Factors that Influence Evolutionarily Significant Unit Boundaries and Status Assessment in a Highly Polymorphic Species, *Oncorhynchus mykiss*, in the Columbia Basin

by

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Executive Summary

NOAA Fisheries Service (NMFS) listed steelhead, the anadromous life history of *Oncorhynchus mykiss*, as threatened or endangered under the Endangered Species Act (ESA) throughout most of the Columbia Basin in the late 1990s. In their original listing decisions, some *O. mykiss* trout populations, the non-anadromous life history of the species, were included in the Evolutionarily Significant Units (ESUs) along with steelhead, but were not listed. As a result of a recent court decision which found that the federal listing agencies cannot list only part of an ESU, NMFS is now reevaluating their original ESA listing decisions for *O. mykiss*. This paper reviews information about the relationship between trout and steelhead populations in the Columbia Basin and the relevance of this relationship to ESU determinations and the assessment of extinction risk of entire ESUs if they include both life histories.

Evolutionary Relationship between Trout and Steelhead

The definition of Evolutionarily Significant Unit (ESU) that has been adopted by NMFS provides the specific criteria of reproductive isolation and evolutionary significance for describing ESU boundaries (Waples 1991, 56 FR 58612). Whether or not trout and steelhead populations, which are the two adult life histories of *O. mykiss*, are in the same ESUs must be evaluated based on these criteria.

The biological evidence about the evolutionary relationship between sympatric steelhead and trout in the Columbia Basin indicates that the life histories are not reproductively isolated to the extent that they would constitute separate ESUs. There is evidence for some interbreeding between the life histories within basins, although in most cases it is likely that sympatric trout and steelhead form demographically independent populations within ESUs, similar to those formed by summer and winter steelhead when they both occur in a basin. The evidence for lack of reproductive isolation between the life histories includes similarity at molecular genetic markers that demonstrate population and ESU structure elsewhere in *O. mykiss*, observations of trout and steelhead spawning on the same redds, and observations and studies that demonstrate both life histories successfully produce offspring that express the alternative life history.

The information about the evolutionary relationship between steelhead below artificial barriers and the *O. mykiss* trout that remain within historic steelhead range above the barriers is weaker but still indicates that the native trout are generally related to the steelhead below the barriers. Populations in the two areas may now be in complete reproductive isolation from each other, although unidirectional gene flow, downstream over the barriers, may still occur. But it is probable that the original relationship between the trout and steelhead when they were sympatric in these blocked areas was the same as that which occurs where the life histories are currently sympatric. Further, the reproductive isolation caused by artificial barriers is recent from the perspective of evolutionary time, less than 100 years, and is anthropogenic. The available genetic evidence demonstrates similarity between trout in many of these areas and steelhead

below the barriers. Potential exceptions may occur where very large areas were blocked by dams, such as the areas above Hells Canyon and Grand Coulee dams. Very little genetics information is available from the upper Snake and upper Columbia, but these large areas may have historically included multiple *O. mykiss* ESUs that contained steelhead. The trout that remain in the uppermost basins in these large blocked areas may have been closely related to steelhead that were historically present but are now entirely extinct. If this were the case, only the trout lower in the basins would be related to the steelhead that still occur below the blockages.

Trout that are above natural barriers such as high waterfalls have been isolated from the trout and steelhead below the barriers since the barriers formed. The geologic ages of such barriers generally are not known, but they may range from several thousands of years to tens of thousands of years or more. The available genetics data indicates that these naturally isolated trout populations have diverged from the populations below the barriers. The combination of long-standing natural reproductive isolation and genetic distinctiveness indicates that such trout populations constitute their own ESUs.

Status of ESUs that Include both Steelhead and Trout

The status or extinction risk of *O. mykiss* in the Columbia Basin can be viewed from several different perspectives. The original NMFS status review focused primarily on steelhead and while trout were acknowledged to be present their contribution to the status of the ESUs was not addressed (Busby et al. 1996). This was partly for jurisdictional reasons since NMFS has jurisdiction only over steelhead. However, if *O. mykiss* ESUs are described according to NMFS criteria and are found to include both steelhead and trout populations, and if the status of the whole ESU is assessed using status indicators such as abundance, distribution, biodiversity and risk avoidance, the extinction risk of the entire ESU may be found to differ significantly from the extinction risk of the steelhead within the ESU.

For example, if the trout that remain above artificial barriers are recognized to be part of the ESUs the distribution of *O. mykiss* increases in all ESUs. Most of the extinctions across historic ranges that are evident for steelhead no longer apply to the ESUs because the species (ESU) is still represented by the trout. This is particularly notable for the Snake and Upper Columbia ESUs if the distributions expand to include at least some of the areas above the Hells Canyon and Chief Joseph/Grand Coulee dam complexes. Also, adult abundance in many of the ESUs increases by an order of magnitude if the trout that are sympatric with steelhead are counted, and increases further if the trout above dams are counted, particularly in the Mid-Columbia, Snake and Upper Columbia ESUs. The available data indicates that trout comprise 90% or more of the adult *O. mykiss* in these ESUs, so adult abundance increases from a few tens of thousands of steelhead to hundreds of thousands of *O. mykiss* if trout are also counted. Finally the ESUs contain a substantially richer biodiversity if trout are included. For example, adult life history diversity expands from only anadromous fish to include resident, fluvial and adfluvial freshwater forms. The high diversity provides both resiliency and adaptability to the ESUs.

Trout also add their own litany of risk factors, such as population fragmentation, ecological displacement by exotic trout, and high sensitivity to local habitat conditions that typically are not as emphasized in steelhead status assessments (e.g. Chilcote 1998, Busby et al. 1996). The status of trout in all the Columbia Basin ESUs is decreased from historic conditions primarily due to impacts to lower basin and mainstem habitats that make the areas particularly inhospitable to resident fish even while steelhead still use them as migration corridors. Evidence from basins where such habitat remains intact for trout, the Deschutes Basin is an example, indicates that these areas were very productive for trout and provided important population connectivity. However trout are still highly abundant in many areas, particularly in headwater areas.

The change in status indicators that occur if trout are recognized to be part of the Columbia Basin ESUs is most pronounced in the three inland ESUs: Mid-Columbia, Upper Columbia and Snake. This is because the increases in distribution and adult abundance caused by counting the trout are substantial. The effect of including trout in the Lower Columbia and Willamette ESUs is more modest. *O. mykiss* trout are not as abundant in these ESUs; instead trout niches are dominated by native coastal cutthroat (*O. clarki clarki*).

While trout are the majority of the *O. mykiss* species in terms of numbers in some of the ESUs, steelhead may still represent a significant part of the ESUs. It is highly probable that the *O. mykiss* species in the three inland ESUs would persist into the foreseeable future without the steelhead life history because the species (ESU) would remain secured by the trout. Certainly the species has persisted, and is often common, in areas above dams from which steelhead have already been excluded. However, it is uncertain that steelhead in these ESUs would persist into the future without the protections provided by the ESA. The loss of the steelhead life history would represent a significant, and possibly irreversible, change in the character of the ESUs. The steelhead phenotype is distinctive from trout and both life histories are an important component of the species. But the evidence indicates that populations in the same geographic areas are not in reproductive isolation from each other and are not evolutionarily diverged from each other as required by the NMFS criteria for defining ESUs. On the other hand, there is no guarantee based on the available information that trout populations alone could reestablish steelhead populations if the steelhead that are currently sympatric with them were lost. An ESA listing decision about a distinctly polymorphic yet reproductively interconnected species like *O. mykiss* is a uniquely complex one.

Introduction

Scope and Intent of this Document:

The species *Oncorhynchus mykiss* expresses a complex array of life histories across much of its range as well as considerable geographic variation. Several subspecies have been proposed (Behnke 1992), although none of them are formally recognized. Two of the proposed subspecies in North America include both trout and steelhead life histories: *O.m. irideus*, or Coastal rainbow/steelhead, and *O.m. gairdneri*, or Inland redband/steelhead. A third subspecies that includes an anadromous life history occurs in Asia, while all other North American subspecies are entirely trout. In the Pacific Northwest, the boundary between the coastal and inland subspecies occurs in the Columbia Gorge, where the Columbia River cuts through the Cascade Mountain Range. The steelhead and trout life histories within these two subspecies are genetically more similar to each other than to fish with the same life history in the other subspecies, indicating that the different life histories within a geographic area share an evolutionary origin (Allendorf 1975). Recent molecular systematic surveys suggest that this proposed taxonomic model of North American *O. mykiss* subspecies may be over simplified and inaccurate (Currens 1997, Busby et al. 1996, F. Utter, U. of Washington); however, it remains the available model until final revisions to the taxonomy are adopted.

The NOAA Fisheries Service (NMFS) further divided *O. mykiss* into multiple "Evolutionarily Significant Units" (ESUs) (Waples 1991, 56 FR 58612, Waples 1995) for listing consideration under the federal Endangered Species Act (ESA). The ESA considers "distinct" populations of taxonomic species to be "species" eligible for legal protection (16 U.S.C. 1532[16]). NMFS adopted the concept of ESUs to serve as distinct population segments in their ESA listing decisions, along with specific criteria for defining them. Evidence for whether or not rainbow trout and steelhead are in the same ESUs is presented in this report according to the criteria provided by NMFS policy (56 FR 58612). The U.S. Fish and Wildlife Service (USFWS) likewise recognizes "Distinct Population Segments" (DPSs) that may be listed under ESA. The agencies share jurisdiction over *O. mykiss* for ESA decisions, with NMFS overseeing the anadromous steelhead and USFWS overseeing the freshwater trout. NMFS has described ESUs for all Northwest steelhead, whether they have been listed or not (Busby et al. 1996); however, the USFWS has not generally described DPSs for Northwest *O. mykiss* trout.

During the original coast-wide status review of steelhead conducted in the 1990s, the NMFS Biological Review Team concluded that, in general, *O. mykiss* trout are part of steelhead ESUs in cases where the two forms are sympatric and have an opportunity to interbreed (Busby et al. 1996). The review team was less conclusive about whether trout above artificial barriers were part of the ESUs. Trout that are sympatric with steelhead were also included in the ESUs by NMFS in the final listing determinations, but they were not listed. The steelhead in five of the ESUs in the Pacific Northwest were listed, including the Lower Columbia (63 FR 13347), Willamette, Mid-Columbia (64 FR

14517), Upper Columbia and Snake ESUs (62 FR 43937), all of which are in the Columbia Basin.

As a result of two recent court cases NMFS is now reexamining the biological relationship between trout and steelhead populations in the ESUs where steelhead are listed and is reassessing the extinction risk of the whole ESUs from the perspective of both life histories. First, the Hogan decision in Oregon concluded that the Services may describe distinct population segments for ESA listing, but once ESUs or DPSs are described, the Services cannot list only part of one of one of them (Alsea Valley Alliance v. Evans [161 F.Supp. 2d 1154, D. Oreg. 2001]). So if NMFS finds trout to be part of an ESU along with steelhead, the Service cannot assess the extinction risk of only the steelhead in the ESU or list only the steelhead. Second, lawsuits in California about non-anadromous *O. mykiss* upstream of man-made barriers (mostly impassable dams) made a similar argument, stating that such populations are related to the steelhead populations below the barriers and should be included in the ESUs and listed (EDC v. Evans, SACV-00-1212-AHS (EEA), United States District Court, C.D. California).

The purpose of this report is to provide more detailed information about trout and steelhead in the Columbia Basin listed ESUs. This report will address two major issues. The first section provides information that will be used to review whether trout and steelhead populations are biologically part the same ESUs, as defined by NMFS criteria. The second section provides information that will be used to review the extinction risks of entire ESUs if trout are considered along with steelhead. A similar, separate report is being prepared for California ESUs where steelhead are listed.

Constraints on data availability:

There is a substantial amount of data about the current and historic distribution, population structure, abundance and productivity of steelhead in the Columbia Basin. However, there is little similar data about trout. In much of the Columbia Basin, particularly where fisheries emphasize anadromous fish, wild trout lack the economic and sports fishing value that agencies use to justify the resources spent on steelhead monitoring. Nor have *O. mykiss* trout outside of the Oregon Great Basins, the Kootenai River and the upper Snake River received attention from ESA petitions or other conservation concerns. Some aspects of trout population dynamics may be simpler to understand than those of steelhead because individual trout populations have a more restricted distribution and are uninfluenced by broader system events in the Columbia mainstem and ocean environments. However, trout abundance is more difficult and more expensive to measure than steelhead abundance. Adult steelhead can be routinely counted as they migrate past fish ladders or weirs and steelhead redd counts can be conducted in some locations. Long time series of steelhead abundance data are available for many Columbia Basin tributaries. Comparable measures of trout abundance are possible only in a few cases. Trout are less migratory so they usually do not pass counting stations, and they usually breed in winter and spring when conditions for viewing small adults and redds on spawning grounds are poor due to snow and high flows. In most cases, a reliable estimate of trout abundance requires labor-intensive

sampling of fish density. The data are collected in sample reaches, usually by multiple-pass electroshocking, and are measured as the number of fish per unit area. Usually the measure is of all fish age one year or older; therefore juveniles as well as breeding adults are included. The fraction of the total population that is adults (the measure that would be similar to the counts of steelhead) can only be determined if age, maturity and size data are also systematically collected. In order to legitimately expand the estimate over an area as large as a large river basin or an ESU, a systematic sampling design with hundreds of sampling locations would be required (see Dambacher et al. 2001 for an example of an abundance survey conducted in the Oregon Great Basins). No such effort has ever been undertaken for *O. mykiss* trout in the Columbia Basin.

There are several further problems in assessing the abundance of trout and steelhead where the two life histories are sympatric. With the exception of steelhead adults and adult trout that are larger than smolts, the two life histories cannot be differentiated in the field. Trout and steelhead look identical as rearing juveniles, although in some cases they may segregate during rearing (Zimmerman and Reeves 2002). Adult trout also may resemble steelhead juveniles since they often can mature and breed when they are as small as 10 to 15 cm and as young as 2 years. Therefore, outside of breeding season, it can be difficult to determine whether adult trout are present among the steelhead juveniles. Steelhead develop some distinction as silvery smolts, although fluvial and adfluvial trout also may become silvery during their in-basin migrations. Age data, measured from scales, can be used to detect small fish that are trout breeding age and older than most smolts, but collection of the data is labor intensive.

There are also some complications about the methods used to expand density data to abundance estimates. The method used by Dambacher et al. (2001) assumed that all the fish observed were resident. Out-migration by part of the population, as would occur where steelhead are present, would introduce a serious error to the abundance estimate (J. Dambacher, ODFW). Also, fish density varies depending on habitat quality (Dambacher and Jones 1995) so fairly detailed information about habitat quality across basins is also necessary to make a valid expansion.

The combination of lesser attention to wild *O. mykiss* trout and monitoring difficulties results in very poor information for addressing this complex issue. This report depends strongly on personal communication from agency and tribal biologists in Oregon, Washington and Idaho. The most robust data sets available are presence/absence surveys and incidental observations that can be used to describe distribution and identify current and historic sympatry between the life histories. A few genetics surveys are available that include samples from known trout. Several specific studies on the relationship between trout and steelhead have occurred in the Yakima, Deschutes and Grande Ronde basins. Trout abundance or *O. mykiss* density data are available from several locations but are not standardized or systematic across the entire Columbia Basin. The density data are often for combined steelhead parr and trout. Only occasionally are the data expanded to a local abundance estimate by the biologists that collected it. Age or size data are occasionally available and can be used to very roughly estimate proportions of adult

trout. For all of these reasons, where measurements of trout abundance that are similar to steelhead abundance can be attempted, they are necessarily crude.

Overview of conditions that influence trout distribution and abundance in the Columbia Basin:

O. mykiss trout distribution and abundance are highly irregular across the Columbia Basin. Input from biologists across the Pacific Northwest indicates the following factors influence the abundance and distribution of *O. mykiss* trout:

- The freshwater life history is more common in the inland subspecies (*O.m. gairdneri*) than in the northern portion of the coastal subspecies (*O.m. irideus*). For example, there is only one resident *O. mykiss* population present along the entire Oregon coast between the Umpqua and Columbia rivers and it occurs above a natural barrier, whereas steelhead are present in every river (Kostow 1995). This difference is similar to the adult steelhead life history differences between the two subspecies in the same geographic area. The northern part of the coastal subspecies is typically winter-run steelhead and there are relatively few populations of summer-run steelhead. The inland subspecies is primarily summer-run steelhead. Trout seem to co-occur most often in association with summer-run steelhead. In the Pacific Northwest portion of the coastal subspecies, trout are sympatric with steelhead only in the larger coastal rivers such as the Klamath, Rogue, Umpqua and Columbia basins, each of which also include *O.m. irideus* summer steelhead populations (Kostow 1995, also Burgner et al. 1992).

