropower construction boom of the 1960s–1970s (NRC 1996, Williams et al. 2001). Nevertheless, there are other ecological consequences of hydropower operations that are not captured by simply measuring the survival of chinook salmon while migrating through the river system (ISG 1996).

Harvest Practices

Commercial and recreational harvests have had clear negative impacts on Pacific salmon (NRC 1996). In addition to direct mortality caused by fishing, indirect mortality owing to hooking fish that are not ultimately landed or catch and release programs have been documented—the Pacific Salmon Commission uses an average hook and release mortality of 30% (PSC 1997). Furthermore, effects of fishing on life history traits—most notably, size-selectivity on adults and resultant reductions in fecundity (Healey 1986; Ricker 1995; Weitkamp et al. 1995; Ratner & Lande 2001; Hard 2002a,b)—can significantly impair population dynamics in ways that are difficult to quantify.

Often, one of the earliest steps taken to redress declines is to reduce harvest. In some cases, reduction in fishing pressure has coincided with a dramatic reversal of salmon declines. Such appears to have been the case for summer chum salmon returning to streams in Hood Canal, Washington (Figure 3). Although the recent rebound in numbers of summer chum salmon escaping to spawn might be attributed to harvest reductions, recent improvements in ocean survival probably also contribute to their increasing numbers. In contrast to the apparent success of harvest management in addressing declines in Hood Canal summer chum populations, reductions in harvest levels have not improved population status of chinook populations a few kilometers across Puget Sound (PSC 2001b). Clearly, other threats to the chinook salmon in northern Puget Sound must be addressed.

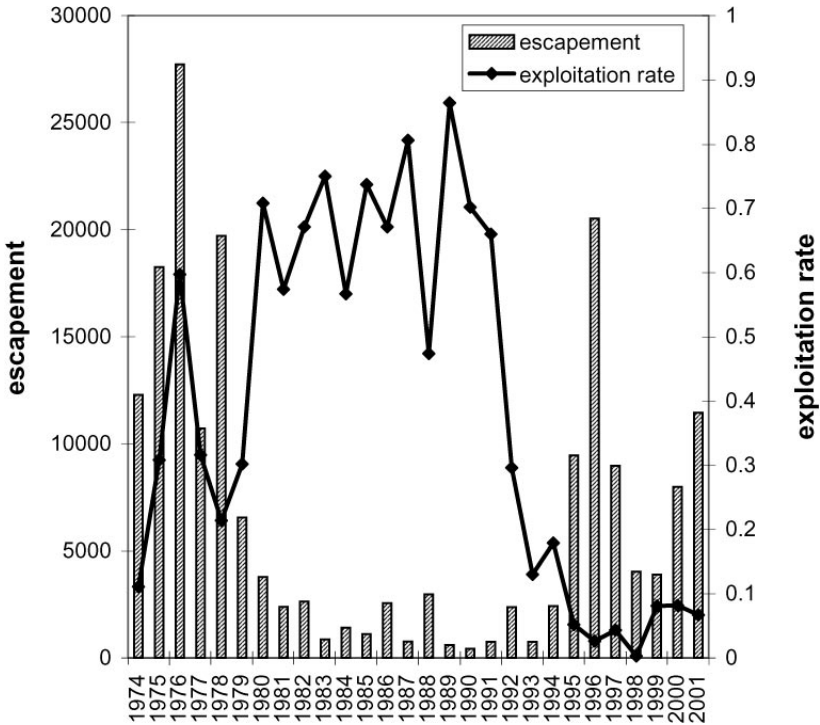


Figure 3 Total exploitation rates (the fraction of total number of summer chum returning to Hood Canal killed owing to direct and incidental harvest in Washington and Canadian waters) and numbers of summer chum salmon escaping to spawn in streams in Hood Canal, WA from 1974–2001 (data from WDFW & PNPTT 2000; T. Johnson, WDFW, personal communication).

Hatchery Propagation of Salmon

A common solution to the ills of salmon populations is to release sometimes enormous numbers of hatchery-reared fish (Lichatowich 1999). Each year hatcheries along the west coast of the United States release nearly 1.2 billion juvenile salmon (Mahnken et al. 1998), with 200 million salmon released annually into the Columbia River alone. There is extensive disagreement over the degree to which hatchery programs contribute to or detract from the viability of wild salmon populations. There are well-documented differences between hatchery and wild Pacific salmon in their survival, reproductive, foraging, and social behaviors, habitat preferences, response to predators, morphology, and physiology (reviewed by Flagg et al. 2000). These differences potentially can affect ecological and genetic interactions between wild and hatchery salmon, and it is clear that negative impacts of hatchery fish do occur in some cases. Misuse of hatcheries has the potential to reduce the

viability of natural salmon populations through effects on vital rates or life history traits such as run timing (Nicholas & Hankin 1988; Fleming & Gross 1993; Hilborn 1992, 1999; Meffe 1992; NRC 1996; Reisenbichler & Rubin 1999; Waples 1999). Translocations of salmon through hatchery programs and subsequent introgression of non-native hatchery-origin genes into wild populations can reduce fitness of wild salmon (e.g., Zinn et al. 1977, Reisenbichler & Rubin 1999). Moreover, reduced smolt-to-adult returns in wild populations of chinook salmon are associated with exceptionally large releases of hatchery fish (Levin et al. 2001).

A risk/benefit analysis of hatchery fish must consider the goals of the hatchery program; generally, hatchery management is designed either to supplement declining wild populations (supplementation programs) or to provide extra salmon for harvest (production programs). Supplementation programs are designed to end—the goal is to produce a naturally self-sustaining population of salmon. Ideally, these programs maximize recovery of wild stocks while minimizing negative genetic or ecological impacts of the hatchery fish. In a recent review, Flagg et al. (2000) identified only three successful supplementation programs (i.e., a self-sustaining population of salmon existed after artificial propagation ended) among scores of candidates (see also Waples et al. 2002). In contrast to supplementation programs, production programs often are designed to exist in perpetuity so that fishers can be assured of catching salmon. Through the late 1980s, in spite of increased hatchery production of coho salmon along the Oregon coast and chinook salmon in Puget Sound, adult returns did not increase as hoped (Stouder et al. 1996; PSC 2001a,b). Risk evaluations on such hatcheries must evaluate the negative ecological and genetic interactions that can occur during juvenile rearing and outmigration stages, threats to adults in mixed hatchery-wild fisheries, competition for spawning sites, and interbreeding between wild and hatchery fish. These potential risks are not trivial—for example, in chinook populations where hatchery fish are marked, escaped hatchery salmon can constitute up to 60% of the spawning population in areas without planned supplementation programs (NMFS, unpublished data).

All Risk Factors Do Not Conveniently Fit into the 4-H Framework

Although scientists and federal agencies tend to emphasize the four H's as keys to salmon recovery (NRC 1996, NMFS 2000b), there are many other sources of salmon population declines. For example, the productivity of the Pacific Ocean varies in decadal oscillations, with sometimes tenfold changes in smolt-to-adult survival (Mantua et al. 1997, Hare et al. 1999, Hollowed et al. 2001). In addition, shorter-term events such as El Niño (occurring every two to seven years) are negatively related to sockeye population sizes in Alaska and British Columbia (Mysack 1986). During prolonged periods of bad ocean conditions, salmon may do so poorly that their populations plummet without any help from human factors (Beamish et al. 1999, McFarlane et al. 2000, Welch et al. 2000).

In addition to the stresses of bad ocean years, salmon face many other natural risks that threaten their persistence. Papers quantifying the effects of either predation or competition on Pacific salmon populations are plentiful (e.g., Reimers 1973, Glova 1984, Ruggerone 1986, Wood 1987, Gearin et al. 1989, Healey 1991, NOAA 1997, Collis et al. 2001). Notably high-profile stories include reports of Caspian terns eating an estimated 7% to 15% of the 100 million salmonid juveniles migrating downstream in the Columbia River (NMFS 1995, Collis et al. 2001) and sea lions eating up to 65% of steelhead adults returning to Lake Washington in Puget Sound, Washington (Gearin et al. 1988, 1989).

Finally, salmon are exposed to another form of environmental degradation that has recently come into the limelight as a global factor: the invasion of ecosystems by exotic species. In the western United States, exotic species now make up to 59% of the fish fauna (Moyle et al. 1986) and are common even in areas that are otherwise pristine (see, e.g., Achord et al. 1997), leading ecologists to suggest that nonindigenous species may rank highest among threats to imperiled species (Vitousek 1994, Simberloff 2000). Levin and colleagues (Levin et al. 2002) showed that survival of juvenile chinook in streams without exotic brook trout was nearly double that in streams with brook trout, even after differences in habitat were taken into account. The difference in juvenile chinook survival between sites with and without brook trout would increase population growth rate (λ) by about 2.5%—an increase sufficient to reverse the negative population growth observed in many chinook populations of the Snake River Basin (McClure et al. 2002).

Furthermore, the effects of nonindigenous species can be much less direct than that of brook trout. For example, one of the most important native predators of juvenile salmon in mainstem rivers and reservoirs as they make their seaward migration is the pike minnow *Ptychocheilus oregonensis* (Rieman et al. 1991). NMFS estimates that each year pike minnow consume 16.4 million salmonids in the Columbia River Basin alone (NMFS 2000c). It is interesting to note that the prominence of the pike minnow as a predator may result from interactions with exotic fishes (Poe et al. 1994). In the absence of nonindigenous fishes, such as small-mouth bass, walleye, or channel catfish, salmonids constituted only 2% of the diet of pike minnow (Buchanan et al. 1981). Instead, crayfish, insects, and sculpins dominated the diet. Poe and colleagues (1994) concluded that a shift in the pike minnow diet to salmon results from competition with exotic predators for sculpins and crayfish. Thus, in the absence of exotic piscivorous fishes, the impact of even native predators such as pike minnow may be reduced.

Management attention to the effects of ecological interactions and ocean conditions on salmon populations has been inconsistent at best. The lack of a systematic consideration of ecological and natural environmental conditions in salmon management plans can be attributed in part to lack of scientific information. For example, in the few cases where ecological impacts of predators on salmon were well documented (e.g., Caspian terns, sea lions, and pike minnow),

management plans included—sometimes even featured—actions designed to reduce predation on salmon (Gearin et al. 1988, Beamesdurfer et al. 1996, Friesen et al. 1999, NWPPC 2001). The contents of salmon management plans thus appear to be guided by serendipitous treatment of these effects by scientists, rather than a more holistic biological vision of threats analysis.

RECOVERY REQUIRES ATTENTION TO INTERACTIONS AMONG RISK FACTORS AND A MIX OF OPTIONS FOR IMPROVEMENT

Although examples exist in which single factors appear to be primarily responsible for the decline of salmon populations, the demise of salmon nearly always results from a constellation of factors throughout their life history (Lawson 1993, NRC 1996, Brodeur et al. 2000, Finney et al. 2000, Levin & Schiewe 2001). The tidy compartmentalization of risks is convenient and analytically tractable, yet it neglects cumulative or interactive effects of risk factors. The alternative—comparing the relative value of a fix to one H to improvements accomplished by instead fixing more than one H (Kareiva et al. 2000)—has never been incorporated into a management plan to our knowledge. Because of the uncertainties inherent in predicting the effects of improvements in the H's on salmon populations, distributing efforts among several known threats increases the chances that hoped-for biological responses will occur. Thus, even if removing all hydropower projects or removing all hatcheries might recover salmon, the more scientifically prudent approach is to consider simultaneous alterations in many of the H's.

For some salmon ESUs, we actually have enough demographic detail in terms of stage-specific mortality rates that one can even use matrix models to examine the impacts of mixed-management activities. For example, Kareiva et al. (2000) found that a mix of modest reductions in juvenile mortality and estuarine mortality together could reverse the declining trends in Snake River spring-summer chinook salmon.

Ecologists are comfortable testing for significant effects. In salmon, all H's exert a significant effect, and the more pertinent question concerns relative importance, which is much harder to estimate. As a first approximation to this issue, currently we are gathering data for a large-scale comparative study designed to explore the combined effects of the threats to population status for salmon in California, Oregon, Idaho, and Washington. We have formulated an a priori set of candidate models that reflect a competing suite of biological hypotheses to explain salmon abundance and trends (Figure 4). Justification for these hypotheses is based on what we know about potential interactions among risk factors as illustrated by the examples below. A strength of this approach is that information theory can be used to select a best approximating model (or set of models) that can then be used to infer the relative importance of those factors thought to impact salmon population trends directly or indirectly (e.g., Hilborn & Mangel 1996, Burnham & Anderson

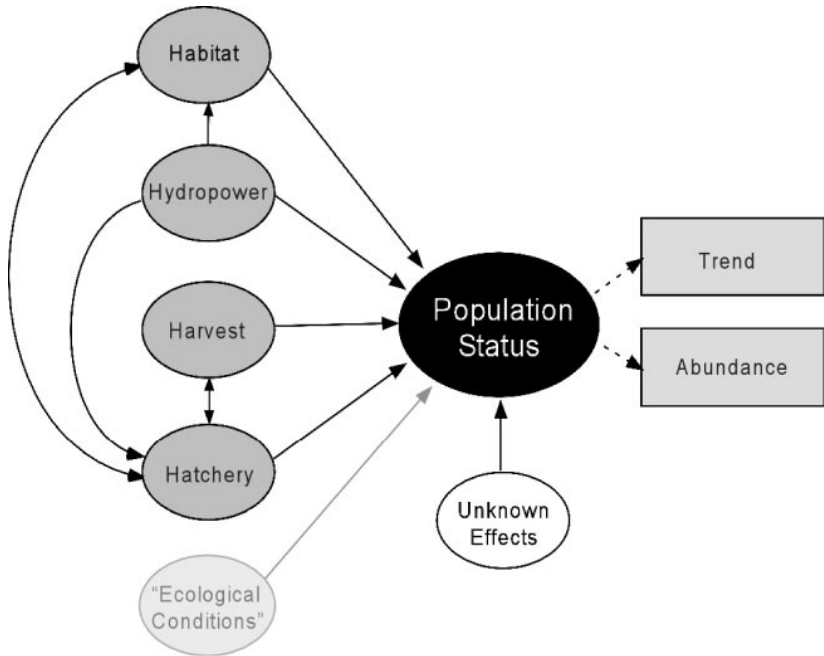


Figure 4 One of several possible model path diagrams depicting the direct and indirect effects of five putative causes of salmon declines (H's—see text) on salmon population status. The four H's (*gray shaded circles*) are modeled here as latent variables that can be estimated by factor analysis from a set of measured environmental parameters thought to collectively describe the factor of interest. A fifth factor (*light gray shaded circle*), defined here as natural ecological conditions (e.g., ocean conditions, interactions with nonindigenous species), could also shape salmon population dynamics, and although not modeled explicitly, could also interact with any of the four H's. The dependent variable, population status, is modeled as a latent variable (*blackened circle*) to be estimated from trend (i.e., λ) and change in abundance of salmon from historical levels. Residual variation (not explained by the combination of predictor variables) is depicted as an unmeasured factor (*open circle*). Arrows indicate the regressions of the H's on population status (direct effects) and on each other (indirect effects). Using model selection criteria, each candidate model (i.e., each combination of paths) represents a biological hypothesis that can be evaluated for fit to collected data to determine the most likely correlative causes of salmon decline.

1998, Anderson et al. 2000). Neither of the holistic analyses we are conducting informs us about how to improve population status, but they do reinforce the value of pursuing improvements simultaneously in multiple life stages and across threats—something that is often overlooked when assigning blame to each of the four H's.

Hatchery and Harvest Interactions

Recent harvest rates on federally listed Pacific salmon populations range from near 0 to 60% (PSC 2001b). As mentioned earlier, in many areas, a major reason fisheries persist is because of hatchery programs that provide fish to be caught. Depending on the extent of ecological and genetic interactions between hatchery and wild fish throughout their life cycle and the degree to which hatchery fish buffer wild fish from threats such as harvest, the net effect of hatchery programs on wild populations could be negative or positive (see “Hatchery Propagation of Salmon,” above).

Aside from the potential direct and indirect negative effects of hatchery salmon on wild salmon, hatchery fish can mask the true status of wild fish in a population. In the Pacific Northwest, hatchery fish currently contribute 70% to 80% of the total salmon catch in coastal fisheries (Flagg et al. 2000). Some argue that the prevalence of hatchery fish in the catch should alleviate concerns about high harvest rates on listed salmon populations. The real test of whether harvest rates are significantly negatively affecting wild salmon populations is to estimate the status of the populations with and without harvest. This seemingly straightforward task is made very difficult because of the often unknown fraction of hatchery fish that are included in estimates of total potential returns to freshwater (recruits), catch, and spawning adults. For most populations of salmon, the proportion of hatchery fish mixed in with a count of total fish is not known—in some cases, estimates are available for a few years, and in very rare cases (e.g., where tagged fish can be automatically counted at dams), time series of hatchery fish in a run are available. In other words, in many cases, it is not possible to estimate the true status of wild salmon populations because of the presence of an unknown fraction of hatchery fish. In populations for which we have time series of estimates of total abundance and hatchery counts, the estimates of λ will always be lower when the presence of hatchery fish is factored out of the calculations in attempts to estimate the status of wild fish. Figure 5 illustrates variation in the effect hatchery fish have on estimates of λ for 15 populations of chinook salmon from Washington, Oregon, Idaho, and California.

Pacific salmon harvest managers must make annual decisions about levels of fishing mortality that do not constitute jeopardy to listed stocks under the ESA, defined as the case where an action does not “reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild” (50 CFR S402.02). All the populations represented in Figure 5 are still harvested at rates greater than 30%—for example, the Nooksack chinook population in northern Puget Sound, Washington (in a listed ESU) had a mean harvest rate of over 52% in the years spanning 1989–1999 (PSC 2001b), and the population growth rate of wild chinook over that same time period was less than one. For populations with unknown fractions of hatchery fish included in total population counts, estimates of appreciable risk from harvest are fraught with uncertainty. This issue is especially pressing in the present political climate, where legal rulings such as the Hogan decision (e.g., *Alsea Valley Alliance v. Evans* 2001) and ongoing petitions to NMFS (Federal

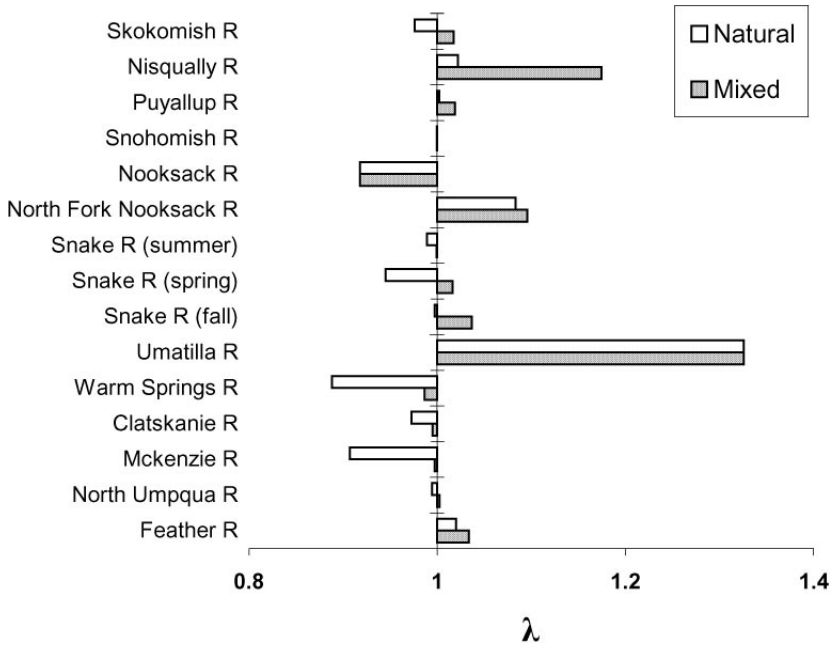


Figure 5 Average annual rate of population growth (λ) for a sample of chinook salmon spawning population counts from Washington, Oregon, Idaho, and California during 1980–1999. λ was calculated two different ways for each population: (a) including naturally spawning fish of hatchery and wild origin (mixed) and (b) counting only wild spawners whose parents were naturally produced (natural). (Source: NMFS, unpublished data.)