- *O. mykiss* trout distribution is influenced by cutthroat trout distribution. Two subspecies of cutthroat trout are naturally sympatric with the Columbia Basin *O. mykiss* ESUs. Coastal cutthroat (*Oncorhynchus clarki clarki*) occur in the Willamette and Lower Columbia ESUs and in the most westerly basins of the Mid-Columbia ESU. Westslope cutthroat (*O.c. lewisi*) are naturally sympatric with *O. mykiss* in the John Day River (Mid-Columbia ESU), in the Clearwater and Salmon rivers (Snake ESU), and in some eastern Washington basins that drain the eastern Cascade Mountains (Upper Columbia ESU). Some introduced westslope cutthroat trout are also present within the native range of *O. mykiss* east of the Cascades (P. Howell, USFS, K. Meyer, IDFG).

  Subbasins tend to have one species of trout or the other, even where steelhead are present throughout. Coastal cutthroat are the dominant trout in most basins west of the Cascade Mountains, including the Willamette River (Kostow 1995). Westslope cutthroat appear to be more readily displaced by other species, including *O. mykiss*, and tend to be restricted to higher elevation, snow melt systems (Kostow 1995, P. Howell, USFS, H. Pollard, NMFS). Ecologically one can expect trout of either species to be more productive if they are allopatric with each other because they seem to share similar, although not identical, niches. *O. mykiss* trout tend to have a higher preference for riffles while cutthroat prosper in the steep boulder plunge-pool habitats that are found in headwater areas (WDFW, ODFW unpublished data). But the reason

why one species is present in one subbasin while the other species is in an adjacent subbasin is not understood.

It appears rare for both species of trout to naturally share a subbasin, but when they do they often form hybrid zones. Hybrids can be detected by molecular genetic analysis. Attempts to identify hybrids by visual assessment can be very misleading (Allendorf et al. 2003). Hybrids have been found among fish that are phenotypically either *O. mykiss* or *O. clarki*, and include F_1 hybrids, recent back-cross hybrids and ancient hybrids that include genomic DNA from one species and mitochondrial DNA from the other (Johnson et al. 1999, Wenburg 1998, Hawkins 1997, Allendorf et al. 2003, F. Utter, U. of Washington, and ODFW, NMFS, WDFW, USFWS, USFS and U. of Montana unpublished data). The most common distribution pattern in many naturally shared basins where genetic testing has occurred is that *O. mykiss* trout occur in lower reaches of a subbasin, *O. clarki* trout are in headwater reaches with a hybrid zone in mid-basin (Howell et al. 2003, U. of Montana and ODFW unpublished data). In areas of natural sympatry, hybrid swarms are usually not observed (Allendorf et al. 2003), however exceptions to this generality have been found in the John Day and Methow basins (Howell et al. 2003, P. Howell, USFS). Hybrids have also been detected among phenotypic steelhead (Wenburg 1998, Hawkins 1997, P. Howell, USFS, F. Utter, U. of Washington).

- It appears that freshwater or anadromous *O. mykiss* life history strategies may be influenced by factors that favor one or the other in a particular geographic area. Agency and tribal biologists across the Pacific Northwest have made the following general observations. More detailed information about many of these points is provided later in this report:

  - Freshwater life histories may be favored in highly productive subbasins; anadromy may be favored in more sterile basins (H. Pollard, NMFS, B. Knox, ODFW).

  - Freshwater life histories may be favored in inland areas where anadromous migrations are long and hazardous. The incidence of residency may increase if migrations become more hazardous.

  - Anadromous females are larger and several times more fecund than freshwater females. Therefore anadromy may be favored in females.

  - Freshwater males have higher survival to breeding age and may be able to adopt successful breeding strategies without growing to large size. Therefore residency may be favored in males.

  - Residency may be an option where anadromy is periodically not possible, for example where natural periodic migration blockages occur or where extremely slow freshwater growth periodically precludes smolting (Mullen 1992).

  - Residency will certainly occur where artificial migration blockages exclude anadromy. Reports from agency and tribal biologists indicate that trout are still present above every artificial barrier within historic steelhead range in the Columbia Basin.

➢ Trout occur above many natural barriers in the Columbia Basin that exclude steelhead. These trout may be very genetically divergent from the *O. mykiss* below the barriers, reflecting the consequences of their long reproductive isolation (e.g. Currens et al. 1990).

➢ Trout abundance may increase if steelhead become rarer, and especially if steelhead are excluded from an area (Bjornn 1978).

➢ The abundance of larger trout, which includes the older and most fecund females, appears to be very sensitive to angling pressure. Consumptive trout fisheries often target larger fish. For example, in some Oregon basins only trout >8 inches (20 cm) can be taken by regulation (ODFW 2003). Some biologists have observed that larger fish may not be seen in populations until wild trout angling becomes catch-and-release (D. Rawding and G. Mendel, WDFW).

➢ Trout abundance appears to be very sensitive to local freshwater habitat conditions and may vary by orders of magnitude with drought cycles, especially in inland desert basins (Dambacher et al. 2001).

➢ Some trout populations appear to be remarkably resilient. They apparently can depress or even skip reproduction in years with poor environmental conditions, then show a large production response when conditions improve (Dambacher et al. 2001).

➢ *O. mykiss* trout express their own wide variety of life histories. They may be strongly resident, moving only a few hundred yards during their life (e.g. Northcote 1992, Northcote and Hartman 1988). But other populations may be fluvial or adfluvial with complex annual migrations among freshwater habitats. The resident trout may be as small as 10 cm as adults while some migratory trout approach 50 cm, the size of small steelhead. This life history and adult size variation affects the productivity of the different trout phenotypes, particularly female fecundity.

The details of how this irregularity and variability occurs across the Columbia Basin ESUs are only partially understood. This irregularity is also why it is risky to expand the few trout abundance and density measurements that are available across an entire basin or across an ESU to develop an estimate of total trout abundance. Nor can information from one basin be assumed to represent conditions in an adjacent basin. Future improvements in the quantity and consistency of trout data across the Columbia Basin may permit a better understanding of the pattern of variation. Meanwhile, one can conclude that the role of trout in the status of ESUs varies depending on location and proceed with a cautious assessment of combined trout and steelhead distribution, abundance and other status indicators.

Information about the Evolutionary Relationship between Trout and Steelhead Populations

Introduction

This section reviews information about the evolutionary relationship between resident trout and steelhead as it pertains to their inclusion in the same ESUs. NMFS developed policy guidance for defining ESUs in the early 1990s (56 FR 58612). According to that guidance, an ESU is "… a population (or group of populations) that 1) is substantially reproductively isolated from other conspecific population units, and 2) represents an important component in the evolutionary legacy of the species" (Waples 1991). Trout and steelhead populations within a geographic area could either be combined in a single ESU, or each group could qualify as their own separate ESU, depending on whether the two criteria in the definition are met. Frequent interbreeding between the life histories is not required in order for the groups to be in the same ESU. ESUs may include sub-structure, including demographically independent populations (McElhany et al. 2000) and significant genetic variation between populations (see the review of genetic variation within steelhead ESUs described by Busby et al. 1996). Complete reproductive isolation between populations within an ESU may occur if it is recent in an evolutionary sense, or gene flow may be only periodic or rare.

The NMFS has already decided to place sympatric winter and summer steelhead populations together in the Lower Columbia ESU. Winter and summer steelhead have distinctive adult life histories that contribute to reproductive isolation between populations. Populations with the different life histories within basins have been shown to differ significantly at allozyme and DNA loci. Examples where studies have occurred include the populations in the Kalama River (Leider et al. 1984) and in the Hood River (Blouin 2003, Ardren 2003, U. of Montana and ODFW unpublished data). Trout populations may differ from steelhead similar to how winter and summer steelhead within a basin differ from each other and it would still be consistent with previous NMFS decisions if they were combined in a single ESU.

It would be easy to argue that steelhead and trout are each distinctive and an "…important component in the evolutionary legacy" of *O. mykiss* simply based on their unique adult life histories. The primary question is whether they meet the first criteria for an ESU and are also "…substantially reproductively isolated." The following discussion therefore focuses on this question.

Genetic Evidence

Genetic surveys of steelhead in the Columbia Basin expanded through the 1990s. Most of the information compiled by the mid-1990s was used by NMFS to originally define the six ESUs in the Columbia Basin and is discussed in detail in Busby et al. (1996). The current Columbia Basin ESUs and historic steelhead range are shown in Figure 1. Additional genetics analysis has been done on steelhead since the 1996 status review. Genetics data for trout are less common, and also have not always been collected

1. Willamette ESU (T)
2. Lower Columbia ESU (T)
3. Mid-Columbia ESU (T)
4. Upper Columbia ESU (E)
5. Snake ESU (T)
6. SW Washington ESU (Not listed)
7. McKenzie "redside" trout
8. Historic steelhead range above Pelton/Round Butte dams
9. Upper Deschutes trout
10. Malheur Lakes trout
11. Historic steelhead range above Hells Canyon dams
12. Shoshone Falls
13. Malad/Wood River trout
14. Historic steelhead range above Dworshak Dam
15. Palouse trout
16. Historic steelhead range above Grand Coulee Dam (extends into Canada to the headwaters)
17. Kootenai trout (also in Canada)

Figure 1. Map of the Columbia Basin showing the distribution of *O. mykiss* and the steelhead ESUs ▢. Several examples are shown of trout populations above dams within historic steelhead range ▢ , and of trout populations above natural barriers ▪ . Many more cases of trout above dams and natural barriers are present in the Columbia (see Table 2).

according to regional consistency protocols that would allow trout data sets to be combined with each other and with steelhead data sets. All available genetics data on inland *O. mykiss* in the Columbia River are currently being complied into an updated report for NMFS (F. Utter, U. of Washington). Since a separate comprehensive report is under preparation, this report only includes a brief summary of the available information as it specifically addresses the relationship between trout and steelhead.

Sympatric steelhead and trout

Only one completed genetics study in the Columbia Basin specifically addressed gene flow between the steelhead and trout life histories in sympatric populations. Pearsons et al. (1998) demonstrated that sympatric trout and steelhead in Teanaway River, a tributary of the Yakima Basin, were genetically indistinguishable based on the allozyme loci they analyzed. They were able, however, to separate the four steelhead populations in the Yakima Basin using their markers. They also used admixture analysis to argue that there was evidence of crosses between trout and steelhead, perhaps partly facilitated by hatchery programs for both species. However, other explanations are available that may explain the apparent hatchery influence that they noted and the markers they attributed to hatchery sources may be natural variation in the Yakima (Utter 2001).

Elsewhere in the Columbia Basin, trout and steelhead in areas where they are sympatric have not generally been distinguished during past genetic surveys. Most sampling in the basin has been of juvenile *O. mykiss* that could have been from either adult life history. In these studies (e.g. Busby et al. 1996, Currens 1997), there was generally little evidence that multiple populations had been included in the samples from any single sampling location where trout and steelhead were in sympatry, although the question was not specifically addressed. However, in all surveys with adequately wide coverage, the most notable genetic differences occurred geographically. All samples from single subbasins were genetically more closely related to each other than to samples from distant subbasins regardless of their possible adult life histories (also see discussion in Busby et al. 1996). These results indicate a genetic affinity between sympatric trout and steelhead within subbasins.

Since the late 1990s the potential for interbreeding between sympatric trout and steelhead has received greater attention. Genetic pedigree studies of steelhead are currently underway in three Columbia Basin tributaries, the Kalama and Hood rivers (Lower Columbia ESU) and the Imnaha River (Snake ESU). Preliminary results are available from the Hood River. This study is discussed in more detail below, but briefly the data indicate that a fairly large number of adult steelhead in the Hood had a non-anadromous parent, and particularly a non-anadromous male parent (Blouin 2003, Ardren 2003). Adult trout have specifically been sampled in an effort to better account for the parentage of fish in the Kalama Basin (C. Sharp, WDFW) and Imnaha Basin (P. Moran, NMFS); however, results from these last two studies are not yet available. Also in more recent steelhead genetic surveys, sampling has specifically targeted either adult fish or fish with clear smolt characteristics in an effort to avoid or distinguish trout (e.g. Pearsons et al.

1998, ODFW unpublished data). Results from some of these more recent sampling efforts will be included in the new comprehensive review by NMFS (F. Utter U. of Washington).

Trout above artificial barriers within historic steelhead range

O. mykiss trout above artificial barriers have been compared to steelhead below the barriers in the upper Snake (area above Hells Canyon Dam, Leary 2001), in the Clearwater (area above Dworshak Dam, R. Waples, NMFS unpublished data), and in the Umatilla (areas above irrigation diversions in Butter and McKay creeks, Currens 1997).

Leary (2001) demonstrated that there was relatively little genetic divergence at the allozyme loci he investigated between the Oxbow and Pahsimeroi steelhead hatchery stocks, which were established using steelhead that had been collected at Hells Canyon Dam, and trout populations in the Powder River and other small tributaries of the Snake just above the Hells Canyon dams. Leary (2001) suggested that some of the trout populations had evidence of introgression with hatchery rainbow trout from the old McCloud hatchery stocks based on the presence of certain alleles, but all samples contained native inland *O. mykiss.* The only samples in Leary (2001) that were from further up the Snake Basin were also from above natural barriers.

The NMFS compared a sample of resident *O. mykiss* collected from the North Fork of the Clearwater above Dworshak Dam to steelhead from Dworshak Hatchery. The purpose of this test was to further explore the uniqueness of the Dworshak Hatchery steelhead stock that had been previously described (Busby et al. 1996). The results demonstrated a genetic affinity between the resident *O. mykiss* above the dam and the Dworshak Hatchery steelhead, which were more similar to each other than to any other Columbia and Snake River samples (R. Waples, NMFS unpublished data).

Currens (1997) compared resident *O. mykiss* from above artificial barriers in McKay and Butter creeks to samples from the Umatilla steelhead and from other locations below barriers in the Umatilla Basin. He found significant differences between most samples, including temporal variation in samples collected from the same locations in different years. However, only the resident *O. mykiss* samples from upper McKay Creek consistently clustered with each other, distinctive from samples from other locations. The Butter Creek samples clustered among the other Umatilla samples. Currens (1997) proposed that the apparent uniqueness of the fish in the upper McKay Creek might have been due to introgression with hatchery rainbow trout or hatchery steelhead from non-local stocks. His Umatilla samples were not compared to samples from other locations in the Columbia Basin.

Two additional surveys of resident *O. mykiss* above artificial barriers in the Columbia Basin have occurred, one in the Deschutes River above Pelton/Round Butte dam complex (Phelps et al. 1998), and the other in the upper Columbia above Chief Joseph/Grand Coulee dams (J. Whalen, WDFW; C. Vail, WDFW). However the samples were not compared to steelhead immediately below the dams, although Phelps et al. (1998) made

some comparisons to steelhead elsewhere in the Columbia Basin. Both studies found the trout to be of the inland subspecies, and both studies found evidence in a few areas that introgression with hatchery rainbow had occurred, based on the presence of certain alleles.

Trout above natural barriers

Several studies have demonstrated that *O. mykiss* trout above natural barriers in the Columbia Basin are highly divergent from the populations below the barriers. These include Currens et al. (1990) who demonstrated the uniqueness of the trout above White River Falls in the lower Deschutes Basin. Currens (1997) also demonstrated the uniqueness of *O. mykiss* trout populations in isolated basins in SE Oregon. These included the population from the Donner und Blitzen River in the Malheur Lakes Basin, which became isolated from the Malheur River, a tributary of the Snake, only about 3 to 5 thousand years ago. The uniqueness of the trout population in the upper South Fork of the John Day above Izee Falls has also been demonstrated as has the uniqueness of several populations in small streams that enter Hells Canyon over waterfalls (Currens 1997, Currens and Stone 1989).

Knudsen et al. (2002) studied the genetic structure of the isolated *O. mykiss* trout population in the Kootenai River. Most of the Kootenai Basin was naturally isolated by falls low in the basin prior to subsequent blockage by dams. Many naturally blocked upper Columbia Basin tributaries, such as the Spokane and Pend Oreille rivers, have native westslope cutthroat above their waterfall barriers. The Kootenai, uniquely for its location, has native *O. mykiss* trout. Kundsen et al. (2002) demonstrated that while the Kootenai populations are clearly of the inland subspecies, each individual population sampled was highly unique.

Leary (2001) also investigated some populations of trout that were above Hells Canyon Dam, but then also above natural barriers. These isolated trout populations were less similar to the Snake River steelhead hatchery stocks than were the populations below the natural barriers yet still above the dams. The Malad/Wood River populations, located above the barrier falls that is near the confluence of the river with the Snake, were particularly distinctive.

A population of *O. mykiss* trout that is isolated by waterfalls and glacial till in Packwood Lake in the upper Cowlitz Basin was studied by Lucas and Chilcote (1982). The trout and steelhead in the lower Cowlitz (Lower Columbia ESU) are coastal *O. mykiss*, but allozyme and morphometric analyses suggested that the Packwood trout population was more similar to the inland subspecies. Similar phenotypically "redband-like" trout have been observed above high waterfalls in the Clackamas, Sandy and Columbia Gorge tributaries in Oregon (all generally within the range of the coastal subspecies, Lower Columbia ESU)(ODFW and U. of Montana unpublished data).