Register 2002) are questioning the means of accounting for hatchery fish in risk evaluations on listed wild salmon populations.

Hydropower and Hatchery Interactions

Much of the massive production of hatchery salmon throughout the Pacific Northwest was motivated by observed or anticipated declines in wild salmon (Lichatowich 1999). A prime example of how hatchery fish were used supposedly to mitigate losses in wild populations is where hatchery programs are associated with hydropower projects. In many cases, unanticipated negative effects of hatchery production on wild salmon species have been documented. For example, most hatchery and wild salmonids from the Snake River are captured at dams, loaded into barges, and transported to the estuary below the eight dams downstream in the Columbia River system they would otherwise have to traverse. Steelhead smolts from Snake River hatcheries average nearly 10 times the size of wild chinook smolts (Levin & Williams 2002), but they are loaded together

into the same barges at densities up to 60 g/L. The result of the shared ride appears to be substantially reduced survival of the wild chinook (Levin & Williams 2002).

Another unintended consequence of hatchery practices is to concentrate salmonid juveniles after their release into freshwater, which can lead to higher susceptibility to predators who cue off of prey densities (reviewed by Flagg et al. 2000, Collis et al. 2001). Because of blockages such as dams and locks, increased predation rates on adult salmon also have been observed (Gearin et al. 1988, 1989; Nash et al. 2000).

Interactions Between Natural Processes and Human Activities

Not only can the effects of the four H's interact with each other, but they also interact with the environment. For example, human activities may interact with the environment by altering the strength of competitive interactions in the sea. Levin et al. (2001) showed that when releases from hatcheries are high and ocean productivity is low, the survival of chinook salmon in the marine phase declines. Similarly, Cooney & Brodeur (1998) found that hatchery effects on wild salmon depend on freshwater habitat capacity and ocean conditions experienced by the wild and hatchery fish. Recent improvements in rearing practices have resulted in hatchery-reared salmon that are now larger than their wild counterparts and exhibit greater marine survival than wild fish (Zabel & Williams 2002).

Another example of interactions between human threats and environmental sources of variability is found in the complicated effects of dams on salmon. The tendency to focus solely on direct mortality of salmon through dams ignores the possibility that factors affecting the fish before or after they pass through hydropower projects act synergistically with dams to reduce survival (Budy et al. 2002). For instance, recent work has highlighted the ecosystem importance of returning salmon that can have positive direct and indirect feedbacks on salmon population dynamics. Nutrients derived from decomposing salmon carcasses are now recognized to play an important role in the ecology of Pacific Northwest riparian habitats (Gresh et al. 2000). For one, the delivery of marine-derived nutrients by salmon returning from the sea appears to be crucial to the growth of juvenile salmon (Bilby et al. 1996, 1998; Larkin & Slaney 1997; Wipfli et al. 1999). Thus, the extreme reduction in salmon abundance caused by dams ostensibly has resulted in a nutrient deficit that could have contributed to reduced size of outmigrating juveniles (compare Bilby et al. 1998). Furthermore, hydropower projects slow the migration of salmon by several weeks, and this delay in migration appears to exacerbate size-selective marine mortality (Zabel & Williams 2002). Together, these independent results suggest that it is possible that the effects of nutrient deficiencies in the freshwater habitat are amplified by dams, resulting in increased marine mortality of juvenile salmon.

An Integrated Threats Analysis for Salmon Recovery

Scientists and managers engaged in salmon recovery increasingly are realizing the importance of whole-life-cycle, whole-ecosystem approaches to identifying significant threats to salmon populations. For example, a recent NRC panel leveled criticism against current practices of stock assessment and management for failing to account adequately for environmental fluctuations in their harvest decisions (NRC 1998), and a group of lead scientists from agencies involved in salmon management trumpeted the need for integrated research on classically isolated problems facing salmon (ISAB 2001a, ISST 2001).

Conducting more relevant research and using better models in making management decisions are relatively obvious things to change about the way risks to salmon populations are managed. Clearly, a widely agreed upon and supported strategic research plan is needed to organize guidance for salmon recovery efforts. More politically and logistically difficult to implement are manipulative, large-scale management experiments followed by thorough monitoring. Impressive experiments such as shutting down harvest or hatcheries or removing dams have been heralded as excellent ways to learn how salmon really would respond to improvements in their complex ecosystems (RSRP 2001). We agree with those pleas for experimentation—but we have not seen any undertaken yet. In the meantime, admitting sources of uncertainty, planning for alternative future states (e.g., Groves 2000), and generating technical analyses that offer a comparison of multiple options for recovering salmon will increase the chances that scientific input informs final recovery decisions designed to abate threats facing the fish.

GETTING REAL—SALMON RECOVERY PLANNING IN PRACTICE

The Art of Recovery Planning for Threatened and Endangered Salmonids: Creating Options

Two technical recovery teams established by the NMFS have been underway for about two years (Puget Sound and Willamette–Lower Columbia River domains), and three others were convened in the fall of 2001 (Interior Columbia Basin, southern Oregon–northern California, and California coastal domains; Figure 1). One of us (MR) is the chair of the Puget Sound recovery team. The technical challenges are a small part of the overall task of developing a recovery plan for listed chinook, chum, and sockeye ESUs within our geographic domain. The recovery teams are multi-stakeholder groups whose members are diverse, but all have the necessary technical backgrounds to satisfy recovery team selection criteria. On the Puget Sound team, we have representatives from federal, state, tribal, and local entities, each of whom views the problem from a distinct perspective. The perspectives of team members come from their experiences in biology spanning harvest management, local government, and basic science backgrounds. In addition, the

member agencies represented on the team have been embroiled in salmon wars for decades—the recent listing under the ESA has merely brought their disputes into sharper focus. Nevertheless, having a diverse set of technical perspectives is the point of setting up multi-stakeholder recovery teams—the hope is that alternative views can be hashed out through the team dynamics, thus producing a relatively harmonized recovery plan that will be easier to communicate to parties on the policy end.

Nonscientists often are unaware of how contentious biological tasks such as those facing the recovery teams can be—truisms such as “numbers don’t lie” lead to expectations that scientific disagreements are relatively easy to resolve. In fact, major technical disagreements stemming from philosophical differences that seem to run as deep as religious beliefs are commonplace in such technical teams. For example, one of our early jobs as a recovery team was to agree on viability criteria for the 21 demographically independent populations of chinook we have identified in Puget Sound (PSTRT 2001). Because of the previous thought and work that had gone into justifying the importance of four key population parameters—abundance, productivity or growth rate, spatial structure, and diversity (McElhany et al. 2000)—there was virtually no debate among team members on what the biological indicators of viability should be.

In contrast, the debate among recovery team members was heated on how best to model viability quantitatively. In particular, strong differences emerged for preferable model structure and complexity, the importance of incorporating density-dependence into population dynamic models, and whether representing uncertainty around model results was important. After a long period of debating the relative merits of alternative approaches, the team agreed to explore a number of different models aimed at addressing the same basic question: How many salmon are needed for a population to have a negligible risk of extinction over 100 years? Preliminary results from two of several planned alternative modeling approaches produced ranges of viable population size that are large and overlapping. Just the simple exercise of displaying these ranges to policy-makers has led to a better understanding of why different scientists produce results that do not agree. The technical team is working with the policy group organizing recovery planning in Puget Sound to decide how best to summarize and communicate these disparate technical results. This seems like such a simple solution to a seemingly unresolvable debate—but it is surprising how rarely a multi-model approach is used in conservation and management applications (Kareiva et al. 1998, Boersma et al. 2001).

Pacific salmon recovery teams are exploring another novel approach—scenarios analysis—to increase the chances that biological results will influence recovery-planning decisions. The idea behind scenario analysis is simple: When uncertainty is enormous, bundle it together in a small number of scenarios (usually three to five) that can then be more easily examined than a complicated model with hundreds or even thousands of unknown parameters. Each scenario should capture a coherent set of assumptions that is embraced by an important stakeholder group or scientific group. An example in the salmon world might be the notion that the major source

of current salmon risk is ocean conditions, and that other risk factors such as hydropower, hatcheries, and habitat explain much less about the recent declines. Given a limited number of scenarios, scientists can then present the data that support or contradict each scenario, and policy-makers can examine the consequences of alternative management actions assuming different scenarios are apt reflections of reality.

Such an approach has been used in a few conservation applications—high-profile examples include the IPCC for global climate change actions and the Millennium Assessment project evaluating the value of global biodiversity under alternative future states—and its popularity is increasing (Reid 2000; Sala et al. 2000; Clark et al. 2001; MA 2001; G. Peterson et al., unpublished data).