Phelps et al. (1998) studied isolated *O. mykiss* populations above Big Falls and North Fork Crooked River Falls in the upper Deschutes. The populations were highly divergent

from each other, and from the several other Columbia Basin populations that were included in the analysis. Little geographic pattern was revealed within the upper Deschutes Basin and some populations were particularly unique with alleles that have not been found elsewhere in the species. A pattern of individual, distinctive populations with little evidence of large-scale structure was also seen in coastal cutthroat trout genetic surveys (Johnson et al. 1998) and in some westslope cutthroat surveys (Howell et al. 2003). These results suggest that the structure of isolated resident trout populations can be highly complex. Many populations are likely under the strong influence of genetic drift caused by periodic severe population bottlenecks and extended periods of complete reproductive isolation. Anthropogenic isolating mechanisms, particularly lethal water temperatures and stream dewatering has been observed during droughts in eastern Oregon streams and severe population size fluctuations have been observed (Dambacher et al. 2001). This combination of population dynamics and high degree of differentiation at neutral genetic markers in individual populations is consistent with populations prone to genetic drift (Nei et al. 1975).

Trout in the upper Willamette

The *O. mykiss* trout in the upper Willamette above the Calapooia subbasin are not isolated from other upper Willamette *O. mykiss*, including the listed steelhead, by any physical barrier. However, the uniqueness of these trout have long been recognized (Fulton 1970). This uniqueness was confirmed by allozyme analysis conducted by NMFS in the late 1990s (D. Teel, NMFS unpublished data). These trout, in the McKenzie and Middle Fork Willamette, appear to be distinctive from all other coastal *O. mykiss*. They show little evidence of hatchery rainbow trout influence, even though hatchery trout have been planted among them. There was some evidence of hybridization with coastal cutthroat trout. The reason why this pattern is maintained, absent a physical barrier and given the close geographic proximity of the populations, is not known.

Otolith Data

Biologists across the Columbia Basin generally agree that otolith microchemistry data would be useful for understanding the relatedness of freshwater and anadromous *O. mykiss*. The method can provide information about whether fish with one life history had a mother with the alternate life history. The method has several limitations, however. First, it requires that the ratio of strontium and calcium in the primordia region of the otolith of a fish be influenced by the saltwater or freshwater growth of the female parent during egg development. Strontium levels are often higher in saltwater causing a higher proportion of it to occur in the otolith primordia of eggs produced by a steelhead. However, there are areas in the Columbia Basin where freshwater strontium levels are also high, which may produce ambiguous results, especially in steelhead which have an extended period of freshwater rearing (J. Ruzycki, ODFW; Volk 1999). Second, otolith chemistry provides information only about the anadromy or residency of the female parent. This is a problem in *O. mykiss* where gene flow between the life histories appears to be particularly facilitated by resident male parents while the offspring tend to express the life history of their mothers (discussed further below). Third, otolith microchemistry

requires lethal sampling and most biologists believe that a large sample size is required in order to obtain unambiguous results. Lethal sampling of large numbers of wild fish for this purpose is not popular among the public so the surveys have not been pursued in many areas (A. Viola, WDFW and H. Bartlett, WDFW). Finally, for the problem explored in this paper, otolith data can be used as evidence of relatedness of trout and steelhead, for example when an anadromous fish is shown to have had a resident mother. This kind of "positive" result provides evidence that the trout and steelhead may be part of the same ESU. However, a "negative" result cannot be used, alone, to conclude that the two life histories belong in different ESUs. For example, an anadromous fish may have had a resident father, which would not be detected in otolith data, or trout and steelhead may simply be forming different populations with infrequent interbreeding within the same ESU.

There is only one completed study of *O. mykiss* otolith microchemistry in the Columbia Basin. Zimmerman and Reeves (2000) analyzed otoliths from 20 adult steelhead and 38 adult trout in the Deschutes River (Mid-Columbia ESU). The strontium level in the Deschutes has been shown to be low enough to allow the method to be effective in this basin (Zimmerman and Reeves 2002). They saw no evidence among their samples that steelhead had resident trout mothers, or that trout had steelhead mothers. They comment, however, that they cannot draw any conclusions about the life histories of fathers. In earlier work in the same area, the same authors documented trout and steelhead spawning together on redds, although such redds were infrequent (Zimmerman and Reeves 1996). They also conducted a similar study on the Babine River in British Columbia, where they saw evidence of interbreeding between the life histories in a sample of 33 steelhead and trout.

In additional work, the same authors demonstrated an apparent segregation of the rearing progeny of steelhead and trout in the lower Deschutes Basin. Samples of juveniles from the mainstem Deschutes mostly had trout mothers, while the juveniles from below falls in several tributaries mostly had steelhead mothers (Zimmerman and Reeves 2002). The study fish were lethally sampled as juveniles; therefore, their own adult life history was never expressed and was thus unknown.

Otoliths have also been collected by ODFW from *O. mykiss* in the Grande Ronde Basin (Snake ESU), but the chemical analysis has not been completed.

Life History Data Pertinent to Interbreeding

The relative spawning times and locations of trout and steelhead may provide evidence of opportunities for interbreeding or reproductive isolation. Spawning time and location data have been collected on the Yakima and Deschutes rivers (Mid-Columbia ESU), and incidental observations have been made in many other basins. The two studies demonstrate that trout spawn over a much wider geographic distribution than steelhead (Pearsons et al. 1998), and over a wider timing distribution than steelhead (Pearsons et al. 1998, Zimmerman and Reeves 2000). Trout can penetrate headwater reaches that are not used by steelhead. Steelhead are restricted by their relative size to mainstems and larger
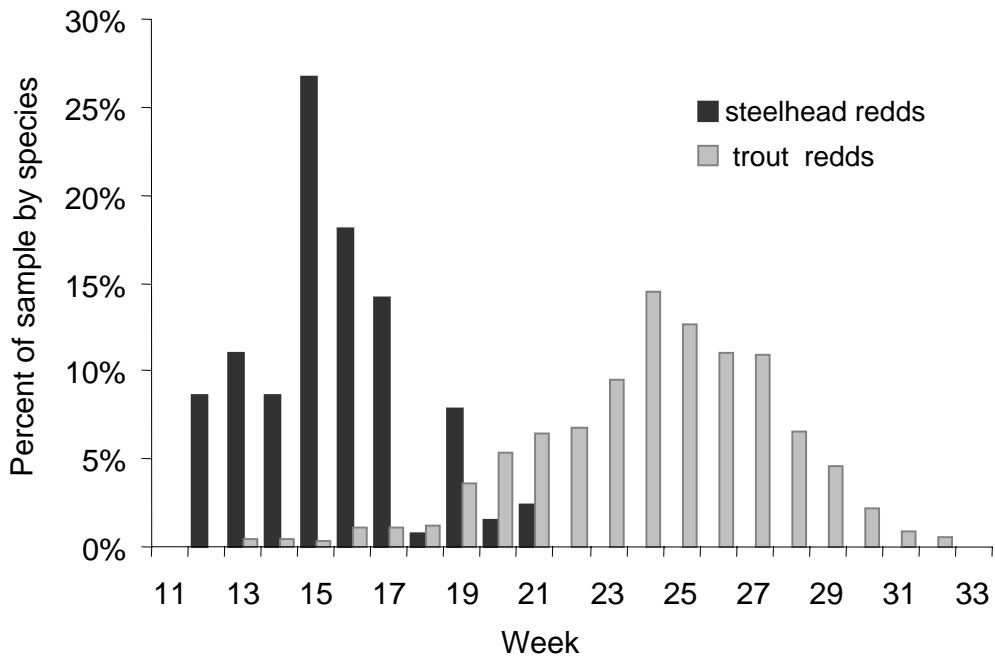
Figure 2a. Proportion of the trout and steelhead populations on the mainstem Deschutes River spawning by week showing different peak spawn times for each life history (data from Zimmerman and Reeves 2000, Table 1).
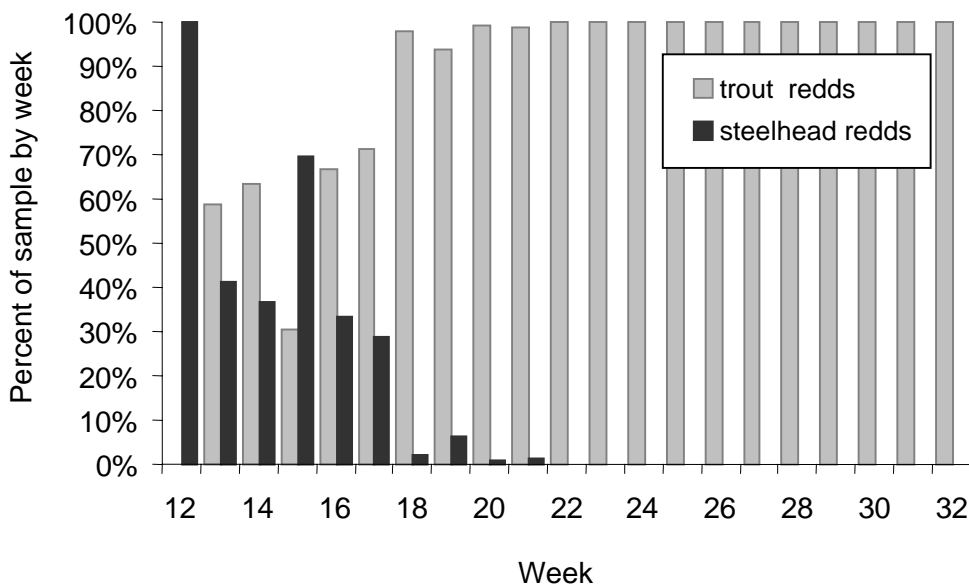
Figure 2b. Proportion of the redds per week that were made by trout or steelhead on the mainstem Deschutes River. Trout produced about 97% of the observed redds and out-numbered the steelhead even during the steelhead peak spawn time (same data as Figure 2a).

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tributaries. Trout can spawn from November to August if summer water quality is sufficient. Peak spawn time for trout can differ in different tributaries of the same basin, probably related to flow and temperature conditions. For example, Zimmerman and Reeves (2000) found the peak spawn time for trout in the mainstem Deschutes to occur in June, but ODFW studies on the Metolius, a tributary of the Deschutes, found the peak spawn time for trout to occur in December (Hemmingsen et al. 1994). Steelhead can also spawn over a wide time period, with summer steelhead spawning earlier (usually February-April) and winter steelhead spawning later (usually April-June) (also see Leider et al. 1984).

Pearsons et al. (1998) demonstrated that there was enough overlap in the spawning time and spatial distributions of trout and steelhead in the Yakima to provide opportunities for interbreeding. The steelhead distributions were generally nested within the trout distributions. Zimmerman and Reeves (2000) believed there was less opportunity for interbreeding in the mainstem Deschutes, mostly because of some differences in microhabitat use during spawning by the two life histories. However, although peak spawning time for the two life histories differed on the part of the Deschutes they surveyed, spawning trout vastly out-numbered steelhead, including during the peak steelhead spawn time (see Figure 2, based on Zimmerman and Reeves (2000), Table 1). Zimmerman and Reeves (1996) also documented several trout x steelhead pairings on redds during the later portion of the steelhead spawn time.

Other Columbia Basin biologists have also noted that trout and steelhead share spawning grounds and have similar spawning times. Intermingling of trout and steelhead redds and spawning fish have been observed on the Washougal (Lower Columbia ESU, D. Rawding, WDFW), on the Klickitat (Mid-Columbia ESU, B. Sharp, YN), on the John Day (Mid-Colombia ESU, T. Unterwegner, ODFW), on the Walla Walla and Umatilla (Mid-Columbia ESU, C. Contor, Umatilla Tribes), on the Tucannon (Snake ESU, M. Schuck, WDFW) on the Grande Ronde and Imnaha (Snake ESU, B. Knox, ODFW) and on the upper Salmon (Snake ESU, T. Curet, IDFG). These spawning ground observations have all been made in the spring. The general perception of the biologists is that the trout appear to spawn somewhat later than the steelhead, perhaps overlapping the later tail of steelhead spawn time. Other areas where steelhead spawning ground counts occur but trout or trout redds have not been seen include the upper Grande Ronde (Snake ESU, J. Zakel, ODFW) and the Santiam (Willamette ESU, S. Mamoyac, ODFW). The lack of observations are likely explained by high flows and otherwise poor conditions at the time that make it difficult to see small trout and redds. Steelhead spawning ground counts do not currently occur in most other geographic areas in the Columbia Basin. In Idaho and the upper Cascades in Washington, many trout and steelhead streams are in remote locations that can be difficult to survey in the winter and streams are often covered by snow at the time spawning occurs.

Observations of Trout Spawning with Steelhead

Pearsons et al. (1998) provided evidence that trout spawned with steelhead in the Yakima Basin. They observed several female steelhead that were on their redds with male trout and apparently spawned with them since no other steelhead were ever seen in the areas.

Spawning between steelhead and trout has also been documented on the Deschutes River (Zimmerman and Reeves 1996). During their survey, the authors counted 48 steelhead redds, 1,430 resident trout redds, and two steelhead x trout redds. They also noted additional polyandrous redds that had both male trout and male steelhead present.

B. Knox, ODFW, also reports seeing spawning between trout and steelhead in the Grande Ronde, particularly in Prairie Creek, a tributary of the upper Wallowa basin. He reports that this creek appears to be a particularly productive one for trout, which are large and abundant. Local biologists have observed spawning in March and have seen all combinations of trout and steelhead inter-spawning. Other biologists have also observed trout spawning with steelhead in other basins. Typically these events involve one or several small male trout with a female steelhead. A male steelhead may also be present and courting the female, with the trout essentially behaving like a small steelhead jack (T. Unterwegner, ODFW, John Day Basin; C. Contor, Umatilla Tribes, Umatilla Basin; D. Rawding, WDFW, Washougal Basin; B. Sharp, YN, Klickitat Basin; T. Curet, IDFG, Salmon Basin).

Evidence that Trout and Steelhead can Produce the Alternate Life History

Some of the strongest evidence that trout are able to produce out-migrating smolts is a breeding study using trout and steelhead from the Grande Ronde basin (Snake ESU) (Ruzycki et al. 2003). The following experimental crosses were produced: rainbow x rainbow, rainbow x steelhead (both gender combinations), steelhead x steelhead and residual females that had been produced by steelhead parents x steelhead or rainbow males. The steelhead used in the study were return adults from an ODFW hatchery stock (Wallowa stock). The trout were collected as wild, mature adults from natural spawning areas in the Grande Ronde. The residual females were the offspring of hatchery steelhead that had been released and then were recollected from the river after they had failed to out-migrate.

Samples of the progeny of the crosses were PIT-tagged and released, and recaptures at PIT tag detectors in mainstem Columbia and Snake river dams were recorded. The results are preliminary, and the releases have been small (the numbers of fish released per treatment group range from 394 to 1,869). However, out-migrants, presumably smolts, from all cross combinations have been detected (Figure 3, based on Ruzycki et al. 2003. Table 3). The steelhead x steelhead crosses had the highest detection rates (39%), while
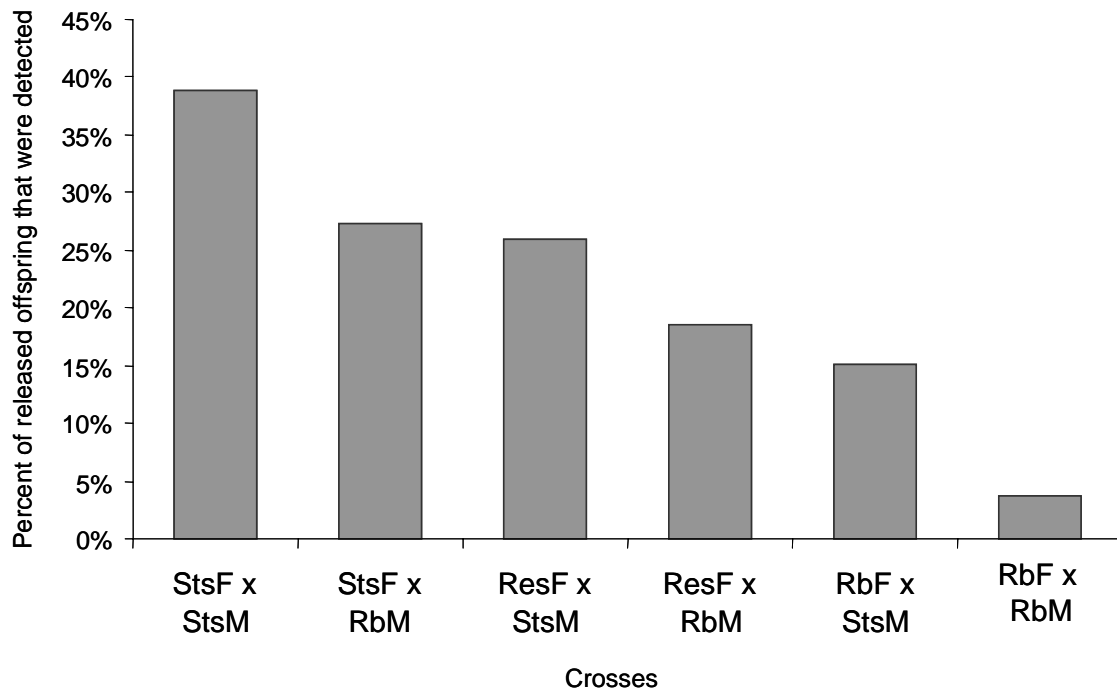
Figure 3.   The rate of detection at Columbia and Snake River dams of PIT-tagged progeny from experimental crosses that were released into the Grande Ronde. Progeny from steelhead x steelhead (Sts) crosses, rainbow x rainbow (Rb) crosses, rainbow x steelhead crosses and from residual females from steelhead parents (Res) and either rainbow or steelhead crosses.   All years of data combined. Based on Ruzycki et al. 2003, Table 3.