Pacific salmon recovery teams are using scenarios to address two main questions: (a) How many and which populations within an ESU must be naturally self-sustaining for the ESU to be considered recovered (i.e., what does recovery look like)? and (b) What actions are necessary to recover populations and ESUs (i.e., how do we get there)? The first question is one that is likely to have multiple answers because most ESUs are comprised of many populations—for example, the Puget Sound chinook ESU has at least 21 demographically independent populations (PSTRT 2001), and it is plausible that not all will need to be viable for the ESU to have a negligible risk of extinction. The Puget Sound technical recovery team is looking at multiple ways of combining population characteristics to describe a recovered ESU. The key to generating multiple solutions is first to set desired ESU-wide targets for abundance, productivity/growth rate, spatial structure, and diversity. Tools such as siting algorithms used in reserve design can help produce biologically equivalent solutions to ESU-level recovery targets (Ruckelshaus et al. 2002). Which ESU viability scenario(s) will be chosen to satisfy regional recovery goals will be decided by a multi-stakeholder policy group in Puget Sound called the Shared Strategy Development Committee (<http://www.sharedsalmonstrategy.org>).

The second type of scenario analysis used in salmon recovery planning is proposing alternative sets of actions whose combined effects will suffice to recover the listed ESUs. Making predictions about the effects of a given action (e.g., reduction in harvest, change in hatchery management practices, protection or restoration of habitat, predator control) on the fate of salmon populations depends on assumptions about future environmental conditions. Previously, detailed simulation models typically have been used to explore different assumptions about the environment and its influence on salmon (ISAB 2001b). Scenario analyses have similar goals as such simulation models, but by collecting assumptions into only a handful of alternatives, they are easier for decision-makers to work with. If one were to consider only three scenarios for salmon recovery, they might be (a) oceanic conditions outside of human control are the dominant factor affecting salmon survival, thus only modest improvements in human-caused risk factors are needed; (b) risks due to human effects are severe, but technical solutions such as hatcheries, better-engineered dams, restored streams, and selective harvest are sufficient to achieve the required survival benefits; and last, (c) the degradation of the

environment is so severe that only massive changes in environmental conditions through restoration of landscape-forming processes and revolutionary changes in harvest and hatchery management will recover salmon. Under each of these scenarios, alternative management actions will have different effects on salmon. The objective for science is to assess the data that support or refute each scenario, to evaluate the internal consistency of each scenario, and to provide an analytical framework that can use new data to resolve critical uncertainties. The ultimate decision about what to do will still come down to trade-offs between economics and ecology or social values and biology, but if scenario analysis is done artfully, those trade-offs will be clear.

It is impossible to predict fish population dynamics precisely and accurately twenty or even five years into the future, with or without management intervention. Uncertainty, lack of basic ecological understanding, and tremendous environmental variability make such an endeavor fruitless. But we can identify management actions that are likely to yield marked improvements in population status under a wide variety of scenarios. Based on what we have learned from recovery planning for Pacific salmonids, we offer the elements in Table 3 as a brief primer on how to incorporate science into a recovery plan effectively (see also Wondolleck & Yaffee 2000, Brick et al. 2001).

Nature and Limitations of Data Underlying Recovery Analyses

Compared to most other imperiled species, there is a plethora of information about salmon—they are counted on fishing boats, at weirs, in snorkel surveys, and at dams. In spite of notebooks and computers full of salmon counts, accessible and well-managed databases for salmon are lacking (Botkin et al. 2000, ISAB 2001a). Science advisory panels note that many questions about salmon recovery could be answered by contrasting populations that experience different risk factors, if only such broad geographic data were available (see, e.g., RSRP 2001). Inadequate monitoring and poor data accessibility are common deficiencies afflicting endangered species management (Kareiva et al. 1998; Campbell, unpublished data). In salmon management, however, there is a more insidious problem—the acceptance of coded expert opinion as a substitute for data. Using expert opinion as a basis for management decisions in the absence of data is a practical necessity—the problem arises when calls for empirical information are forgotten once a decision has been made.

Two expert opinion approaches have come to be widely embraced as scientific support tools for salmon management. The first, Ecosystem Diagnosis and Treatment (EDT), is used to evaluate habitat capacity for salmon. EDT uses 45 habitat descriptors to predict the capacity of different streams and watersheds to support salmon. The 45 habitat variables represent scores on a scale of zero to four that are typically filled in by experts or derived from written reports but almost never entail a scientist actually going to the sites to take repeatable, standardized measurements. The method thus involves making guesses about habitat attributes

TABLE 3 Elements of successful participation in a recovery planning exercise. We define “success” as creating a situation where biological information influences ultimate decisions made in designing a recovery plan for imperiled species

1. Work hard in advance to clearly write down the first principles of population and conservation biology that will guide your technical approaches to recovery planning. Codified conceptual guidance and the next step—well-documented, tested and transparent technical approaches to addressing key questions—go a long way toward settling disputes that inevitably arise in technical teams.
2. Be choosy about the level of technical detail you delve into in addressing questions posed to your group. Each of the questions posed to salmon recovery teams could involve several lifetimes of research and analyses to answer. Use guidance from policy staff involved in recovery planning to help you decide which questions are key to the decisions they will make. In the end, deadlines will be the ultimate check in deciding which analyses you undertake and how to balance a mix of quantitative assessments, proxy information, and biological intuition to justify your conclusions.
3. Plan to present technical results as scenarios rather than “the answer” to a particular question. There can be many potential solutions to questions such as “Which populations must be viable for an ESU to be recovered?” and “Which actions are necessary for ESU recovery?”, and expecting a technical team to present a single answer is unwise for at least two reasons. First, presenting a single result makes it very difficult to see how sensitive results are to policy assumptions (e.g., probability of persistence, time frame used in viability models; degree of certainty in the effects of actions on population status). Second, single answers from a technical team box decision-makers into a corner, reducing the chances that biological input will influence ultimate decisions that must also consider political, social, and logistical factors.
4. Resist the temptation to walk away from the group when it gets frustrating. Abandoning ship is an option open to most academics—when one scientist disagrees with another on a technical matter, it is relatively easy to write the offender off as naïve, off-base, or just plain stupid. Attempting to provide useful scientific guidance for real conservation applications requires that you stay at the table to ensure that your opinions on analytical approaches and interpretation of results are included in the final analysis.
5. Invest the time to work with policy- or decision-makers who will influence how scientific results are used in the design of the final recovery plan. Interacting with policy-makers who typically lack a scientific background can appear to slow your progress, will almost surely reorder your priorities for technical analyses, and will generally try your patience. The reality is that political, social, and logistical constraints on recovery solutions are powerful drivers when a recovery plan is being designed—in the end, policy staff are your best hope for incorporating hard-won points of scientific agreement into recovery solutions.

and then running those “data” through a model that predicts population performance. The EDT model includes so many unknown parameters that it is prone to large error propagation (Burnham & Anderson 1998), and it is extremely difficult to validate. Although this approach has been criticized by a “blue ribbon” panel of ecologists (RSRP 2000), it remains popular as a management tool.

A similar expert opinion scientific tool is the “matrix of pathways and indicators” that the NMFS developed for conducting consultations under the ESA (NMFS 1996). The matrix consists of 18 habitat attributes such as sediment, chemical contaminations and nutrients, pool frequency, width/depth ratio, and floodplain connectivity, each of which is scored as properly functioning, at risk, or not properly functioning. Although these attributes could be directly measured, the more typical pattern is that a consultant or agency biologist visits the site and fills in the matrix using his or her professional judgement. It may be possible to fill in a matrix without even visiting the watershed (simply by looking at previous reports and maps). It is not surprising then that attempts to see how well the matrix scores relate to measures of salmon abundance or productivity have detected no relationships (T. Good et al., unpublished data). Both EDT and the NMFS habitat matrix are honest efforts to inform decisions pertaining to salmon habitat actions in the absence of data. The problem is that the public, and even some scientists, have ended up being too satisfied with an absence of data, and have been willing to accept the expert opinion systems as a permanent substitute for empirical information.

In fact, the largest and best-funded ecological database for the Columbia Basin, the Interior Columbia Basin Ecosystem Management Plan (ICBEMP) database, is replete with “data layers” that are only thinly related to anything that might be measured (Quigley & Arbelbide 1997, <http://www.icbemp.gov>). For example, one of the variables in the databases, “riparian integrity index,” is derived using models of models, and cannot be interpreted as anything that could be directly measured. Even a variable like “road” in the ICBEMP data, which could conceivably be directly measured, is a categorical variable that results from two conditional inequalities (see metadata regarding field *ROAD in ICBEMP). ICBEMP also used Bayesian belief networks to summarize the quality of habitats in the Columbia basin for salmonids, and in turn the opportunities for aiding fish recovery via habitat restoration or protection (ISAB 2001b). Analyses of measured data were lacking from this exercise. Again, the derived nature of the data and the degree to which data are expert opinion or empirical are difficult to discern—these important details are often forgotten by those using the database for management.

Finally, even in those cases where measured data exist, they can be fraught with problems. For example, the most fundamental of all data for salmon are population counts, which are key to determining the status and risk of different ESUs. In most management models, these counts are befuddled by two major sources of error that are rarely given the attention they deserve. First, counts are usually made of redds, carcasses, or live fish in small index streams that may be chosen simply because they are easily accessed. These index counts are then used to estimate total population size along two to three dimensions of extrapolation: multiplying index stream length by a factor to get total anadromous stream miles, expanding the number of redds or carcasses into a number of live fish, and somehow translating counts made over a limited period to a number representing the entire returning population (by area-under-the-curve methods, or making assumptions about the longevity of a

redd) (e.g., Smith & Castle 1994). All of these extrapolations are prone to huge errors. For example, total anadromous stream miles can err by 30% to 75% (Bahls & Ereth 1994) and even the simplest redd counts have sampling errors on the order of 25% to 75% (Holmes 2001). If these sampling errors are not accounted for, estimates of population risk could be greatly inflated (because variability owing to sampling error often gets translated as environmental variability and hence elevated extinction risk).