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the trout x trout crosses had the lowest (4%), but even they produced offspring that out-migrated past the downstream dams. The female steelhead x male trout crosses, which is the combination most often observed when the two life histories appear to be interbreeding on natural spawning grounds, produced the second highest detections (27%). The offspring of residual females had intermediate detection rates.

The authors noted that the offspring of female trout were significantly smaller than those of female steelhead, regardless of the male parent phenotype. Juvenile size and growth rate at the time of release will influence smoltification (Wagner et al. 1963). These results suggest that the female phenotype may have more influence on the production of out-migrating offspring, although the male phenotype also had an effect. The authors also observed that different trout populations appeared to produce different rates of out-migrants.   The trout population that was used as the source of adults in 1998-2000 produced more out-migrants than the one that was used in 2001 (less than 1% of offspring detected as out-migrants in 2001 compared to 10% in 1998 - 2000). The results hint at a possible genetic basis underlying smolting, but if this is true the necessary genetic variation was present among trout as well as in steelhead.   One confounding factor was that the size of eggs was influenced by the size of females such that the eggs

from trout were generally smaller than those from steelhead. Egg size may influence juvenile size and growth rate. Also, the experimental fish were all produced in a hatchery where growth rates and juvenile size phenotypes, and therefore smoltification, can be modified environmentally (Kostow 2003). The trout progeny may have experienced an environmentally induced growth spurt under these conditions that increased their smolting beyond what would naturally occur in a stream. But, regardless of the genetic, maternal or environmental basis, the results were clear that trout, including both males and females and crosses between the two without a steelhead parent involved, can and do produce out-migrants. Crosses that include a steelhead parent increased the production of out-migrants.

This study is still in early stages and adult offspring have not yet returned. The sample sizes were so small and smolt-to-adult survival of Snake River steelhead is so low, that it will be unlikely that very many adult offspring of any treatment group will return. The authors note, however, that the final test of whether trout were able to produce steelhead will require a demonstration that they were able to produce adult steelhead offspring.

The pedigree results from the Hood River study mentioned previously also provided strong evidence that non-anadromous parents contributed to the adult steelhead populations in this basin during the 1990s. All of the adult steelhead that spawned in the Hood River were intercepted and sampled at Powerdale Dam since 1992. Because of the configuration of the dam and trap, all steelhead must enter the trap before they can pass upriver, so the possibility of missing a steelhead that passed into the spawning grounds was extremely small. Also the reliability of assigning an offspring to a parent was very high in this study. The researchers were able to assign 84% of the adult steelhead returning to Powerdale Dam to a steelhead parent that was known to have spawned in the basin. However, about 40% of the fish could only be assigned to a female parent, while about 10% could only be assigned to a male parent (Blouin 2003, Ardren 2003). The other parent in these cases was apparently a non-anadromous fish since it had to have been one that was above the dam but did not pass the dam. At this time, it is not clear which non-anadromous parents, among several possible candidates, participated in the production of these offspring. The results were pooled for summer and winter steelhead and for naturally-produced fish that were offspring of either wild or hatchery parents. Native *O. mykiss* trout are sympatric primarily with the summer steelhead above Punchbowl Falls in the West Fork Hood River, while coastal cutthroat are the dominant trout elsewhere in the basin. Hatchery rainbow trout were being stocked in the East Fork Hood River, where the wild winter steelhead spawn, during part of this study. Finally, the steelhead hatchery programs may be producing some residuals that survive to spawn. Further analysis of the data is planned and may clarify these questions.

There are several natural examples of resident trout apparently producing steelhead in the Columbia Basin. One example occurred on the Methow River (Upper Columbia ESU). A power dam was constructed near the mouth of the river in 1915. Mullen et al. (1992) reported that chinook were dip netted below the dam and passed upriver "…but there is no evidence that steelhead and coho were so passed." Resident *O. mykiss* remained above the dam. Soon after the dam was removed in 1929, steelhead began to return
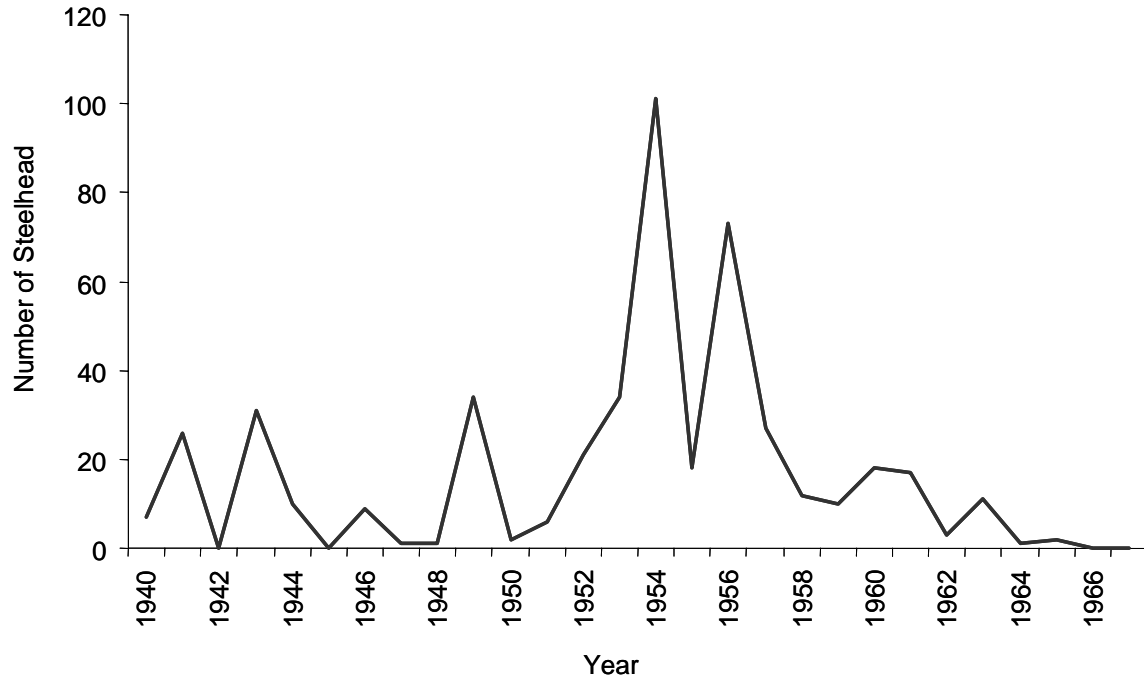
Figure 4. Number of adult steelhead counted at Roza Dam in the upper Yakima Basin between 1940 and 1967. Data provided by P. Monk, YBJB.

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naturally to the area above the dam site. Local biologists believe this rapid recolonization, which was unique to steelhead compared to other salmonids historically in the basin, was facilitated by the trout producing steelhead once the migration barrier was removed (H. Bartlett, WDFW).

Another possible example of trout contributing to steelhead production occurred in the upper Yakima Basin above Roza Dam. The upper Yakima basin was historically the most productive part of the basin for steelhead. Steelhead passage at Roza Dam was very poor between 1940 and 1967, dropping to two or fewer fish in some years (Figure 4). After passage was improved the steelhead returned to the area, causing local biologists to speculate that the resident *O. mykiss* that had remained above the site contributed to the rapid recolonization (Berg 2001). Trout are still the dominant *O. mykiss* life history above Roza Dam.

A similar blockage occurred at Faraday Dam on the mainstem Clackamas River between 1917 and 1939 (Kostow 1995). Anadromous fish naturally recolonized the upper basin after passage was restored. ODFW now estimates that 80% of the wild winter steelhead population occurs above the site of the historic blockage (ODFW 1992). The role of resident trout in reestablishing steelhead to the upper Clackamas is uncertain, although trout were and still are present in the portions of the upper basin used by the steelhead. In addition to steelhead, both coho and spring chinook also recolonized the upper

Clackamas without any contribution by resident fish, indicating that populations below such blockages will also contribute to recolonization.

Trout populations occur in all locations in the Columbia Basin where dams or other artificial blockages have eliminated access by steelhead. In most of these areas, trout were historically present with the steelhead and it is difficult to determine whether steelhead residualized and contributed to these populations, or whether the trout populations simply continued or perhaps increased on their own after steelhead were excluded.

But there are a few cases where robust trout populations now exist in areas where fish with a freshwater life history were rare or perhaps absent historically. A good example is the Bull Run subbasin on the Sandy River (Lower Columbia ESU). The Sandy Basin has a winter steelhead population, but cutthroat trout are the dominant trout species in all areas sympatric with steelhead (ODFW and U. of Montana unpublished data). Dams in the Bull Run subbasin blocked an area that was historically used by steelhead. Robust populations of adfluvial *O. mykiss* trout have become established in the reservoirs, spawning and rearing as young juveniles in inlet tributaries and then migrating to rear in the reservoirs (J. Massey ODFW, retired). This watershed is unique in that it is closed to public access because it is the water supply for the City of Portland. This closure means there is no history of planting hatchery trout in the reservoirs and no trout angling. It is highly likely that the source of the trout populations was the steelhead.

Another basin where trout populations apparently have become established from steelhead after closure of a dam is in the North Fork Clearwater above Dworshak Dam (Snake ESU). It is thought that westslope cutthroat were historically the dominant resident trout in the basin, although it is likely that some *O. mykiss* trout were also present. *O. mykiss* trout populations are now well established above Dworshak Dam (C. Corsi, IDFG). Genetic analysis confirms the similarity of the trout above Dworshak and the steelhead below the dam and at Dworshak hatchery (R. Waples, NMFS unpublished data).

Robust adfluvial trout populations have also become established in Lake Roosevelt above Grand Coulee Dam, although trout were historically present and perhaps abundant in this area. Genetics analyses have demonstrated that the Lake Roosevelt trouts are native rather than introduced hatchery fish (J. Whalen, WDFW). A healthy *O. mykiss* trout population is also present above Condit Dam on the White Salmon River, possibly related to the historic steelhead population in the basin (P. Connolly, USGS). In most cases, however, the historic presence of wild trout, a history of hatchery trout plantings and high angling pressure confound the origin of trout populations in reservoirs.

Steelhead may produce some resident fish even where their migrations are not blocked. Many authors have recorded the incidence of residual, precocial steelhead among hatchery steelhead (e.g. Viola and Schuck 1995, McMichael et al. 1999). Although residual hatchery steelhead may occur anywhere, they seem to be more common in the upper Columbia and Snake basins. They are most often males. They do not migrate to

the ocean, and they are often ripe and ready to spawn at the time they are released. They are generally viewed as a problem. The behavior appears to be influenced by environmental manipulation since increasing growth rates near the time of release can apparently induce smolting and decrease the incidence of the behavior (Wagner et al. 1963), although excessive growth and size of smolts can increase it (C. Sharp, WDFW). However, these fish may also be expressing life history variation that allows some steelhead, particularly males, to assume residency and breed without anadromy under some conditions.

Another observation that suggests that *O. mykiss* life histories may differ by gender is that steelhead sex ratios are often skewed strongly toward females, particularly in summer steelhead populations. For example, the wild summer steelhead population in the Hood River is about 70% female (adult returns to Powerdale Dam)(Olsen and French 2000), while about 40% of the steelhead in the Hood have been shown to have non-andromous male parents (Blouin 2003, Ardren 2003). Interestingly the skewed sex ratio is only seen in wild fish. Hood River hatchery fish, which were derived from local wild fish, returned to the basin in a 50:50 sex ratio during the 1990s.

Skewed sex ratios have also been observed in other basins. The Yakima summer steelhead populations have ranged from 63% to 73% female (Berg 2001, Hymer et al. 1992). The population of steelhead in the Pahsimeroi, a tributary of the Salmon River in the Snake, are about 59% female (adult returns to a weir)(D. Engemann, IDFG). The steelhead populations in the Entiat and Methow have ranged from 72% to 82% female (Hymer et al. 1992). Peven et al. (1994) recorded that out-migrating steelhead smolts, captured in the Rocky Reach juvenile bypass, were 63% female indicating that the sex ratio skew in steelhead is not just an adult phenomenon. In all these cases, the steelhead populations were sympatric with trout populations. Burgner et al. (1992) reported that steelhead captured in ocean sampling, which included fish from many different populations including some that were not sympatric with trout, were 54% female.

There may be several reasons why there are fewer male than female steelhead in addition to the possibility that some males may assume resident life histories. Males may consistently suffer much higher mortality rates than females. Also, in lower Columbia Basin steelhead populations, the proportion of repeat spawners among wild steelhead can reach 10% or more and repeat spawners can be biased toward females (Burgner et al. 1992, Olsen and French 2000, WDFW unpublished data). Repeat spawning is less common in inland steelhead populations. Only about 2% of the wild adults passing Bonneville Dam were repeat spawners in 2000 through 2002 (ODFW unpublished data, also Burgner et al. 1992).

Migratory trout populations also tend to have sex ratios that are biased toward females. One example is the fluvial population that is monitored on the Pahsimeroi (Salmon Basin, Snake ESU) which was 70% female (D. Engemann, IDFG) and another is the adfluvial Packwood Lake population (Cowlitz Basin, Lower Columbia ESU) which was 63% female (Lucas and Chilcote 1982). Possibly some of the males in these populations were resident, rather than migratory trout.

Major Barriers and the Historic Distribution of Steelhead

The Columbia Basin has many natural and artificial barriers to steelhead, and *O. mykiss* trout are present above many of them. The natural barriers include waterfalls, natural sinks, closed basins, and lava dams that have excluded anadromous fish passage since they were formed. The natural barriers may range from several thousands of years old to more ancient, unknown ages. Native *O. mykiss* trout are not present above all natural barriers in the Columbia Basin, but they occur above some of the oldest, such as the closed Great Basins in southeastern Oregon, several of which have no demonstrated historic connection to other water bodies (Kostow 1995). Given the age of the natural barriers, and based on several genetics studies of the *O. mykiss* trout isolated above them (e.g. Currens et al. 1990, Currens 1997, Nielsen et al. 1999, Leary 2001), it is likely that the trout populations that are isolated by these natural features each constitute unique evolutionary lineages of their own, separate from steelhead or from any other trout populations.

Artificial barriers that now block anadromous fish from areas they used historically range from large dams to culverts and small irrigation berms and occur throughout the Columbia Basin. The large dams are well known and some of them block large areas, such as much of the Snake Basin, which is blocked by the Hells Canyon complex of dams. The small artificial barriers are numerous, widespread and generally not well accounted for. They may block only a few miles of historic anadromous fish habitat. The artificial barriers are recent. The oldest extant large dams date to the early 1900s, while the newest were closed in the 1970s. In the Columbia Basin, *O. mykiss* trout are reported to occur above artificial barriers in all areas that historically had steelhead. Recent genetic events, like founder affects and bottlenecks, may have caused some of the trout populations to diverge, but generally their evolutionary relationship with the steelhead below the artificial barriers is recent.

The NMFS has identified three categories that describe the relationship between anadromous steelhead and non-anadromous trout:

Category 1. The two life histories are currently sympatric. They co-occur in the same basin with no apparent physical barrier to interbreeding.

Category 2. Resident fish occur above a natural, long-standing barrier to anadromous fish and interbreeding has not occurred since the formation of the barrier. Although one-directional gene flow down stream may be possible in some cases, studies of long-standing isolated trout populations demonstrate that they eventually loose the segment of the population that out-migrates and adopt strongly resident life history characteristics (Northcote and Hartman 1988). They can also develop distinctive genetic characteristics (e.g. Currens et al. 1990).

Table 1. Distribution of *O. mykiss* trout by category in the Columbia Basin ESUs, based on information provided by agency and tribal biologists. Only major barriers are noted; numerous small barriers, both natural and artificial, also exist. *O. mykiss* trout distribution may be restricted or otherwise influenced by the presence of native *O. clarki* trout in some basins. The generalized listing of basins and subbasins does not imply that these constitute single trout populations or that trout distribution is continuous throughout the areas listed.

ESU	Category 1 (Sympatric)	Category 2 (Major Natural Barriers)	Category 3 (Major Artificial Barriers)
Willamette	Pudding/Molalla Lower Santiam Calapooia Tualatin (Gales Cr.)	All subbasins upstream of Calapooia: McKenzie MFk. Willamette	NFk. Santiam (Big Cliff/Detroit dams) SFk Santiam (Green Peter Dam)

Table 1 *cont.* Distribution of *O. mykiss* trout by category in the Columbia Basin ESUs.