Data can be divided into four categories: measured data, extrapolated or inferred data, modeled data, and expert opinion. Salmon management relies primarily on expert opinion and extrapolated or inferred data. As a temporary solution this approach is sensible; yet excessive reliance on expert opinion relaxes the pressure to collect data.

CONCLUSIONS

The elegant experiment, clear hypothesis, and simple model are icons of good science. But when science enters the arena of endangered species recovery, the science is rarely elegant, clear, or simple. Although engaging in political and economic discussions can be frustrating to biologists, the much-maligned role of science in endangered species management has as much to do with the shortcomings of science as it does with the perils of politics. We have uncovered many shortcomings in the science underlying salmon recovery. Even the most basic question of identifying relevant units for conservation at the population level warrants more thoughtful consideration. For example, when populations are targeted for priority protection, multiple biological criteria need to be involved when defining those units, in concert with a compelling vision of exactly what one is attempting to preserve (e.g., future evolutionary potential or medium-range ecological persistence). Once conservation units have been delineated, tools for estimating their viability are relatively well developed and understood. What we lack are tools for translating different management scenarios into likely changes in viability. The difficulty in assessing the merits of different management scenarios emerges from salmon facing multiple sources of risk simultaneously; risks that interact with one another and with a backdrop of natural hazards and fluctuating environmental conditions. Finally, our data management simply is not sufficiently developed to support the numerical analyses we wish we could do. Salmon, especially Pacific salmon, are the subject of thousands of papers in scientific journals over the past decade. Nonetheless, the most fundamental data regarding abundance and distribution are not readily accessible. And for subtler data—such as habitat quality—managers rely all too often upon expert opinion and obscure extrapolations. Expediency dictates that management decisions are made based on insufficient data, nevertheless, calls for empirical data to redress the gaps in our understanding cannot be too insistent.

We are experimenting with approaches, such as scenario planning and multi-stakeholder technical recovery teams, for delivering scientific guidance in the face of data shortcomings and great uncertainty. There is a dire need for research aimed

at determining what makes the infusion of science into decision-making sometimes work and sometimes fail miserably (Kinzig et al. 2000). One place to begin would be a systematic review of the effectiveness of science at influencing policy.

Finally, for salmon recovery, the most crucial questions are not purely scientific. Our experience has taught us that participants bring such different values to the table, that even when given exactly the same data and information, they come up with dramatically different solutions. The need for collaboration, consensus, compromises, and an accounting for values make the science/policy interface an uncomfortable environment for most scientists. Yet it is primarily in this environment that science can make the biggest difference—by making clear the likely biological consequences of actions, and stopping short of saying anything about what “should” be done.

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LITERATURE CITED

- Achord S, Eppard MB, Hockersmith EE, Standford BP, Matthews GM. 1997. *Monitoring the migrations of wild Snake River spring/summer chinook salmon smolts 1996*. Bonneville Power Admin. Rep. Proj. 91-028, Portland, OR
- Anderson DR, Burnham KP, Thompson WL. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *J. Wildl. Manag.* 64:912-23
- Avise JC. 1989. A role for molecular genetics in the recognition and conservation of endangered species. *Trends Ecol. Evol.* 4:29-281
- Bahls P, Ereth M. 1994. *Stream typing error in Washington water type maps for watersheds of Hood Canal and Southwest Olympic Peninsula*. *Tech. Rep. 94-2*. Point-No-Point Treaty Council, Kingston, Wash.
- Barlow GW. 1995. The relevance of behavior and natural history to evolutionarily significant units. See Nielsen 1995, pp. 169-75
- Beamesderfer RC, Ward DL, Nigro AA. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Can. J. Fish. Aquat. Sci.* 53:2898-908
- Beamish RJ, Noakes DJ, McFarlane GA, Klyashtorin L, Ivanov VV, Kurashov V. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56:516-26
- Beckham SD. 1977. *The Indians of Western*

- Oregon: *This Land was Theirs*. Coos Bay, OR: Arago Books
- Bednarek AT. 2001. Undamming rivers: a review of the ecological impacts of dam removal. *Environ. Manag.* 27:803–14
- Beechie TJ, Beamer E, Collins B, Benda L. 1996. Restoration of habitat-forming processes in Pacific Northwest watersheds: A locally adaptable approach to salmonid habitat restoration. In *The Role of Restoration in Ecosystem Management*, ed. DL Peterson, CV Klimas, pp. 48–67. Madison, WI: Soc. Ecol. Restor.
- Beechie TJ, Beamer E, Wasserman L. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for restoration. *N. Am. J. Fish. Manag.* 14:797–811
- Beechie TJ, Bolton S. 1999. An approach to restoring salmonid habitat-forming processes in Pacific Northwest watersheds. *Fisheries* 24:6–15
- Beechie TJ, Roni R, Steel EA. 2002. *Ecosystem recovery planning for listed salmon: an integrated assessment approach for salmon habitat*. NOAA Tech. Memo. NMFS-NWFSC, Northwest Fish. Sci. Cent., Seattle, WA. In press
- Beissinger SR, McCullough DR, eds. 2002. *Population Viability Analysis*. Chicago, IL: Univ. Chicago Press
- Bilby RE, Fransen BR, Bisson PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* 53(1):164–73
- Bilby RE, Fransen BR, Bisson PA, Walter JK. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. *Can. J. Fish. Aquat. Sci.* 55:1090–118
- Boersma PD, Kareiva PM, Fagan WF, Clark JA, Hoekstra JM. 2001. How good are endangered species recovery plans? *BioScience* 51:643–49
- Botkin D, Peterson D, Calhoun J. 2000. *The scientific basis for validation monitoring of salmon for conservation and restoration plans*. Olympic Nat. Resource Cent. Tech. Rep., Forks, WA
- Bowen BW. 1998. What is wrong with ESUs? *The gap between evolutionary theory and conservation principles*. *J. Shellfish Res.* 17:1355–58
- Bowen BW. 1999. Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Mol. Ecol.* 8:S5–10
- Boyle B. 2002. Restoring credibility to government science. *Seattle Times*, Feb. 27
- Bradford MJ, Irvine JR. 2000. Land use, fishing, climate change, and the decline of Thompson River, British Columbia, coho salmon. *Can. J. Fish. Aquat. Sci.* 57:13–16
- Brick P, Snow D, Van De Wetering S. 2001. *Across the Great Divide. Explorations in Collaborative Conservation and the American West*. Washington, DC: Island
- Brodeur RD, Boehlert GW, Casillas E, Eldridge MB, Helle JH, et al. 2000. A coordinated research plan for estuarine and ocean research on Pacific Salmon. *Fisheries* 25(6):7–16
- Brook BW, O'Grady J, Chapman A, Burgman M, Akcakaya HR, Frankham R. 2000. Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–86
- Brown B. 1983. *Mountain in the Clouds: A Search for the Wild Salmon*. Seattle: Univ. Wash. Press. 249 pp.
- Buchanan DV, Hooton RM, Moring JR. 1981. Northern squawfish (*Ptychocheilus oregonensis*) predation on juvenile salmonids in sections of the Willamette River Basin, Oregon. *Can. J. Fish. Aquat. Sci.* 38:360–64
- Budy P, Thiede GP, Bouwes N, Petrosky CE, Schaller H. 2002. Evidence linking delayed mortality of Snake River salmon to their earlier hydrosystem experience. *N. Am. J. Fish. Manag.* 22:35–51
- Burnham KP, Anderson DR. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. New York: Springer-Verlag

- Busby PJ, Wainwright TC, Bryant GJ, Lierheimer LJ, Waples RS, et al. 1996. *Status review of west coast steelhead from Washington, Idaho, Oregon, and California*. NOAA Tech. Memo. NMFS-NWFSC-27. Northwest Fish. Sci. Cent., Seattle, WA
- Busby PJ, Wainwright TC, Waples RS. 1994. *Status review for Klamath Mountains Province steelhead*. NOAA Tech. Memo. NMFS-NWFSC-19. Northwest Fish. Sci. Cent., Seattle, WA
- Clark JS, Carpenter SR, Barber M, Collins S, Dobson A, et al. 2001. Ecological forecasts: An emerging imperative. *Science* 293:657–60
- Collings MR, Smith RW, Higgins GT. 1972. *Hydrology of four streams in western Washington as related to several Pacific salmon species: Humptulips, Elochoman, Green and Wynoochee rivers*. U.S. Geol. Serv. open file rep., Tacoma, Wash.
- Collis K, Roby DD, Craig D, Ryan BA, Ledgerwood RD. 2001. Colonial waterbird predation on juvenile salmonids tagged with passive integrated transponders in the Columbia River estuary: vulnerability of different salmonid species, stocks, and rearing types. *Trans. Am. Fish. Soc.* 130:385–96
- Cone J. 1995. *A Common Fate: Endangered Salmon and the People of the Pacific Northwest*. Corvallis: Oregon State Univ. Press
- Cone J, Ridlington S, eds. 1996. *The Northwest Salmon Crisis: A Documented History*. Corvallis: Oregon State Univ. Press
- Connelly M. 2001. Home is where they'll lay me down. *Orion* (Summer):17–25
- Cooney RT, Brodeur RD. 1998. Carrying capacity and North Pacific salmon production: stock enhancement implications. *Bull. Mar. Sci.* 62:443–64
- Craig JK, Foote CJ. 2001. Countergradient variation and secondary sexual color: phenotypic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). *Evolution* 55:380–91
- Crandall KA, Bininda-Emonds ORP, Mace GM, Wayne RK. 2000. Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* 15:290–95
- Dalton R. 2002. Fur flies over lynx survey's suspect samples. *Nature* 415:107
- Doremus H. 2000. Delisting endangered species: An aspirational goal, not a realistic expectation. *Environ. Law Rep.* 30:10434
- Fed. Regist. 1996. Policy regarding the recognition of distinct vertebrate population segments under the Endangered Species Act. *Fed. Regist.* 61:4721–25
- Fed. Regist. 2002. Endangered and threatened species: Findings on petitions to delist Pacific Salmonid ESUs. *CFR Fed. Regist.* 50:223–26. 67(28)
- Feist BE, Steel EA, Pess GR, Bilby RE. 2002. What is the correct scale for habitat analyses aimed at prioritizing restoration efforts for salmon? *Anim. Conserv.* In review
- Finney BP, Eaves G, Sweetman I, Douglas J, Smol MSV. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science* 290:795–99
- Flagg TA, Berejikian BA, Colt JE, Dickhoff WW, Harrell LW, et al., eds. 2000. *Ecological and behavioral impacts of artificial production strategies on the abundance of wild salmon populations—a review of practices in the Pacific Northwest*. NOAA Tech. Memo. NMFS-NWFSC-4, Northwest Fish. Sci. Cent., Seattle, WA
- Fleming IA, Gross MR. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. *Ecol. Appl.* 3:230–45
- Ford MJ. 1998. Testing models of migration and isolation among populations of Chinook salmon (*Oncorhynchus tshawytscha*). *Evolution* 52:539–57
- Ford MJ, Budy P, Busack C, Chapman D, Cooney T, et al. 2001. *Upper Columbia River steelhead and spring chinook salmon population structure and biological requirements*. <http://www.nwfsc.noaa.gov/>
- Frank BJR. 2002. Salmon need better habitat. *Seattle Post-Intelligencer*, Jan. 11

- Fraser DJ, Bernatchez L. 2001. Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol. Ecol.* 10:2741–52
- Friesen TA, Ward DL. 1999. Management of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. *N. Am. J. Fish. Manag.* 19:1008–19
- Frissell CA, Nawa RK. 1992. Incidence and causes of physical failure of artificial habitat structures in streams of western Oregon and Washington. *N. Am. J. Fish. Manag.* 12:182–97
- Gearin P, Pfeifer R, Jeffries S, Delong R. 1989. California sea lion predation depletes a steelhead run in Washington State. *Proc. Bien. Conf. Biol. Mar. Mammals, Dec. 7–11, Pacific Grove, CA* (Abstr.)
- Gearin P, Pfeifer R, Jeffries S, Delong R, Johnson M. 1988. *Results of the 1986–87 California sea lion-steelhead trout predation control program at the Hiram M. Chittenden Locks*. Seattle, WA: NMFS Northwest Alaska Fish. Cent. Process. Rep. 88–30. 111 pp.
- Glova GJ. 1984. Management implications of the distribution and diet of sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams in British Columbia, Canada. *Prog. Fish Cult.* 46:269–77
- Gore AJR. 1992. *Earth in the Balance. Ecology and the Human Spirit*. New York: Penguin
- Gresh T, Lichatowich J, Schoonmaker P. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem. *Fisheries* 25:15–21
- Groot C, Margolis L. 1991. *Pacific Salmon Life Histories*. Vancouver: Univ. Br. Columbia Press
- Groves C. 2000. *Designing a Geography of Hope: A Practitioner's Handbook to Ecoregional Conservation Planning*. Washington, DC: The Nat. Conserv. Press
- Gustafson RG, Wainwright TC, Winans GA, Waknitz FW, Parker LT, Waples RS. 1997. *Status review of sockeye salmon from Washington and Oregon*. NOAA Tech. Memo. NMFS-NWFSC-33. Northwest Fish. Sci. Cent., Seattle, WA
- Hard JJ. 2002a. Case study of Pacific salmon. In *Fisheries-Induced Adaptive Change*, ed. U Dieckmann, OR Godø, M Heino, J Mork. Cambridge, UK. In press
- Hard JJ. 2002b. Response of chinook salmon life history to selection under harvest. In *Salmonid Perspectives on Evolution*, ed. A Hendry, S Stearns. Oxford, UK: Oxford Univ. Press. In press
- Hard JJ, Kope RG, Grant WS, Waknitz FS, Parker LT, Waples RS. 1996. *Status review of Pink salmon from Washington, Oregon, and California*. NOAA Tech. Memo. NMFS-NWFSC-25. Northwest Fish. Sci. Cent., Seattle, WA
- Healey MC. 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. *Can. Spec. Publ. Fish. Aquat. Sci.* 89:39–52
- Healey MC. 1991. Diets and feeding rates of juvenile pink, chum and sockeye salmon in Hecate Strait, British Columbia. *Trans. Am. Fish. Soc.* 120:303–18
- Hendry AP. 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290:516–18
- Hilborn R. 1992. Hatcheries and the future of salmon in the Northwest. *Fisheries* 17:5–8
- Hilborn R, Mangel M. 1997. *The Ecological Detective*. Princeton, NJ: Princeton Univ. Press
- Hollowed AB, Hare SR, Wooster WS. 2001. Pacific Basin climate variability and patterns of Northeast Pacific Marine fish production. *Prog. Oceanogr.* 49:257–82
- Holmes EE. 2001. Estimating risks in declining populations with poor data. *Proc. Natl. Acad. Sci. USA* 98:5072–77
- Holmes EE, Fagan WF. 2002. Validating population viability analyses for corrupted data sets. *Ecology* In press
- Independent Sci. Advis. Board (ISAB). 2001a. *A Review of Salmon Recovery Strategies for the Columbia River Basin, ISAB Rep. 2001–7*. Northwest Power Plan. Council., Portland, OR

- Independent Sci. Advis. Board (ISAB). 2001b. *ISAB Model Synthesis Report. An Analysis of Decision Support Tools Used in Columbia River Basin Salmon Management. ISAB Rep. 2001-Ja*. Northwest Power Plan. Council, Portland, OR
- Independent Sci. Group (ISG). 1996. *Return to the river: restoration of salmonid fishes in the Columbia River ecosystem*. Northwest Power Plan. Council, Portland, OR
- Independent Sci. Group (ISG). 1999. Scientific issues in the restoration of salmonid fishes in the Columbia River. *Fisheries* 24:10–19
- Interagency Sci. Salmon Team (ISST). 2001. *Identified Research Needs for Salmon Recovery*. 15 pp.
- Johannesson K. 2001. Parallel speciation: a key to sympatric divergence. *Trends Ecol. Evol.* 16:148–53
- Kareiva PM, Anelman S, Doak D, Elder D, Groom M, et al. 1998. *Using science in habitat conservation plans*. <http://www.nceas.ucsb.edu/projects/hcp>
- Kareiva PM, Marvier M, McClure M. 2000. Recovery and management options for spring/summer chinook salmon in the Columbia River Basin. *Science* 270:977–79
- Kinnison MT, Bentzen P, Unwin MJ, Quinn TP. 2002. Reconstructing recent divergence: evaluating nonequilibrium population structure in New Zealand Chinook salmon. *Mol. Ecol.* 11:739–54
- Kinzig AP, Carpenter S, Dove M, Heal G, Levin S, et al. 2000. *Nature and Society: An Imperative for Integrated Environmental Research*. <http://lweb.la.asu/akinzig/NSFReport.pdf>
- Lande R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am. Nat.* 142:911–27
- Lande R, Shannon S. 1996. The role of genetic variation in adaptation and population persistence in a changing environment. *Evolution* 50:434–37
- Larkin G, Slaney PA. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. *Fisheries* 22(11):16–24
- Lawson PW. 1993. Cycles in ocean productivity, trends in habitat quality, and the restoration of salmon runs in Oregon. *Fisheries* 18:6–10
- Levin PS, Achord S, Feist B, Zabel RW. 2002. Non-indigenous brook trout and the demise of threatened Snake River salmon: a forgotten threat? *Proc. R. Soc. London Ser. B.* 269:1663–70
- Levin PS, Schiewe MH. 2001. Preserving salmon biodiversity. *Am. Sci.* 89:220–27
- Levin PS, Tolimieri N. 2001. Differences in the impacts of dams on the dynamics of salmon populations. *Anim. Conserv.* 4:291–99
- Levin PS, Williams JG. 2002. Interspecific effects of artificially propagated fish: an additional conservation risk for salmon. *Conserv. Biol.* In press
- Levin PS, Zabel RW, Williams JG. 2001. The road to extinction is paved with good intentions: negative associations of fish hatcheries with threatened salmon. *Proc. R. Soc. London Ser. B* 268:1–6
- Lichatowich J. 1999. *Salmon Without Rivers*. Washington, DC: Island
- Lynch M, Lande R. 1993. Evolution and extinction in response to environmental change. In *Biotic Interactions and Global Change*, ed. P Kareiva, JG Kingsolver, RB Huey, pp. 234–50. Sunderland, MA: Sinauer
- Mahnken C, Ruggerone G, Waknitz W, Flagg T. 1998. A historical perspective on salmonid production from Pacific Rim hatcheries. *North Pac. Anadromous Fish. Comm. Bull.* 1:38–53
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Am. Meteor. Soc. Bull.* 78:1069–79
- Mapes LV. 2001. Lynx-fur furor focuses on science role. *Seattle Times*, Dec. 30
- Mayden RL, Wood RM. 1995. Systematics, species concepts, and the evolutionarily significant unit in biodiversity and conservation biology. See Nielsen 1995, pp. 58–113
- McClure MM, Cooney T, Marvier M. 2001. Assessing the role of dams in salmon recovery. *Hydro Rev.* 20:36–45