ESU	Category 1 Trout Populations (Sympatric)	Category 2 Trout Populations (Major Natural Barriers)	Category 3 Trout Populations (Major Artificial Barriers)

Lower Columbia	Historic use of lower basins by trout may have been greater
	
	Wind
	Clackamas:
	     Collawash
	Hood:
	     West Fk
	     Middle Fk
	Sandy[1]
	Upper Cowlitz
	Upper Kalama
	EFk and upper Lewis
	Upper Washougal
		Clackamas:
		     Roaring R.
		     North Fk
		     South Fk
		     Memaloose[1]
		
		Sandy:
		     Little Sandy
		     Salmon[1]
		
		Some Columbia Gorge tributaries
			Cowlitz (Mayfield Dam)[2]
			
			Lewis (Merwin Dam)
			
			Sandy (Bull Run dams)

[1] Expected presence of *O. mykiss* trout, but not confirmed by reliable field observations.
[2] Volitional passage does not occur, but steelhead are currently trucked above this dam.

Table 1 *cont*. Distribution of *O. mykiss* trout by category in the Columbia Basin ESUs.

ESU	Category 1 Trout Populations (Sympatric)	Category 2 Trout Populations (Major Natural Barriers)	Category 3 Trout Populations (Major Artificial Barriers)

Mid-Columbia	Historically all areas where steelhead are/were present. Trout distributions currently more restricted, especially in lower mainstems
	
	Lower Big White Salmon
	
	Fifteenmile:
	        Eightmile
	
	Deschutes
	Klickitat
	Umatilla
	John Day
	Walla Walla
	
	Yakima:
	        Upper Yakima
	          Naches
	
	Some other small tributaries
		All natural barriers upstream of White Salmon and Deschutes basins:
		
		Little White Salmon
		
		Deschutes:
		        White River
		    Upper Deschutes (Big Falls)
		      Upper NFk Crooked R.
		
		John Day:
		     Upper SFk John Day
			Trout distributions currently more restricted than historically
			
			White Salmon (Condit Dam)
			
			Deschutes (Pelton/Round Butte dams):
			        Metolius
			       Squaw Cr.
			      Crooked River
			
			Umatilla (irrigation dams):
			       Willow Cr.
			        Butter Cr.
			        McKay Cr.

Table 1 *cont*. Distribution of *O. mykiss* trout by category in the Columbia Basin ESUs.

ESU	Category 1 Trout Populations (Sympatric)	Category 2 Trout Populations (Major Natural Barriers)	Category 3 Trout Populations (Major Artificial Barriers)

Snake	Potentially all areas that are/were used by steelhead.
	
	Tucannon
	Asotin
	Grande Ronde
	Imnaha
	
	Salmon:
	    Lwr to mid-basin tribs.
	     Little Salmon
	      South Fk.
	      Middle Fk.
	       Lemhi
	      Pahsimeroi
	       East Fk.
	
	Clearwater:
	      Selway
	      Lochsa
		Palouse River
		
		Malad/Wood River
		
		Several Hells Canyon tributaries
		
		Several tributary falls in lower Salmon and Imnaha basins
		
		Upper Malheur Basin "recent" disconnect from lower Malheur Lakes Basin
			Trout distributions currently more restricted than historically
			
			North Fork Clearwater (Dworshak Dam)
			
			Mainstem Snake (Hells Canyon Dam):
			      Powder
			      Burnt
			      Malheur
			      Owyhee
			      Weiser
			      Payette
			      Boise
			      Bruneau
			    Salmon Falls Cr.
			   Mainstem and several
			    small tributaries to
			    Shoshone Falls

Table 1 *cont..* Distribution of *O. mykiss* trout by category in the Columbia Basin ESUs .

ESU	Category 1 Trout Populations (Sympatric)	Category 2 Trout Populations (Major Natural Barriers)	Category 3 Trout Populations (Major Artificial Barriers)
Upper Columbia	Potentially all areas that are/were used by steelhead Wenatchee Lower Entiat Methow Okanogan	Upper Entiat Upper Kootenai Methow: Chewuch[3] Lost Okanogan: Enloe Falls[3]	Trout distributions currently more restricted than historically Okanogan Basin: Conconully Dam Enloe Dam[3] Chief Joseph Dam: Lower Spokane to Post Falls Sanpoil Several small tributaries Lower Pend Oreille to Z-Canyon Columbia mainstem and lower tributaries to headwaters in Canada

[3] Uncertain whether steelhead were historically able to pass these features.

Category 3. Resident *O. mykiss* are isolated from steelhead above an artificial barrier, but are within known historic steelhead range. These trout now may be in total reproductive isolation from the steelhead, although downstream gene flow may still occur. However, the isolation event is recent, usually less than 100 years. Prior to the artificial blockage, when the trout and steelhead were historically sympatric, their relationship was likely similar to that which occurs in areas of current sympatry (Category 1).

A general summary of the distribution of trout as they fall into these three categories is provided in Table 1.

The following section is a description of the current and historic distribution of trout and steelhead in each of the listed Columbia Basin ESUs. Major barriers are identified, including both artificial barriers that now exclude steelhead from their historic range and major natural barriers that were the historic upstream boundary of anadromous steelhead. The information is summarized in Table 2. Additional barriers, both natural and artificial, that block small areas also exist but their locations are poorly documented so they are not included in the table or discussion.

Willamette ESU

The Willamette ESU in Oregon covers a small geographic area, but it is occupied by a very distinctive group of winter steelhead within the coastal subspecies (Busby et al. 1996, D. Teel, NMFS). The lower boundary of the ESU is Willamette Falls, which was historically passable only by anadromous fish with a specific run-time that corresponded to optimal passage flows. High, steep drainages with snow-influenced flows characterize the Cascade slopes of the eastern valley. Low coastal mountains with more gradual drainages and rain-influenced flows are to the south and west.

In geologic history, two stream captures occurred between Oregon coastal rivers and the upper Willamette Basin (Baldwin 1964). A portion of the upper Willamette was captured by the Umpqua Basin sometime in the late Cenozoic. Then the Willamette captured the Long Tom River from the Siuslaw River sometime during the Pleistocene. These events certainly influenced non-game fish distribution and biodiversity along the mid-Oregon coast and upper Willamette Valley (e.g. Markle et al. 1991), but the effect on *O. mykiss* distribution and biodiversity is not known. More recently, the basin was inundated by the series of Missoula or Bretz floods 12 to 15 thousand years ago that formed Lake Allison between the current sites of Portland and Eugene (Allen et al. 1986). The floods may have contributed to the formation of Willamette Falls, but in any case they were the last major geological disruption of fish distribution in the valley. Recent lava flows associated with the Sisters volcanic center in the central Oregon Cascades have disrupted drainages in the upper Santiam and McKenzie basins, but these areas are outside of historic steelhead range.

Steelhead have an unusual distribution in the Willamette because they are naturally absent from much of the basin, even though there are no physical barriers that preclude

Table 2. Major artificial and natural barriers to anadromous fish in the Columbia Basin.

ESU	Subbasin	Tributary	Artificial Barriers			Natural Barriers		
			Name	River km	Trout above?	Name	River km	Trout above?
Willamette	Santiam	North Fork	Big Cliff/ Detroit Dams	93	*O. mykiss* and *O clarki*			
		South Fork	Foster/ Green Peter Dams	60	*O. mykiss* and *O clarki*			
	Pudding	Silver Cr.				Silver Falls		unknown
	Luckimute	L. Luckimute				Falls	~15	*O clarki*
	Mainstem					Natural Distribution Break	~130	*O. mykiss* and *O clarki*
Lower Columbia	Cowlitz	Mainstem	Mayfield Dam	83	*O. mykiss* and *O clarki*			
	Kalama	mainstem				Falls	59	*O. mykiss*

Table 2 *Cont..* Major artificial and natural barriers to anadromous fish.

ESU	Subbasin	Tributary	Artificial Barriers			Natural Barriers		
			Name	River km	Trout above?	Name	River km	Trout above?
Lower Columbia (cont.)	Clackamas	Mainstem				Natural Distribution Break	~70	*O clarki*
		Roaring				Falls	< 2	*O. mykiss*
		North Fork				Falls	< 2	*O. mykiss*
		South Fork				Falls	< 2	*O. mykiss* and *O clarki*
		Memaloose				Falls	< 2	*O. mykiss*?
		Eagle Cr.				Falls	< 2	*O clarki*
		Oak Grove Fk				Falls	< 4	*O clarki*
	Lewis	North Fork	Merwin Dam	31	*O. mykiss* and *O clarki*	Falls	115	*O. mykiss*
		East Fork				Falls	52	*O. mykiss* and *O clarki*
	Sandy	Bull Run	Bull Run Dam	10	*O. mykiss* and *O clarki*	Falls	~30	*O clarki*
		Little Sandy				Falls	~20	*O. mykiss*
		Salmon River				Falls	~20	*O. mykiss*?

Table 2 *Cont..* Major artificial and natural barriers to anadromous fish.

ESU	Subbasin	Tributary	Artificial Barriers			Natural Barriers		
			Name	River km	Trout above?	Name	River km	Trout above?
Lower Columbia (cont.)	Columbia Gorge falls	All small tributaries in Oregon				Gorge Falls	< 4	*O. mykiss* or *O clarki*
	Hood	East Fk, Dog R.				Falls	~ 8	*O clarki*
Mid-Columbia	Fifteenmile	Threemile				Falls		*O clarki*
	Little White Salmon	mainstem				Falls	3	*O. mykiss*
	White Salmon	mainstem	Condit Dam	5	*O. mykiss* and *O clarki*	Falls	25	*O. mykiss*
	Deschutes	White River				Falls	~ 1	*O. mykiss*
		mainstem	Pelton/Round Butte dams	165	*O. mykiss*	Big Falls	~200	*O. mykiss*
		Crooked River, North Fork				Falls	~30	*O. mykiss*
	John Day	South Fork				Izee Falls	48	*O. mykiss*

Table 2 *Cont..* Major artificial and natural barriers to anadromous fish.

ESU	Subbasin	Tributary	Artificial Barriers			Natural Barriers		
			Name	River km	Trout above?	Name	River km	Trout above?
Mid-Columbia (cont.)	Umatilla	Willow Cr	irrigation dam		*O. mykiss*			
		Butter Cr	irrigation dam		*O. mykiss*			
		McKay Cr	irrigation dam	~10	*O. mykiss*			
Snake	Palouse	Mainstem				Falls	~ 16	*O. mykiss*
	Hells Canyon area	Small tributaries to the Snake and to the lower Imnaha and Salmon				Falls		*O. mykiss*
	Mainstem	Mainstem	Hells Canyon Dam	395	*O. mykiss*	Shoshone Falls	985	*O clarki*
	Malad/ Wood	Mainstem				Falls	~ 6	*O mykiss*
	Clearwater	North Fork	Dworshak Dam	3	*O. mykiss* and *O clarki*			
Upper Columbia	Mainstem	Mainstem	Chief Joseph Dam	547	*O. mykiss* and *O clarki*			
	Wenatchee	Icicle Cr	Leavenworth Hatchery		*O. mykiss*			

Table 2 *Cont..* Major artificial and natural barriers to anadromous fish.

ESU	Subbasin	Tributary	Artificial Barriers			Natural Barriers		
			Name	River km	Trout above?	Name	River km	Trout above?
Upper Columbia (cont.)	Entiat	Mainstem				Falls	~ 45	*O. mykiss*
	Chelan	Mainstem				Falls	~ 5	*O clarki*
	Methow	West Fork				Falls	~ 25	*O clarki*
		Chewuch				Falls	~ 50	*O clarki*
		Lost				Sink		uncertain
	Okanogan	Salmon Cr	Conconully Dam	~5	*O. mykiss*			
		Similkameen	Enloe Dam	~5	*O. mykiss*	Enloe Falls?	Inundated by Enloe Dam	historic steelhead passage uncertain
	Pend Oreille	Mainstem	Boundary Dam	~15	Potential mix due to inundation of natural barrier	Z-Canyon or Albany Falls	Inundated by Boundary Dam	*O clarki*
	Spokane	Mainstem				Post Falls	~120	*O. clarki*
	Kootenai	Mainstem				Falls	~20	*O. mykiss* and *O clarki*

them. They are present in the Pudding/Molalla, Santiam, and Calapooia subbasins, which drain from the Cascades. They are also present, although in very low numbers, in several of the coast-range tributaries (Tualatin, Yamhill, Rickreall, Luckimute and perhaps the Marys rivers)(Kostow 1995). There is some debate whether steelhead are more recently established in the Coast Range drainages (Busby et al. 1996, also see Fulton 1970), although genetics data indicates that they were not simply introduced from hatchery plants (D. Teel, NMFS). But steelhead are notably absent, currently and historically, from the entire Willamette Basin above the Calapooia, including from large subbasins like the McKenzie and Middle Fork Willamette which are or were occupied by spring chinook (Fulton 1970). The reason why steelhead did not penetrate further into the Willamette basin is not known.

The *Oncorhynchus* trouts of the upper Willamette Basin are also extraordinary. Coastal cutthroat are the dominant trout in most of the basin, including exclusively in all of the Coast Range drainages except in one tributary of the Tualatin (Gales Creek), and in the high Cascades where they are often isolated above lava dams and waterfalls. But the upper Willamette Basin, including the McKenzie and Middle Fork Willamette tributaries, are occupied by a very unique *O. mykiss* trout, locally known as "McKenzie redsides". These are sympatric with coastal cutthroat and will hybridize with them. But they are very genetically distinct from the Willamette steelhead and from the rest of the coastal subspecies (D. Teel, NMFS unpublished data) even though no physical barrier separates them. Other resident rainbow trout are sympatric with the steelhead in the Calapooia, Santiam, Pudding/Molalla and parts of the Tualatin. It is not known whether these trout share an evolutionary legacy with the steelhead or with the McKenzie redsides, or whether they are a mix of them or some other unique group of their own. The assumption, lacking data, is that they are likely more closely related to the steelhead since they share the same distribution.

The Santiam River was historically the major steelhead-producing drainage in the Willamette, but both the North and South Forks are now blocked by dams. Big Cliff/Detroit dams form a complete blockage of the upper North Fork. Foster/Green Peter dams block the upper South Fork. A passage facility is installed at Foster Dam that passes some steelhead, but it is of poor design. Some steelhead habitat remains between Foster Reservoir and Green Peter Dam. There have been past attempts to pass steelhead above Green Peter Dam, but no passage occurs at this time. *O. mykiss* trout are still present above the dams up to the numerous small natural falls that block the headwaters of most tributaries. There are no other major artificial barriers to steelhead within their range in the Willamette Basin. Some smaller structures on the Calapooia and in some other locations may cause intermittent passage problems or block small areas. Natural waterfall or lava dam barriers that isolate cutthroat populations occur throughout the headwaters of the Cascade tributaries, but none of them block large subbasins or isolate *O. mykiss* trout.

Lower Columbia ESU

The Lower Columbia ESU is located along both sides of the Columbia River in Washington and Oregon. It extends from the Cowlitz River to the Wind River in Washington, and from the Willamette River (the basin below Willamette Falls, including the Clackamas River) to the Hood River in Oregon. The ESU includes the Columbia Gorge where the Columbia River cuts through the Cascade Mountains, and constitutes the most inland distribution of *O.m. irideus* in the Pacific Northwest. It includes both winter-run and summer-run steelhead, although the winter-run life history is the most prevalent. Coastal cutthroat trout are sympatric with steelhead through most of the ESU, with a few exceptions. *O. mykiss* trout are also sympatric with steelhead through most of the ESU, again with a few exceptions. *O. mykiss* trout persist in all historic steelhead ranges above dams. Hybrids between cutthroat and *O. mykiss* occur in many areas. Allopatric *O. mykiss* and cutthroat trout populations are also present in this part of the Columbia Basin, isolated by an exceptional number of natural barriers.

The Oregon side of this ESU has only three major basins, the Clackamas, Sandy and Hood rivers, all of which drain steeply from Mt. Hood. These basins have primarily winter-run steelhead. Only one summer-run population is present in a tributary of the Hood River, West Fork Hood, above Punchbowl Falls which is a partial migration barrier. The Oregon side is also characterized by having an exceptional number of high waterfalls that are total barriers to anadromous fish, both in the three major basins and on all the other Oregon-side tributaries to the Columbia (see Table 2). The Clackamas, in particular, has many waterfalls and steelhead distribution is very restricted. A complex, and poorly understood, pattern of either cutthroat or *O. mykiss* trout are distributed above these falls. All of the falls are at least 10,000 years old, and many are probably older.

In Washington, the Cowlitz, Kalama, Lewis, Washougal and Wind rivers, plus several smaller tributaries, drain more gradually from the area around Mt. St. Helens. Fewer high waterfalls occur in these basins and anadromous fish historically had access to most of the area. Several low waterfalls form partial migration barriers that influenced steelhead life history, including Lower Kalama Falls on the Kalama, Lucia Falls on the East Fork Lewis, and Shipherd Falls on the lower Wind River. Summer steelhead populations are associated with these low waterfalls because they prohibit the passage of winter steelhead and sometimes also the passage of other salmon species, but summer steelhead passage is possible during lower flows. For example, all anadromous species except summer steelhead were excluded from much of the East Fork Lewis River by Lucia Falls because passage was feasible only during low flow conditions (WDFW unpublished data). Cutthroat trout are probably the dominant trout in upper, high gradient headwater reaches and in small isolated areas above upper tributary falls in most Washington rivers (C. Sharp, WDFW).

The pattern of trout distribution in areas where they are sympatric with steelhead is variable in this ESU (Table 3). Cutthroat trout are very rare or absent in the Wind River above Shipherd Falls (P. Connolly, USGS) and in the West Fork Hood River above

Table 3. Pattern of resident *O. mykiss* and *O. clarki* trout distribution in areas where they are sympatric with steelhead, Lower Columbia ESU.

River	Notable features	Steelhead life history below barriers	*O. mykiss* trout occurrence	*O. clarki* trout occurrence
Cowlitz	Mayfield Dam	Winter and summer steelhead	Present in upper basin and above dams	Dominant species in high gradient areas
Kalama	Lower Kalama Falls, partial barrier	Winter and summer steelhead	Rare but present in upper basin	Dominant species in high gradient areas
NFk. Lewis	Merwin Dam	Winter and summer steelhead	Present in upper basin and above dams	Dominant species in high gradient areas
EFk. Lewis	Lucia Falls, partial barrier	Winter and summer steelhead	Present in upper basin	Dominant species in high gradient areas
Clackamas	Extensive waterfalls	Winter steelhead	Dominant species in Collawash	Dominant species elsewhere in upper basin
Sandy	Bull Run dam complex	Winter steelhead	Present above dams; rare or absent in other areas that have steelhead	Dominant species
Washougal		Winter and summer steelhead	Present in upper basin	Dominant species in high gradient areas
Wind	Shipherd Falls, partial barrier	Winter and summer steelhead	Only species	Apparently absent
Hood	Punchbowl Falls in WFk. partial barrier	Winter and summer steelhead	Only species above Punchbowl; rare in MFk. rare or absent in EFk.	Dominant species except in the upper WFk., where they are apparently absent.

Punchbowl Falls. Both systems have steelhead and *O. mykiss* trout populations. The Collawash tributary in the upper Clackamas also appears to be dominated by *O. mykiss,* and includes both trout and steelhead. But in most other basins where steelhead are currently present, the dominant trout species appears to be cutthroat trout. *O. mykiss* trout may be absent from some areas.

Two basins in this ESU suffered extensive drainage disruptions due to volcanic eruptions within the last 200 years. The Cowlitz Basin was impacted in the early 1980s by the eruption of Mt. St. Helens. An extensive mudflow passed down the Toutle River to the mouth of the Cowlitz. Although steelhead were briefly excluded from the basin, human intervention quickly reopened passage into the Cowlitz and steelhead quickly returned to the basin (Lucas 1985, Leider 1989). Resident fish in the path from the Toutle to the mouth were probably destroyed. The Sandy River was disrupted during the 1800 eruption of Mt. Hood. The eruption sent a large mudflow down the Zig Zag River to the mouth of the Sandy. The Lewis and Clark journals report that the mouth of the Sandy (they called it Quicksand River) was still plugged with mud and sand when they visited it in the winter of 1805-6 (DeVoto 1953). Entry by steelhead into the Sandy may have been disrupted for several years and resident populations in the path from the Zig Zag to the mouth were probably destroyed.

The basins in this ESU were also affected by the Missoula/Bretz floods, 12 to 15 thousand years ago. The floods backed up in the narrow Columbia Gorge and influenced the formation of the high, hanging falls on the Oregon side (Allen et al. 1986). The more gradual basins on the Washington side were inundated to various degrees.

Dams are present on the mainstems and on some tributaries of nearly every major basin in this ESU. Some of them are passable to steelhead. Major passable dams include the North Fork dam complex (Clackamas River), Marmot Dam (Sandy River) and Powerdale Dam (Hood River). The North Fork dam complex was impassible from 1917 to 1939, after which new fish passage facilities were installed. Major impassable dams include the Mayfield Dam (Cowlitz River), Merwin Dam (Lewis River) and the Bull Run dam complex (Sandy River). Steelhead are currently being passed above Mayfield Dam by truck. Resident *O. mykiss* trout are still present, and sometimes common to abundant, above the three major impassable dam complexes. Other small passage barriers, ranging from culverts to small dams to fish hatchery weirs, are present throughout this ESU, but block relatively small areas.

Mid-Columbia ESU

The Mid-Columbia ESU straddles the Columbia River from the Little White Salmon River to the Yakima Basin in Washington, and from Fifteenmile Creek in Oregon to the Walla Walla Basin, which is shared by Oregon and Washington. It is likely that the historic downstream boundary of this biological unit was Celilo Falls, which was inundated by the reservoir behind The Dalles Dam. One consequence of inundating a natural barrier is that the populations above and below it are mixed, blurring the original biological boundary. The major tributaries in this ESU include the White Salmon and

Klickitat rivers and Fifteenmile Cr., which are below the historic falls and include the only winter steelhead populations in the ESU. The Deschutes, John Day, Umatilla, Walla Walla, and Yakima basins are above the historic falls and are all inland subspecies and summer steelhead. Coastal cutthroat trout are present in Fifteenmile Creek and in some smaller tributaries below historic Celilo Falls. A unique, isolated pocket of native westslope cutthroat trout (*O.c. lewisi*) is present in the upper John Day basin in tributaries of the upper mainstem above the confluence of the South Fork. Steelhead and resident *O. mykiss* are in the mainstem and lower tributaries of this area, cutthroat are in the headwaters of tributaries, and extensive hybrids zones occur between them (ODFW, P. Howell USFS and U. of Montana unpublished data). Westslope cutthroat are also present in some parts of the upper Yakima but they are probably introduced there (P. Howell USFS). Otherwise native cutthroat are absent from this ESU. *O. mykiss* trout are sympatric with all current steelhead distributions, they occupy all areas of historic steelhead range above dams and other artificial barriers, and they are present above all natural barriers in basins from the Deschutes and Klickitat upstream. Their distribution typically extends beyond the steelhead distribution into small headwater tributaries even when physical barriers other than stream size are absent.

The rivers in this ESU drain the eastern Cascades (part of the Deschutes, Klickitat, Yakima, and White Salmon basins), or the Blue Mountains in Northeast Oregon (part of the Deschutes, John Day, Umatilla and Walla Walla basins). Major recent volcanic eruptions associated with the Sisters and Newberry Crater volcanic areas in central Oregon have modified drainages in the upper Deschutes Basin, although all of the most recently affected areas are above historic steelhead range. The major eruptions that affected the Metolius and Crooked River watersheds are more ancient, dating to the Pliocene and early Pleistocene, 1.6 million years ago or older. Although the basins were largely blocked by lava flows at that time, the rivers reestablished their original channels by eroding through the lavas, but leaving the extensive network of springs that still influence the Metolius, lower Crooked and lower Deschutes river flows (Orr et al. 1992). The Missoula/Bretz floods backed up at The Dalles and at Wallula Gap, creating periodic lakes that flooded the lower reaches of the basins in this ESU, potentially disrupting fish distributions. Unique fish biogeography patterns in the upper South Fork John Day indicate that an historic stream capture occurred between the South Fork and Silvies River, which is in the Malheur Lakes Basin, a Southeast Oregon Great Basin (Bisson and Bond 1971). This event appears to have affected *O. mykiss* diversity in the South Fork John Day (Currens and Stone 1989).

Natural barriers are less common in this ESU (Table 2). The most important ones occur in the Deschutes Basin, associated with the erosion of the early Pleistocene lavas. White River Falls blocks the entire White River, one of the major tributaries of the lower Deschutes. The *O. mykiss* trout above this falls are highly distinctive (Currens et al. 1990). A second important falls, Big Falls, occurs on the mainstem Deschutes not far upstream from the reservoir behind Round Butte Dam. This falls historically blocked all anadromous fish access to the upper Deschutes Basin. A third waterfall blocked most of the North Fork Crooked River basin. Natural falls also blocked the upper South Fork of the John Day River, some tributaries of Fifteenmile Creek and most of the Little White

Salmon Basin. Several low waterfalls on the mainstem Deschutes, Klickitat and Umatilla (the latter is now under Threemile Dam) were passable by steelhead. Otherwise, there are no other major physical blockages to steelhead in this ESU, although they probably did not penetrate upper most headwater areas.

The major artificial barrier in this ESU is the Pelton/Round Butte dam complex on the Deschutes. These dams blocked access to major steelhead production areas in the upper basin, including the Crooked River, Metolius River and Squaw Creek. Condit Dam, just a few miles above the mouth of the White Salmon River, blocked access to that basin. Irrigation dams in the Umatilla blocked access to several tributaries. Otherwise, the numerous water diversion structures in this ESU are currently passable to steelhead, although some of them may cause passage problems.

Snake ESU

The Snake ESU is geographically large, covering areas in Idaho, eastern Oregon and southeast Washington. All of the steelhead are summer-run and inland subspecies. Subbasins in the ESU that currently have native steelhead include the Tucannon and Asotin (Washington), The Grande Ronde and Imnaha (Oregon), and the Clearwater and Salmon (Idaho).

A major dam complex on the mainstem Snake River in Hells Canyon blocks access to much of the area historically used by steelhead in the Snake Basin. Historically, steelhead penetrated the Snake River up to Shoshone Falls, a natural barrier to all anadromous fish on the mainstem Snake in central Idaho (Chandler and Chapman 2001). Major subbasins that historically had Snake River steelhead populations include the Powder, Burnt, Malheur and Owyhee (Oregon), and the Weiser, Payette, Boise, Bruneau and Salmon Falls Creek (Idaho). Steelhead were also present in some smaller basins.

The NMFS Biological Review Team did not come to any definitive conclusion about the relationship between the *O. mykiss* above the Hells Canyon complex and the steelhead below it. One could reasonably argue that the Snake historically included two *O. mykiss* ESUs with steelhead (Figure 5). The first would be a large ESU that occupied the forested mountain rivers of central Idaho and Northeast Oregon/Southwest Washington, part of which remains as the listed Snake ESU. A second ESU may have occupied desert basins from about the Malheur River upstream to Shoshone Falls. The two areas certainly have different climates, ecology and geologic histories. However, steelhead above Hells Canyon Dam became extinct long before the kinds of modern genetic surveys that have been used to describe ESUs were conducted. Recent genetic analysis of *O. mykiss* trout from tributaries that enter the Snake just above the dams and of several Snake River steelhead hatchery stocks demonstrated that the trout populations below natural barriers above Hells Canyon Dam are closely related to the steelhead hatchery stocks (Leary 2001). However, only one middle Snake tributary, the Malad/Wood River Basin, was sampled in this study. This trout population was very distinctive from the lower river populations, but it also was isolated by a natural waterfall (Leary 2001).

Figure 5. Map of potential Snake River *O. mykiss* ESUs based on environmental features and limited genetics data (Leary 2001, Currens 1990, Waples 1998). The currently described Snake ESU is shown (1) along with areas of historic steelhead distribution that may have been part of the existing ESU (2). The middle subbasins of the Snake, up to Shoshone Falls, may have formed their own ESU from which steelhead are now completely extinct (3). Several areas of trout distribution are isolated by natural features (4).

Several other studies suggest that the trout that remain in the desert subbasins of the mid-Snake are distinctive and uniquely adapted to their desert ecosystems. Currens (1990) demonstrated that the trout populations in Succor Creek and the Owyhee Basin were highly unique compared to other Snake River trouts. Wishard et al. (1984) also studied the native trouts in the Owyhee and noted their unique adaptations to severe desert environments.

The northern Oregon and Washington basins primarily drain the Blue Mountains, the central Idaho basins primarily drain the granitic Idaho Batholith and the desert basins above Hells Canyon primarily drain the Owyhee Mountains. The largest recent drainage modification occurred in the Malheur Basin. Geologic evidence indicates that Malheur Lake, which is now in Malheur Lakes Basin, a closed Great Basin, drained into the South Fork Malheur River as recently as three to five thousand years ago. This event is associated with a genetic affinity between the *O. mykiss* trout in the Donner und Blitzen River and the Malheur River (Currens 1997). The Snake River basins were not glaciated during the Pleistocene, except for some mountain glaciers. The only Pleistocene to Recent volcanic activity occurred in the Owyhee Basin, near Jordan Creek, and in the upper Snake Basin above the range of steelhead. The Missoula/Bretz floods only affected the lowest part of the basin in Washington, although their local impact was probably high. The floods probably contributed to the formation of Palouse Falls, which isolates that tributary from anadromous fish (Allen et al. 1986, M. Schuck, WDFW). The Bonneville flood, which drained Lake Bonneville in northern Utah about 15,000 years ago, primarily affected the upper Snake Basin above the distribution of anadromous fish. However, it inundated Shoshone Falls, possibly contributing to the formation of the falls, and evidence of the flood is present along the mainstem Snake as far down river as the Boise area (Jarrett and Malde 1987).

Other natural barriers to steelhead are uncommon in this ESU, except for a cluster of falls on small tributaries in Hells Canyon and in the Imnaha and lower Salmon basins that have resident *O. mykiss* trout above them (Leary 2001, B. Knox, ODFW, H. Pollard, NMFS). A major falls blocks access to the entire Malad/Big Wood River system in South-central Idaho (C. Corsi, IDFG, Chandler and Chapman 2001). *O. mykiss* trout in the Malad/Big Wood basins are notably unique (Leary 2001). Other falls block small subbasins and some headwater streams have steep gradients that are not accessible to steelhead.

The Hells Canyon dam complex is the major artificial barrier in this ESU. Another important artificial barrier is Dworshak Dam, which blocks most of the North Fork Clearwater River. Several smaller dams historically blocked tributaries of the Clearwater (Lewiston and Stites dams), although Lewiston Dam passed steelhead. Sunbeam Dam on the upper mainstem Salmon also blocked steelhead passage. These three dams have been removed (S. Yundt, IDFG).

O. mykiss trout are the only native *Oncorhynchus* trout species in much of the Snake ESU, with the exception of two major basins. Native westslope cutthroat are the dominant trout species throughout most of the Clearwater Basin and in much of the

Salmon Basin. Cutthroat are not native elsewhere in the Snake River Basin except above Shoshone Falls. Native *O. mykiss* are not present above Shoshone Falls and the native cutthroat is a different subspecies, Yellowstone cutthroat (*O.c. bouvieri*).

The US Fish and Wildlife Service, in cooperation with other agencies, have mapped the distribution of native westslope cutthroat, including areas where they hybridize with *O. mykiss*, as part of an ESA review of the cutthroat trout (Shepard et al. 2003). The issue of co-occurrence of *O. mykiss* and *O. clarki* became an important one for the cutthroat listing consideration because the two species form hybrid zones in many areas where they overlap. The USFWS was legally challenged about not properly evaluating the implication of the hybrid zones during an earlier listing review (L. Kaeding, USFWS, Civil Action No. 00-2521, March 2002). Westslope cutthroat are naturally allopatric to *O. mykiss* through most of their native range including many subbasins in the upper Columbia such as the Pend Oreille and upper Spokane. The hybrids in these areas are caused by introduced hatchery rainbow trout and are artificial and invasive (Allendorf et al. 2003). There are also several basins in eastern Washington and western Idaho where cutthroat have been introduced on top of native *O. mykiss* with potential hybrid implications. However, the two species are naturally sympatric in four basins that have native ESA-listed steelhead: the Clearwater, Salmon, Methow and John Day basins, and hybrids between sympatric native species have been found in all basins where genetic investigations have occurred (Shepard et al. 2003, Howell et al. 2003, USFS, ODFW and U. of Montana unpublished data). It is possible that the formation of "natural" hybrids is a recent event that has been facilitated by habitat changes and/or declines in population sizes (F. Allendorf, University of Montana), although evidence of more ancient hybrid events have also been found among phenotypic *O. mykiss* in the Tucanon River (F. Utter, University of Washington).

Genetics analyses in the Clearwater Basin indicate that there are fewer hybrids present in that basin, as compared to other areas of natural sympatry in Oregon and Washington (Shepard et al. 2003, Howell et al. 2003). This result is consistent with observations by local biologists who note that westslope cutthroat trout appear to be the dominant trout species in most of the basin. IDFG biologists estimate that cutthroat occupy the upper two-thirds of most tributaries, extending into the headwaters (C. Corsi, IDFG). Steelhead are in the mainstems and lower portions of the tributaries. *O. mykiss* trout populations are also present in some locations currently occupied by steelhead, such as the Selway and Lochsa, and they are present in the artificially blocked North Fork Clearwater.