- McClure MM, Holmes EE, Sanderson BL, Jordan CE. 2002. A large-scale, multi-species assessment: Anadromous salmonids in the Columbia River Basin. *Ecol. Appl.* In press
- McCusker MR, Parkinson E, Taylor EB. 2000. Mitochondrial DNA variation in rainbow trout (*Oncorhynchus mykiss*) across its native range: testing biogeographical hypotheses and their relevance to conservation. *Mol. Ecol.* 9:2089–108
- McElhany P, Ruckelshaus MH, Ford MJ, Wainwright T, Bjorkstedt E. 2000. *Viable salmonid populations and the recovery of evolutionarily significant units.* NOAA Tech. Memo. NMFS-NWFSC-42. Washington, DC: US Dep. Comm. 156 pp.
- McFarlane GA, King JR, Beamish RJ. 2000. Have there been recent changes in climate? Ask the fish. *Prog. Oceanogr.* 47:147–69
- Meffe GK. 1992. Techno-arrogance and half-way technologies: salmon hatcheries on the Pacific coast of North America. *Conserv. Biol.* 6:350–54
- Millennium Ecosyst. Assess. (MA). 2001. *Objectives, audience, process and conceptual framework.* Presented at MA Tech. Design Workshop, Bilthoven, The Netherlands
- Mills LS. 2002. False samples are not the same as blind controls. *Nature* 415:471
- Milstein M. 2002. Fish, lynx flubs hit agencies' credibility. *The Oregonian*, Feb. 5
- Moritz C. 1994. Defining "evolutionarily significant units" for conservation. *Trends Ecol. Evol.* 9:373–75
- Moritz C. 2002. Strategies to protect biodiversity and the evolutionary processes that sustain it. *Syst. Biol.* 51:238–54
- Morris W, Doak D, Groom M, Kareiva PM, Fieberg J, et al. 1999. *A Practical Handbook for Population Viability Analysis.* Washington, DC: The Nat. Conserv.
- Moyle PB, Li HW, Barton BA. 1986. *The Frankenstein Effect: Impact of Introduced Fishes on Native Fishes in North America*, pp. 415–26. Bethesda, MD: Am. Fish. Soc.
- Myers J, Busack C, Rawding D. 2002. *Identifying historical populations of chinook and chum salmon and steelhead with the Lower Columbia River and Upper Willamette River Evolutionarily Significant Units.* Willamette/Lower Columbia River Tech. Recovery Team. Tech. Rev. Draft
- Myers JM, Kope RG, Bryant GJ, Teel D, Lierheimer LJ, et al. 1998. *Status review of Chinook salmon from Washington, Idaho, Oregon, and California.* NOAA Tech. Memo. NMFS-NWFSC-35. Northwest Fish. Sci. Cent., Seattle, WA
- Mysak LA. 1986. El Nino, interannual variability and fisheries in the northeast Pacific ocean. *Can. J. Fish. Aquat. Sci.* 43:464–97
- Nash CE, Iwamoto RN, Mahnken CVW. 2000. Aquaculture risk management and marine mammal interactions in the Pacific Northwest. *Aquaculture* 183:307–23
- Natl. Mar. Fish. Serv. (NMFS). 1991. Notice of policy: Policy on applying the definition of species under the Endangered Species Act to Pacific salmon. *Fed. Regist.* 56:58612–16
- Natl. Mar. Fish. Serv. (NMFS). 1995. *Biological opinion for reinitiation of consultation on 1994–1998 operation of the Federal Columbia River Power System and juvenile transportation program in 1995 and future years.* NMFS Northwest Reg., Portland, OR
- Natl. Mar. Fish. Serv. (NMFS). 1996. *Making ESA determinations of effect for individual or grouped actions at the watershed scale.* Environ. Tech. Serv Div., Habitat Conserv. Branch, Portland, OR
- Natl. Mar. Fish. Serv. (NMFS). 2000a. *Recovery planning guidance for Technical Recovery Teams.* <http://www.nwfsc.noaa.gov/cbd/trt/about.htm>
- Natl. Mar. Fish. Serv. (NMFS). 2000b. *Reinitiation of consultation on operation of the Federal Columbia River power system, including the juvenile fish transportation program, and 19 Bureau of Reclamation projects in the Columbia Basin.* Seattle, WA
- Natl. Mar. Fish. Serv. (NMFS). 2000c. *Predation on salmonids relative to the Federal Columbia River Power System.* Northwest Fish. Sci. Cent., Seattle, WA
- Natl. Oceanic Atmospheric Administration

- (NOAA). 1997. *Impacts of California sea lions and Pacific harbor seals on salmonids and on the coastal ecosystems of Washington, Oregon and California*. NOAA Tech. Memo. NMFS-NWFSC-28. Northwest Fish. Sci. Cent., Seattle, WA
- Natl. Res. Council. (NRC), ed. 1995. *Science and the Endangered Species Act*. Washington, DC: Natl. Acad. Press
- Natl. Res. Council. (NRC), ed. 1996. *Upstream: Salmon and Society in the Pacific Northwest*. Washington, DC: Natl. Acad. Press
- Natl. Res. Council. (NRC), ed. 1998. *Improving Fish Stock Assessments*. Washington, DC: Natl. Acad. Press
- Natl. Res. Council. (NRC). 2002. *Scientific Evaluation of Biological Opinions on Endangered and Threatened Fishes in the Klamath River Basin: Interim Report*. Washington, DC: Natl. Acad. Press
- Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. *Fisheries* 16(2):4–21
- Nicholas JW, Hankin DG. 1988. *Chinook salmon populations in Oregon coastal river basins: Description of life histories and assessment of recent trends in run strengths*, Fish. Div. Inf. Rep., No. 88–1. Portland, OR: Oreg. Dep. Fish Wildl. 359 pp.
- Nielsen JL, ed. 1995. Evolution and the aquatic ecosystem: defining unique units in population conservation. *Proc. Am. Fish. Soc. Symp.*, 17th. Bethesda, MD: Am. Fish. Soc.
- Nielsen JL, Fountain MC, Wright JM. 1997. Biogeographical analysis of Pacific trout (*Oncorhynchus mykiss*) in California and Mexico based on mitochondrial DNA and nuclear microsatellites. In *Molecular Systematics of Fishes*, ed. TD Kocher, CA Stepien, pp. 53–69. New York: Academic
- Northwest Power Plan. Council. (NWPPC). 2001. *20th annual report of the Pacific Northwest Electric Power and Conservation Planning Council*. Council. Doc. 2001–3. Northwest Power Plan. Council., Portland, OR
- Pac. Salmon Comm. (PSC). 1997. *Incidental fishing mortality of chinook salmon: mortality rates applicable to Pacific salmon commission fisheries*. Rep. TCCHINOOK (97)-1. Vancouver, BC, Can.: Pac. Salmon Comm.
- Pac. Salmon Comm. (PSC). 2001a. *Catch and escapement of chinook salmon under Pacific Salmon Commission jurisdiction 1997–2000*. Rep. TCCHINOOK (01)-1. Vancouver, BC, Can.: Pac. Salmon Comm.
- Pac. Salmon Comm. (PSC). 2001b. *Annual exploitation rate analysis and model calibration*. Rep. TCCHINOOK (01)-2. Vancouver, BC, Can.: Pac. Salmon Comm.
- Pascual M, Bentzen P, Rossi CR, Mackey G, Kinnison MT, Walker R. 2001. First documented case of anadromy in a population of introduced rainbow trout in Patagonia, Argentina. *Trans. Am. Fish. Soc.* 130:53–67
- Paulsen CM, Fisher TR. 2001. Statistical relationship between parr-to-smolt survival of Snake River spring-summer chinook salmon and indices of land use. *Trans. Am. Fish. Soc.* 130:347–58
- Pearcy WG. 1992. *Ocean Ecology of North Pacific Salmonids*. Seattle, WA: Wash. Sea Grant
- Pess GR, Montgomery DR, Steel EA, Bilby RE, Feist BE, Greenberg HM. 2002. Landscape characteristics, land use, and coho salmon (*Oncorhynchus kisutch*) abundance, Snohomish River, Wash. *Can. J. Fish. Aquat. Sci.* 59:613–23
- Poe TP, Shively RS, Tabor RA. 1994. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake Rivers. See Stouder et al. 1994, pp. 347–60
- Puget Sound Tech. Recovery Team (PSTRT). 2001. *Independent populations of chinook salmon (Oncorhynchus tshawytscha) in Puget Sound*. Public Rev. Draft NMFS, Seattle, WA. <http://www.nwfsc.noaa.gov/cbd/trt/popid.pdf>
- Quigley TM, Arbelvide SJ, eds. 1997. *An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins*. Gen. Tech. Rep. PNW-GTR-405. Pac. Northwest Res. Stn., Portland, OR

- Quinn TP, Kinnison MT, Unwin MJ. 2001. Evolution of Chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 113:493–513
- Quinn TP, Unwin MJ, Kinnison MT. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. *Evolution* 54:1372–85
- Ratner S, Lande R. 2001. Demographic and evolutionary responses to selective harvesting in populations with discrete generations. *Ecology* 82(11):3093–104
- Raymond HL. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer chinook salmon and steelhead in the Columbia River Basin. *N. Am. J. Fish. Manag.* 8:1–24
- Recovery Sci. Rev. Panel (RSRP). 2000. *Report from the RSRP Meeting held Dec. 3–4*. <http://www.nwfsc.noaa.gov/cbd/trt/rsrpdoc2.pdf>
- Recovery Sci. Rev. Panel (RSRP). 2001. *Report from the RSRP Meeting held March 13–14*. <http://www.nwfsc.noaa.gov/cbd/trt/rsrpdoc1.pdf>
- Reeves GH, Everest FH, Nickelson TE. 1989. *Identification of physical habitats limiting the production of coho salmon in western Oregon and Washington*. Gen. Tech. Rep. PNW-GTR-245, Pac. Northwest Res. Stn., Portland, OR
- Reeves GH, Hall JD, Roelofs TD, Hickman TL, Baker CO. 1991. Rehabilitating and modifying stream habitats. In *Influences of Forest and Rangeland Management on Salmonid Fishes and Their Habitats*, ed. WR Meehan, pp. 519–57. Bethesda, MD: Am. Fish. Soc.
- Regetz J. 2002. Landscape-level constraints on recruitment of chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin, USA. *Aquat. Conserv.* In press
- Reid WV. 2000. Ecosystem data to guide hard choices. *Issues Sci. Tech.* <http://www.nap.edu/issues/>
- Reimers PE. 1973. *The length of residence of juvenile fall chinook salmon in Sixes River, Oregon*. *Oregon Fish Comm. Res. Rep.* 4(2). Portland: Oregon Dep. Fish Wildl. 43 pp.
- Reisenbichler RR, Rubin SP. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES J. Mar. Sci.* 56:459–66
- Ricker WE. 1995. Trends in the average size of Pacific salmon in Canadian catches. *Can. Spec. Publ. Fish. Aquat. Sci.* 121:593–602
- Rieman BE, Beamesderfer RC, Vigg S, Poe TP. 1991. Estimated loss of juvenile salmonids to predation by Northern Squawfish, Walleyes, and Smallmouth Bass in John Day Reservoir, Columbia River. *Trans. Am. Fish. Soc.* 120:448–58
- Rohlf DJ. 1989. *The Endangered Species Act: A Guide to Its Protections and Implementation*. Stanford, CA: Stanford Environ. Law Soc.
- Ruckelshaus MH, McElhany P, Ford MJ. 2002. Recovering species of conservation concern: Are populations expendable? In *The Importance of Species: Setting Conservation Priorities*, pp. 305–29, ed. PM Kareiva, S Levin. Princeton, NJ: Princeton Univ. Press. In press
- Ruggerone GT. 1986. Consumption of migrating juvenile salmonids by gulls foraging below a Columbia River dam. *Trans. Am. Fish. Soc.* 115:736–42
- Ryder OA. 1986. Species conservation and systematics: the dilemma of subspecies. *Trends Ecol. Evol.* 1:9–10
- Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–74
- Schaller HA, Petrosky CE, Langness OP. 1999. Contrasting patterns of productivity and survival rates for stream-type chinook salmon (*Oncorhynchus tshawytscha*) populations of the Snake and Columbia Rivers. *Can. J. Fish. Aquat. Sci.* 56:1031–45
- Schluter D. 1998. Ecological causes of speciation. In *Endless Forms: Species and Speciation*, ed. DJ Howard, SH Berlocher, pp. 114–29. Oxford, UK: Oxford Univ. Press
- Seattle Times. 2002. Leery of grizzly tests,

- legislator demands review of all endangered-species studies. *Seattle Times*, Jan. 10
- Simberloff DS. 2000. Nonindigenous species: a global threat to biodiversity and stability. In *Nature and Human Society: The Quest for a Sustainable World*, ed. P Raven, T Williams, pp. 325–34. Washington, DC: Natl. Acad. Press
- Smith C. 1979. *Salmon Fishers of the Columbia*. Corvallis: Oregon State Univ. Press
- Smith CJ, Castle P. 1994. *Puget Sound chinook salmon (Oncorhynchus tshawytscha) escapement estimates and methods—1991*. Washington Dep. Fish Wildl. Proj. Rep. Ser. No. 1. Wash. Dep. Fish. Wildl., Olympia, WA
- Smith CT, Nelson RJ, Wood CC, Koop BF. 2001. Glacial biogeography of North American coho salmon (*Oncorhynchus kisutch*). *Mol. Ecol.* 10:2775–85
- Stokstad E. 2002. Fur flies over charges of misconduct. *Science* 295:250–51
- Storfer A. 1996. Quantitative genetics: a promising approach for the assessment of genetic variation in endangered species. *Trends Ecol. Evol.* 11:343–48
- Stouder DJ, Bisson PA, Naiman RJ, eds. 1996. *Pacific Salmon and Their Ecosystems: Status and Future Options*. New York: Chapman & Hall
- Stouder DJ, Fresh KL, Feller RJ, eds. 1994. *Theory and Application in Fish Feeding Ecology*. Columbia: Univ. SC Press
- Strassel KA. 2002. The missing lynx. *The Wall Street J.*, Jan. 24
- Tallman RF, Healey MC. 1991. Phenotypic differentiation in seasonal ecotypes of chum salmon, *Oncorhynchus keta*. *Can. J. Fish. Aquat. Sci.* 48:661–71
- Tallman RF, Healey MC. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon. *Can. J. Fish. Aquat. Sci.* 51:577–88
- Taylor EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Atlantic and Pacific salmon. *Aquaculture* 98:185–207
- Tear TH, Scott JM, Hayward PH, Griffith B. 1993. Status and prospects for success of the Endangered Species Act: A look at recovery plans. *Science* 262:976–97
- Tear TH, Scott JM, Hayward PH, Griffith B. 1995. Recovery plans and the Endangered Species Act: Are criticisms supported by data? *Conserv. Biol.* 9:182–95
- Teel DJ, Milner GB, Winans GA, Grant WS. 2000. Genetic population structure and origin of life history types in Chinook salmon in British Columbia, Canada. *Trans. Am. Fish. Soc.* 129:194–209
- US v. Washington. The Boldt Decision*. 384 F. Suppl. 312; 1974 U.S. Dist. LEXIS 12291
- Utter F, Milner G, Ståhl G, Teel D. 1989. Genetic population structure of Chinook salmon, *Oncorhynchus tshawytscha*, in the Pacific Northwest. *Fish. Bull.* 87:239–64
- Verhovek SH. 2002. “Saving” wild salmon’s bucket-born cousins. *New York Times*, Feb. 4
- Vitousek PM. 1994. Beyond global warming: ecology and global change. *Ecology* 75: 1861–76
- Waples RS. 1991. Pacific salmon (*Oncorhynchus* spp.) and the definition of “species” under the Endangered Species Act. *Mar. Fish. Rev.* 53:11–22
- Waples RS. 1995. Evolutionarily significant units and the conservation of biological diversity under the Endangered Species Act. See Nielsen 1995, pp. 8–27
- Waples RS. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *J. Hered.* 89:438–50
- Waples RS. 1999. Dispelling some myths about hatcheries. *Fisheries* 24:12–21
- Waples RW, Ford MJ, Schmitt D. 2002. Empirical results of salmon supplementation: a preliminary assessment. In *Ecological and Genetic Implications of Aquaculture Activities*, ed. T Bert. The Netherlands: Kluwer Academic. In press
- Waples RW, Gustafson RG, Weitkamp LA, Myers JM, Johnson OW, Busby PJ, et al. 2001. Characterizing diversity in salmon from the Pacific Northwest. *J. Fish Biol.* 59(Suppl.A):1–41
- Wash. Dep. Fish Wildl. Point-No-Point Treaty

- tribes (WDFW & PNPTT). 2000. *Summer Chum Salmon Conservation Initiative. An implementation plan to recover summer chum in the Hood Canal and Strait of Juan de Fuca region*. Olympia, WA: WDFW. 424 pp.
- Wash. Dep. Fish Wildl. West. Wash. Treaty Indian Tribes (WDFW & WWTIT). 1993. *1992 Washington State Salmon and Steelhead Stock Inventory*. West. Wash. Treaty Indian Tribes. Olympia, WA: WDFW
- Weber B. 2002. Wildlife society clarifies its role in lynx studies. *The Wall Street J.*, Feb. 12
- Weitkamp LA, Wainwright TC, Bryant GJ, Milner GB, Teel DJ, et al. 1995. *Status Review of Coho salmon from Washington, Oregon, and California*. NOAA Tech. Memo. NMFS-NWFSC-24. Northwest Fish. Sci. Cent., Seattle, WA
- Welch DW, Ward BR, Smith BD, Eveson JP. 2000. Temporal and spatial responses of British Columbia steelhead (*Oncorhynchus mykiss*) populations to ocean climate shifts. *Fish. Oceanogr.* 9:17–32
- Williams JG, Smith SG, Muir WD. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia River hydropower system 1966–1980 and 1993–1999. *N. Am. J. Fish. Manag.* 21:310–17
- Williams JG, Tuttle ME. 1992. The Columbia River: fish habitat restoration following hydroelectric dam construction. In *Restoring the Nation's Marine Environment*, ed. GW Thayer, pp. 405–22. College Park: Maryland Sea Grant
- Willson MF, Gende SM, Marston BH. 1998. Fishes and the forest. *BioScience* 48:455–62
- Willson MF, Halupka KC. 1995. Anadromous fish as keystone species in vertebrate communities. *Conserv. Biol.* 9:489–97
- Wipfli MS, Hudson JP, Chaloner DT, Caouette JR. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. *Can. J. Fish. Aquat. Sci.* 56(9):1600–11
- Wondolleck JM, Yaffee SL. 2000. *Making Collaboration Work. Lessons from Natural Resource Management*. Washington, DC: Island
- Wood CC. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on Eastern Vancouver Island. I: Predation during seaward migration. *Can. J. Fish. Aquat. Sci.* 44:941–49
- Wood CC. 1995. Life history variation and population structure in sockeye salmon. See Nielsen 1995, pp. 195–216
- Wood CC, Riddell BE, Rutherford DT, Withler RE. 1994. Biochemical genetic survey of sockeye salmon (*Oncorhynchus nerka*) in Canada. *Can. J. Fish. Aquat. Sci.* 51:114–31
- Zabel RW, Williams JG. 2002. Selective mortality in chinook salmon: what is the role of human disturbance? *Ecol. Appl.* 21(1):173–83
- Zinn JL, Johnson KA, Sander JE, Fryer JL. 1977. Susceptibility of salmonid species and hatchery stocks of chinook salmon (*Oncorhynchus tshawytscha*) to infections by *Ceratomyxa shasta*. *J. Fish. Res. Board Can.* 34:933–36

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ERRATA

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