Local biologists also assume that hybrid zones are uncommon in much of the Salmon Basin (Shepard et al. 2003) although very little genetics investigation has occurred in that basin to confirm or dispute the assumption. Westslope cutthroat are prevalent in many parts of the Salmon Basin, particularly in upper headwater areas. However, several subbasins, such as the Little Salmon, South Fork, Lemhi, Pahsimeroi, and parts of the Middle Fork Salmon, also have *O. mykiss* trout populations. A recent presence/absence survey by IDFG of native trouts in 84 streams in the upper Salmon Basin found *O. mykiss* in 48% of the streams surveyed and westslope cutthroat in 43% of the streams surveyed. Hybrids between the two species were found in 13% of the streams based on visual

identification (Brimmer et al. 2002, T. Curet, IDFG). Local biologists have observed that when cutthroat trout and *O. mykiss* trout and steelhead are all present together in a basin, the species and life histories seem to sort themselves into different areas. Steelhead tend to be in mainstems and the lower parts of larger tributaries, *O. mykiss* trout tend to be in the larger and lower tributaries, and the cutthroat trout tend to be in the smaller headwater tributaries, although complete overlap may also occur (S. Yundt, IDFG, H. Pollard NMFS). There are also fluvial *O. mykiss* and *O. clarki* in the Middle Fork Salmon and in tributaries of the mid-Salmon basin. In these cases, the two species mingle in the rearing areas, but separate when they enter the tributaries to spawn, with the *O. mykiss* trout spawning lower in the tributaries and the *O. clarki* migrating into upper reaches (T. Curet, IDFG).

Outside of the Salmon and Clearwater, resident *O. mykiss* trout are present in all of the current and historic steelhead basins in the Snake ESU. Leary (2001) found evidence of hatchery rainbow trout in several locations above Hells Canyon Dam, based on the occurrence of certain alleles, but in all cases native trout were also present. The trout populations in many of the desert basins in the middle Snake are depressed and fragmented due to local habitat impacts, especially hydrological changes caused by irrigation. They are absent from many areas that were historically used such as the lower mainstems of the Malheur, Owyhee and Bruneau rivers. However, they remain well distributed in many upper basins and in most headwater areas outside of the Salmon and Clearwater basins, in both current and historic steelhead range.

Upper Columbia ESU

The Upper Columbia ESU extends from the confluence of the Snake into the upper Columbia Basin in eastern Washington. All of the steelhead are summer-run and inland subspecies. Steelhead populations currently occur in the Wenatchee, Entiat, Methow and lower Okanogan basins, all of which drain from the North Cascade Mountains. The basins above Grand Coulee Dam that historically had steelhead drain from the North Cascades to the west or from the Rocky Mountains to the east. *O. mykiss* trout are sympatric with the steelhead throughout their current range and also occur throughout the historic range of steelhead above artificial barriers.

The *O. mykiss* species was not native above many of the natural barriers in the upper Columbia, which instead have native westslope cutthroat trout. The Lake Chelan basin has a natural barrier to anadromous fish that forms the lake outlet only a few miles upstream of the Columbia River and has westslope cutthroat trout above it. Native westslope cutthroat also occur above natural barriers that blocked anadromous fish passage in several major basins above Grande Coulee Dam, including the Spokane and Pend Oreille basins. *O. mykiss* trout have been introduced in many of these areas. A small area of natural sympatry between westslope cutthroat trout and steelhead occurs in the Methow, and there is extensive hybridization there (Howell et al. 2003). Westslope cutthroat and *O. mykiss* trout are also naturally sympatric in the upper Kootenai. In all other cases, the two species in the upper Columbia are naturally allopatric.

Chief Joseph/Grand Coulee dams now block all access to much of the upper Columbia Basin that was historically used by steelhead. In the United States, these included the Spokane River up to Post Falls and several smaller tributaries such as the Sanpoil. The Pend Oreille had only limited steelhead production in the lower basin because access was blocked by natural barriers at either Z Canyon or Albany Falls (J. Whalen, WDFW). Steelhead were present in Canada to the headwater lakes. Similar to the Hells Canyon dam complex on the Snake, the NMFS Biological Review Team did not form any conclusions about the relationship between *O. mykiss* in the upper Columbia Basin above Chief Joseph Dam and the steelhead below it. Also similar to the Snake, it is possible that two *O. mykiss* ESUs that included steelhead were present above Chief Joseph Dam, taking into consideration the distribution into Canada. In the upper Columbia, historic Kettle Falls was a likely ESU boundary. Kettle Falls was a partial migration barrier that may have affected *O. mykiss* similarly to the way historic Celilo Falls and Willamette Falls did. Kettle Falls was inundated by Lake Roosevelt behind Grand Coulee Dam. If Kettle Falls was an ESU boundary, the upper Columbia ESU boundary would have been just short of the U.S./Canada boarder, while the second ESU would have included the species distribution in Canada. Again similar to the Snake, genetics data are not available from the upper Columbia to study this question.

Other artificial dams and weirs blocking historic steelhead areas are present in the Wenatchee and Okanogan. The issue of whether steelhead passed Enloe Falls, the current site of Enloe Dam in the Okanogan Basin, is debated. First Nation elders in Canada argue that anadromous fish did not pass above the falls, but others believe that steelhead may have been able to do so (H. Bartlett, WDFW). One dam on the Methow River that may have blocked steelhead from most of that basin has been removed (H. Bartlett, WDFW).

The Upper Columbia ESU is the most severely, recently disrupted system in the Columbia Basin from a geological perspective. The Okanogan Lobe of the Cordilleran Ice Sheet extended well into northern Washington as recently as 13,000 years ago. As a result fish were completely absent from most northern Cascades basins down to the Wenatchee (Mullen et al. 1992). As the glaciers receded, huge proglacial lakes formed along their margins (Pielou 1991). Lake Missoula was one such lake. It covered the area now occupied by the upper Clark Fork of the Pend Oreille in the vicinity of Missoula, Montana. As glacial lobes extended and retreated into northern Washington 15,000 to 12,000 years ago, the lake burst in a cycle of about every 60 years, sending catastrophic floods across eastern Washington. The floods were contained at Wallula Gap, near the confluence of the Snake River, and then rushed on down the Columbia. Eastern Washington was left scarred and streaked with dry coolies and rocky scab lands, remnants of the old flood channels (Allen et al. 1986). The entire area could not have been very hospitable to fish until the floods and ice were well past.

However, *O.m. gairdneri*, possibly in resident form, must have persisted in some areas at least periodically through these difficult periods. A unique resident population managed to become isolated above the barriers in the upper Kootenai (Knudsen et al. 2002). Stream exchanges between the Fraser and the upper Columbia during the period of

proglacial lakes, particularly the capture of the Thompson River by the Fraser from the Columbia, is presumed to be the source of Inland subspecies *O. mykiss* in the upper Fraser River (McPhail and Lindsey 1970). However, it can be assumed that many areas in the Upper Columbia ESU were colonized relatively recently.

Implications of Hatchery Trout Stocking

The stocking of hatchery *O. mykiss* trout in the Columbia Basin raises two questions associated with defining ESUs. The first question is whether the trout that are present in a basin are native, or whether they were all introduced by hatchery stocking. The second question is whether any of the trout hatchery stocks are closely related to local populations and might also be included in the ESUs.

There is a possibility that some trout populations were introduced. Hatchery rainbow trout, and other trout species, have been stocked essentially everywhere in the Columbia Basin starting in the late 1800s. The original stocking programs were by federal fisheries agencies and states assumed responsibility only in the early 1900s (Taylor 1999). Old trout stocking records are very poor. The early stocking techniques were crude, including transporting fry or fingerlings in aerated milk cans by backpack and mule.

It is clear that many of these early trout stocking efforts "took" in spite of their crudeness, based on the wide distribution of exotic eastern brook trout (*Savelinus fontinalis*) and European brown trout (*Salmo trutta*) in the Columbia Basin. However, the effect of the hatchery rainbow trout stocking is more obscure since native *O. mykiss* were wide spread and abundant in the Columbia Basin prior to the stocking. Rainbow trout have certainly become established outside of their native range in the Columbia Basin, such as in western Montana above natural barriers that historically had only cutthroat trout (Shepard et al. 2003). But in areas where *O. mykiss* were historically present, a history of hatchery stocking cannot be taken as evidence that the current trout populations were merely introduced by hatchery programs.

Evidence that *O. mykiss* historically occupied a basin is a better indication that native trout are still present, as compared to an argument that a record of hatchery stocking means that all the trout populations are introduced. Lacking other information, in all areas in the Columbia Basin where both trout and steelhead are currently sympatric, it would be consistent with previous NMFS decisions to assume that the naturally-produced trout are native. This same determination has been made for all the steelhead in the Columbia Basin ESUs even though they also have been stocked with hatchery fish, including fish from outside of the ESUs (63 FR 13347; 64 FR 14517; and 62 FR 43937). In areas where steelhead are now excluded by artificial barriers, but trout remain, the question is more difficult. Even if trout were not naturally present in such areas historically, local steelhead may have residualized and established native resident populations. This may have occurred in areas such as the Bull Run River, tributary of the Sandy River (Lower Columbia ESU) and in the North Fork Clearwater (Snake ESU). It would also be consistent with previous NMFS decisions, lacking other evidence, that naturally-produced trout within historic steelhead range are assumed to be native.

Hatchery rainbow trout that are used in the Columbia Basin have primarily been "McCloud" stock, "Kamloops" stock, or mixture of these stocks. These hatchery stocks were founded from populations in geographic areas outside of the Columbia Basin ESUs. The "McCloud" stock is from the upper Sacramento Basin in California and the "Kamloops" stock is from Kootenay Lake, Canada in the Columbia River headwaters, but above a natural barrier (Category 2 trout population). According to criteria developed by NMFS, these trout hatchery stocks are "Category 4" hatchery stocks based on their origin from geographic areas outside of the ESUs (SSHAG 2003).

Implications of *clarki/mykiss* Hybrid Zones

Cross species hybrids are usually viewed as a negative event, even though in fish, including between *clarki* and *mykiss*, the hybrid offspring are often viable and fertile (Allendorf et al. 2003, Rhymer and Simberloff 1996). Possibly our taxonomic concept of "species", which predates the theory of evolution, creates an artificially rigid expectation that organisms should stay in the groups we have assigned them to. Some biologists suggest that natural hybrid zones between native species should be viewed as their own kind of natural biodiversity (E. Taylor, University of British Columbia, also Redenbach and Taylor 2003). Others suggest that hybridization is now occurring at unnatural levels among native species, caused by habitat degradation or population declines (F. Allendorf, University of Montana, also Allendorf et al. 2003). In any case, the existence of hybrids is a difficult issue under ESA. Since it is difficult to clearly assign hybrid fish to a species, it becomes further difficult to assign them to an ESU or DPS. The USFWS recently addressed this issue as it pertains to westslope cutthroat concluding that hybrid fish that are phenotyically "westslope cutthroat" would be counted as westslope cutthroat (68 FR 46989). Presumably those fish that are phenotypcially *O. mykiss*, whether steelhead or trout, would be counted as *O. mykiss*, consistent with this finding. The USFWS has also produced maps of the range of native westslope *clarki* and *mykiss* and their hybrids in the John Day, Methow, Clearwater and Salmon rivers (Shepard et al. 2003). Hybrid zones are also an issue for the lower Columbia and Willamette *O. mykiss* ESUs where the hybrids involve native coastal cutthroat trout. Although hybrids have been found in these ESUs everywhere they have been looked for, in a few cases at quite high frequencies (e.g. over 30% of a sample, ODFW and U. of Montana unpublished data) hybrid zones have not been systematically mapped or quantified in these coastal ESUs.

Conclusions

The biological evidence about the evolutionary relationship between steelhead and resident *O. mykiss* trout where they are sympatric (category 1) supports the original decision by the NMFS Biological Review Team that the trout and steelhead life histories in the same geographic areas are in the same ESUs. Although the two life histories are distinctive, they are not reproductively isolated to the extent required by the NMFS criteria for ESUs (Waples 1991, 56 FR 58612). There is evidence for interbreeding between the life histories within basins. The evidence includes similarity at molecular

genetic markers that demonstrate population and ESU structure elsewhere in *O. mykiss*, observations of the potential for interbreeding, and observations and studies of both life histories successfully producing offspring that express the alternative life history.

The evidence about the evolutionary relationship between steelhead below artificial barriers and the *O. mykiss* trout that still exist above the barriers (category 3) is weaker, but still supports a conclusion that in many cases the trout populations above the barriers and the steelhead below the barriers are in the same ESUs. The fish in the two areas may now be in complete reproductive isolation from each other. But, it is probable that the original relationship between the trout and steelhead when they were sympatric in these blocked areas was the same as that which occurs where the life histories are currently sympatric. There is some genetic evidence that indicates similarity between trout in these areas and steelhead below the barriers (Leary 2001, Currens 1997, NMFS unpublished data). A reasonable argument could be made that the large blocked areas above Grand Coulee and Hells Canyon dams historically supported more than one *O. mykiss* ESU that had steelhead. If this were the case, only the lower subbasins above the blockages would be in the same ESU as the fish below the dams. A decision that the steelhead below artificial barriers are in the same ESUs as the trout above the barriers would also be consistent with current management planning to reestablish steelhead passage over some of these barriers.

The next section of this paper assumes that all naturally-produced *O. mykiss* trout that are currently sympatric with steelhead (category 1), or that remain in areas historically used by steelhead (category 3), are part of the listed ESUs. This includes all areas above Hells Canyon Dam and all areas in the USA above Grand Coulee Dam, even though NMFS has not made a final decision about the extent of ESU boundaries above these features. The discussion then proceeds to report information about the status of the trout and their contribution to the status and extinction risks of ESUs that contain both life histories. This approach is necessary in order to provide all of the available information that could influence the status of ESUs if the trout that are sympatric with steelhead or that are within the historic range of steelhead were found to be part of the ESUs, even though NMFS may ultimately decide to exclude some category 1 and 3 trout populations from the ESUs.

In contrast, trout that are isolated by natural barriers (category 2) are assumed to be in their own ESUs or DPSs. In these cases, the state of reproductive isolation is natural and long-standing, and numerous genetic surveys support the conclusion that the isolated trout populations are distinctive (e.g. Currens et al. 1990, Currens 1997, Leary 2001, Knudsen et al. 2002). Information about the status of category 2 trout populations is not provided in the following sections. This approach presupposes that NMFS will exclude all of these trout populations from the ESUs. Excluding a discussion of these isolated trout populations from this document does not imply anything about their own status or extinction risk, but simply recognizes that they are probably not part of the steelhead ESUs that are being reviewed by NMFS. The trout populations that are in Canada, above Grand Coulee Dam in the upper Columbia Basin, also are not discussed in this report because they are outside of the jurisdiction of the ESA.

Information about the Status of ESUs with both Trout and Steelhead

Introduction

A status review that effectively assesses the extinction risk of an ESU that contains both trout and steelhead, as opposed to only steelhead, is complex and difficult particularly given the uneven information available about the various forms of *O. mykiss*. Most past status assessments focused only on steelhead (e.g. Chilcote 1998), or recognized trout only briefly (e.g. Busby et al. 1996). Status reviews generally assess current and historic species distribution, population abundance, productivity and structure, diversity, and specific risk factors that affect the species (McElhany et al. 2000). Information about these factors is much more available for steelhead than for trout. Further, our understanding of this species is not good enough for us to determine whether the status of an entire *O. mykiss* ESU is just the sum of the statuses of the two life histories, or whether we should expect some synergy between them. There is evidence of interbreeding and interactions between the life histories in some parts of the Columbia Basin, which are presumably beneficial. However, there are examples in coastal rivers where steelhead naturally flourish without trout and there are many examples in the Columbia Basin and elsewhere where trout populations naturally flourish without steelhead. Therefore it is not evident that the two life histories necessarily depend upon each other for persistence; in fact they might compete with each other (Bjornn 1978). An interpretation of status of such a polymorphic species under ESA is complex. It is possible that an ESU may be at low risk of actual extinction (i.e. of the whole species (ESU) disappearing), but at a high risk of significant change due to the loss of a valued life history (i.e. of steelhead disappearing). How the ESA addresses a significant change in the character of an ESU, as opposed to the extinction of it, is unclear.

The following sections provide overviews of the current and historic distribution of sympatric trout and steelhead in the Columbia Basin, and of factors that influence their productivity, population structure and diversity. These sections are followed by a discussion of trout and steelhead abundance for each ESU summarized at the broad level that is necessary to legitimately address the trout. Finally several risk factors that are important for trout are discussed. Additional risk factors that are particular to steelhead, plus substantially more detailed information about steelhead status, are discussed in Busby et al. (1996) which is being updated in a new steelhead status review by NMFS.

Current and Historic Distribution

If one concludes that the trout that remain above artificial barriers are part of the ESUs that contain the steelhead below the barriers, the distributions of all ESUs expand significantly, with the greatest changes in the Snake and Upper Columbia ESUs. All apparent extinctions in portions of the species range that are evident if only steelhead are counted are no longer valid because the species (ESU) is still represented in all areas by trout. Biologists in the Columbia Basin did not report a single example where the entire species of *O. mykiss* has disappeared above a major artificial barrier that blocked steelhead (see Tables 1 and 2, and Figure 1).

Trout distribution has decreased within most basins, including in areas where they are currently sympatric with steelhead, primarily due to losses in mainstem reaches and the withdrawal of trout populations into headwater areas. Trout populations are no longer present in the lower mainstems of major inland basins such as the Yakima, John Day or Umatilla, which were likely highly productive reaches for trout historically, similar to the current condition on the lower mainstem Deschutes. The lower reaches of some coastal subbasins, such as the Clackamas, are also thought to have been more productive of *O. mykiss* trout historically than currently (D. Cramer, PGE).

Aspects of Trout and Steelhead Life Histories that Influence Productivity

The productivity of steelhead populations has been assessed in several Oregon subbasins in the Columbia Basin (Chilcote 2003). These assessments require substantial data sets, including long time series of annual abundance data and information about harvest, survival and age structure. Similar data is not available for any trout population in the Columbia; therefore, a similar assessment of trout productivity cannot be conducted. It can only be observed that some studies of trout abundance over time suggest that their populations can be remarkably resilient (Dambacher et al. 2001).

Some information can be obtained by reviewing how life history differences influence the relative productivity of trout and steelhead. The two life histories demonstrate different, successful approaches to balancing optimal survival and optimal reproduction. Trout have much higher survival to adults and more reproductive events; but steelhead – especially females – are more productive in each reproductive event. Table 4 summarizes and generalizes several life history characteristics that influence the productivity of the two life histories.

Steelhead are able to spawn multiple times, a characteristic which distinguishes them from most other Pacific anadromous salmonids but which they share with trout. Repeat spawning is generally more common among females, and in coastal populations. While quite high incidences of repeat spawning is reported in the literature for some geographic areas (Burgner et al. 1992), steelhead populations that have been aged by scales in the lower Columbia (Kalama and Hood) have only about a 10% incidence of it (based on data from E. Olsen, ODFW and C. Sharp, WDFW). Repeat spawning in inland Columbia Basin steelhead populations is currently very rare (Burgner et al. 1992). Only about 2% of the wild inland steelhead aged by scales at Bonneville Dam in 2000-2001 were repeat spawners (ODFW unpublished data). Historic out-migrant data on the Clackamas River (Lower Columbia ESU) indicates that kelts were much more common in the 1960s than they are currently (based on data provided by D. Cramer, PGE), suggesting that the incidence of repeat spawning has decreased in this population.

Table 4. A comparison of some Columbia Basin *O. mykiss* life history characteristics that influence productivity. Information from Schroeder and Smith 1989, Pribyl and Hosford 1985, Pearsons et al. 1994, Busby et al. 1996, Burgner et al. 1992, and unpublished ODFW and WDFW data. Information is generalized.

Characteristic	Steelhead	Trout
Fecundity (eggs/female)	3,000 to 5,600	150 to 1,500 migratory trout tend to be more fecund
Age at first spawning	4 – 5 years	2 – 4 years migratory trout tend to be older at first spawning
Migration	anadromous (long distant)	resident, fluvial or adfluvial (none or short distance)
Survival from age 1 parr to age 2 fish	~ 50% to smolts	~ 50% to adults in many populations
Survival from smolt to first spawning adult	0.5 – 20% inland populations tend to have lower survivals; survival is influenced by variable marine conditions	Generally not applicable, although some trout start breeding at an older age
Survival of adults after first spawning	~10% mostly females	45 - 80%
Incidence of repeat spawning	2 - 10% once or twice; more common in coastal populations, among females, and more prevalent historically	25 - 40% one to three times
Maximum age	6 – 7 years	4 – 10 years
Response to local catastrophes	Migrate elsewhere to spawn and then recolonize later	Survive as adults if possible and put off breeding until later

Trout productivity varies depending on their life history and on the conditions under which they live. Observations in Oregon indicate that resident fish in cold, unproductive or distressed streams may have lower fecundity, shorter life spans and undergo only one or two breeding cycles. Resident fish in highly productive systems may be more fecund and have longer life spans. Migratory female trout, whether fluvial or adfluvial, grow to much larger sizes and are more fecund. In some trout populations, the migratory fish appear to more often be female (D. Engemann, IDFG, Lucas and Chilcote 1982). Inland steelhead also have sex ratios that are skewed toward female, while resident parents of steelhead or residual offspring of steelhead are more often males (Blouin 2003, Ardren 2003, Berg 2001, Olsen and French 2000, Pearsons et al. 1998).

Trout appear to be more flexible about when they breed than steelhead. Individual trout are able to skip breeding years (Schroeder and Smith 1989). Surveys of Oregon desert trout populations during the 1990s indicated that little or poor reproduction occurred during severe droughts, followed by very high productivity in wet years (Dambacher and Jones 1995, Dambacher et al. 2001). The trout appear to respond to extreme environmental cycles by skipping one or more years of breeding, with many adults surviving to breed when conditions improve. Individual steelhead, in comparison, must precede spawning by a long migration and cannot respond to local environmental conditions by skipping breeding episodes. Instead individuals have a more rigid life span, although the population may express a diversity of ages.

Steelhead are better able to avoid local catastrophes by flexibility in their migrations, and they are much more capable of natural recolonization after a local population or breeding patch has been lost. Leider (1989) observed that steelhead responded to the severe impacts in the Cowlitz system caused by the Mt. St. Helens eruption by straying to other, adjacent basins to spawn. They recolonized the Cowlitz several years later. The resident trout in the path of the Toutle mud slides were probably lost and it may take some years for them to recolonize the basin.

Aspects of Trout Population Structure that Influence Status

The life history, distribution and population structure of trout make them exceptionally prone to the effects of population fragmentation. Fish with resident life histories may move only a few hundred yards during their lifetimes so local conditions must meet all their life cycle needs (Northcote 1992, Northcote and Hartman 1988). Migratory fish, like steelhead or fluvial trout, are able to pass through marginal habitat when conditions permit, but resident fish require good quality local habitats year-round. Gene flow and other metapopulation functions between highly resident populations requires a continuous distribution of both good habitat and fish as well as no passage barriers, otherwise interactions between patches drop to zero. Seasonal habitat problems, such as poor water quality, high summer temperatures, or seasonal dewatering, make long reaches of streams inhospitable to resident fish and can cause local extinctions and disrupt distributions and gene flow. The typical result is a pattern of population fragments that are completely isolated from each other in headwater reaches. Even though the total abundance of trout in a basin may be quite high, the size and the degree

of isolation of the individual patches determine their actual vulnerability to extinction (Higgins and Lynch 2001).

Population fragmentation is a particular problem for trout in desert basins where most mainstem reaches are highly impacted by irrigation withdrawals and artificial passage barriers. Trout in these habitats also tend to go through extreme abundance cycles in accordance with drought cycles, which further lower their effective population sizes (Dambacher et al. 2001). It is therefore important, when assessing the status of resident trout, to look beyond total abundance and consider how the fish are distributed across the landscape and how they are behaving. A mosaic of life histories may be very important for extinction avoidance. Fluvial trout populations, and possibly steelhead, may provide a mechanism for gene flow to occur between otherwise isolated resident patches, which can restore the adaptive genetic variation that can be lost to genetic drift. They also provide the means for recolonization to occur if individual breeding patches become extinct due to local catastrophes. Therefore the loss of the migratory life histories, even if they make up only a small portion of the total abundance, may disproportionably increase the vulnerability of the species to extinction.

It is also important to note that the dams and other artificial barriers that exclude steelhead from their historic ranges also impose complete reproductive isolation on the trout populations that remain above them. Although downstream gene flow, out of the populations, may still occur, fish are not able to move upstream into the populations. Other artificial barriers, including major dams, smaller irrigation diversions, culverts and dewatered reaches further subdivide trout populations above many of the barriers to steelhead. As long as the barriers are in place, the local trout population sizes must be large enough to sustain them in isolation (Higgins and Lynch 2001). The isolated trout populations are also very vulnerable to local catastrophic events since there is no possibility of natural recolonization from outside of the blocked area.

Breeding populations of steelhead have been defined by the Northwest states using various criteria (e.g. Kostow 1995, Leider et al. 1994). Boundaries of steelhead populations are currently being redefined by Technical Review Teams under the NMFS recovery planning process using criteria provided by McElhany et al. (2000). However, trout populations have not been generally described (see discussion about trout populations in Oregon in Kostow 1995). Although the general distribution of *O. mykiss* trout is known, their detailed distribution and barriers and other features that would influence population boundaries have not been mapped. Detailed information on the extent of population fragmentation is lacking. Further, the demographic relationship between various trout life histories, which are often sympatric, is not known. For example, fluvial and resident trout may be forming independent populations when they are sympatric, or they may be part of a single polymorphic population.

The discussion below about trout abundance is presented by tributary or subbasin since that is the level at which abundance information is available. This approach does not imply that all the trout within a tributary or subbasin are in a single breeding population.

In most cases the trout within basins are sub-divided into numerous local breeding populations, some of which are in complete reproductive isolation from others.

Diversity in ESUs with both Trout and Steelhead

O. mykiss ESUs are considerably more diverse if trout are recognized to be part of the ESUs along with steelhead. This increase is evident in adult life history diversity, as adult options increase from winter and summer steelhead to also include resident, fluvial and adfluvial freshwater life histories. These behavioral variants are accompanied by morphological and physiological variants, particularly expressed as variation in adult size and in the physiological ability to spawn with or without anadromy. Extremes in environmental tolerance are very evident among *O. mykiss* trout, as various populations in the Columbia Basin spend their entire life cycle in conditions ranging from rain forests in the western Cascades to severe desert climates in the inland basin (see Northcote 1992, Northcote and Hartman 1988, and Wishard et al. 1984 for several discussions of various micro-adaptations by resident trout). Although variation in juvenile life history associated with adult life history variation is not generally apparent, careful studies have demonstrated that juvenile trout and steelhead may use different micro-environments within basins where they are sympatric (Zimmerman and Reeves 2002). Trout are certainly able to use headwater areas that are not available to steelhead (Pearsons et al. 1998). These significant contributions by trout to the variation in life history and adaptations of the species increase the resiliency and adaptability of the species compared to a condition where only steelhead are present.

The limited genetics data that is available indicate that trout populations also carry extremely high levels of molecular genetics diversity as compared to steelhead or any other anadromous species. Surveys by Phelps et al. (1998), Kundsen et al. (2002) and Currens (1997) demonstrated the remarkable level of genetic divergence between trout populations, particularly as compared to that between steelhead populations (the analyses by Phelps et al. 1998 and Currens 1997 included both life histories). These studies also demonstrate a high level of genetic diversity among trout including the occurrence of rare and unique alleles. Trout populations that are sympatric with steelhead appear to have less differentiation and uniqueness than isolated trout populations (Phelps et al. 1998, Currens 1997, also Pearsons et al. 1998), probably due to the homogenizing effects of gene flow facilitated by the migratory steelhead.

There has probably been some decrease in life history diversity among trout populations, primarily losses of migratory life histories caused by anthropogenic passage barriers and habitat impacts that have made many river mainstems inhospitable. Migratory trout are the largest, and therefore the most productive trout life history, and they provide connectivity between resident populations that otherwise can become fragmented and isolated. Therefore the loss of migratory trout may increase the vulnerability of the species more than what may be expected based on numbers alone. Successful desert trout rehabilitation projects in southeast Oregon have demonstrated that complex migratory life histories can be quickly restored by providing safe, reliable passage at culverts, water diversions and other small passage barriers (ODFW unpublished data).

This suggests that the ability to migrate may be retained in resident populations for a number of years even if the behavior is not being expressed.

Abundance of Trout and Steelhead by ESU

A measure of the total abundance of *O. mykiss* in an ESU needs to count both the steelhead and the trout. Annual adult steelhead abundance data, measured by either dam counts or redd counts, are available for all Columbia Basin ESUs. However, similar data for *O. mykiss* trout are unavailable for most tributaries in the Columbia Basin. Only two redd count data sets and one weir count data set are available for trout. The most common trout data are fish density data that are generally collected in the summer. The densities may be by area (fish/m^2) or linear (fish/km). If densities have been measured in enough index areas, and if habitat area, quality and occupation are adequately known, the densities may be expanded to a quantitative abundance estimate for a basin. However often the information is not adequate to make an expansion. Where trout and steelhead are sympatric, both life histories may be included in the density measurements confounding any abundance estimate, and in fact most *O. mykiss* density measurements in the Columbia Basin have been an attempt to estimate juvenile steelhead production.

An estimate of the density or abundance of adult trout is of most interest since steelhead abundance data are for adults. Many density data sets are for all fish age 0+ or 1+ and so are a mix of juveniles and adults. In some cases, size or age data are also available so that it is possible to focus on the portion of the populations that might be adult trout. Many trout can begin to breed at age 2+ and at about 10cm, while most steelhead in the Columbia Basin are 2-year smolts. Although older smolts have been detected as out-migrants (Peven et al. 1994), ages measured from adult scales indicate that older smolts are rare in most areas. About 10% (Kalama) to 20% (Hood) of the fish in the Lower Columbia ESU had been age 3 smolts based on ages measured from adult scales during the 1990s (E. Olsen, ODFW; C. Sharp, WDFW). About 10% of the wild inland summer steelhead sampled at Bonneville Dam had been age 3 smolts based on adult scales. Adults that had been older smolts were less than 1% of all observations (ODFW unpublished data, 2000 - 2002 samples). The older inland steelhead smolts are thought to be primarily from the Upper Columbia and Snake ESUs where productivity is thought to be lower. Since older smolts are generally rare, the presence of 2+ *O. mykiss*, sampled in the summer after 2-year old smolts have out-migrated, are used in this report to indicate the presence of adult trout. Neave (1944), Bjornn (1978), and Berg (2001) used similar criteria to document the presence of trout.

In the following section, two conventions for a qualitative estimate of trout abundance are used in basins where quantitative abundance data are unavailable. The first convention depends on the existence of some density data. Dambacher and Jones (1995) established three qualitative benchmarks for trout abundance interpreted from density data of 1+ resident *O. mykiss* in eastern Oregon desert streams:

- "low abundance" (< 0.05 fish/m^2),
- "moderate abundance" (0.06 – 0.19 fish/m^2), and

- "high abundance" (>0.20 fish/m^2).

These benchmarks are used as reference points in this document, even though the data in this review may differ from that used by Dambacher and Jones (1995) in the following ways:

- A 1+ population includes a substantial proportion of sub-adults, perhaps as many as 50%. If age or size data are available so that the densities of potential adult trout (2+ fish) are known, the benchmarks will underestimate abundance.
- In some cases, the only data available is of 0+ fish. These measurements typically include a large number of young-of-the-year fish, which are usually the most abundant life stage present. Therefore the benchmarks will overestimate abundance.
- Where trout and steelhead are sympatric, many 0+ or 1+ fish are steelhead parr rather than trout. Therefore the benchmarks will overestimate the abundance of trout.

It is also not certain whether the three benchmarks are meaningful outside of the desert stream environments for which they were established. Highly productive streams may be well under carrying capacity at these densities, while pristine but sterile, high-elevation streams may be at carrying capacity at much lower densities.

There are no trout data of any kind available from much of the Columbia Basin, including for some entire ESUs. The second convention for a qualitative estimate of abundance depends on the professional judgment of biologists in basins where no density or abundance data are available. Four qualitative estimates are used:

- "Absent" refers to conditions where no *O. mykiss* large enough (>10cm) or old enough (2+ or older) to be trout have been seen. In many of these areas it appears that only steelhead are present, and/or other species of trout are present.
- "Rare" refers to conditions where *O. mykiss* trout are known to be present but are infrequently seen or difficult to find.
- "Common" refers to conditions where *O. mykiss* trout are present and can be reliably found, but do not appear to occur in large numbers.
- "Abundant" refers to conditions where *O. mykiss* trout can be readily found and appear to occur in large numbers.

Willamette ESU

An accurate measure of the total number of wild winter steelhead adults entering the Willamette ESU is available from counts at the Willamette Falls fish ladder. However, no information is available about the abundance of *O. mykiss* trout in the portions of the Willamette Basin where they are sympatric with, and likely related to, steelhead. Trout are present and it is likely that their natural historic distribution was smaller than that of steelhead. They appear to be confined to the middle reaches of a few of the Cascades subbasins and one tributary of the Tualatin (Gales Creek). They remain above the dams

in the Santiam that currently block steelhead passage, but they do not extend into headwater areas. All other areas in the Willamette are occupied by other native trouts. No abundance data is available for the trout; however, they are routinely observed during snorkel surveys in the basin. In the expert opinion of Willamette Basin biologists, resident *O. mykiss* are common in the Santiam, Calapooia, and Molalla subbasins (S. Mamoyac, ODFW).

The life history of Willamette Basin *O. mykiss* trout is not known. Historically, they may have been fluvial, migrating from breeding areas in the tributaries to rearing areas in the highly productive mainstem Willamette. This kind of life history is known to occur in both cutthroat trout and bull trout (*Savelinus confluentus*) in the Willamette. Some of the *O. mykiss* trout above the Santiam dams may be adfluvial, migrating to rear in the reservoirs. Other trout probably have resident life histories. Adult trout that are larger than steelhead smolts are observed during snorkeling or other surveys. Local biologists suspect that small breeding adults may also be present that cannot be distinguished from steelhead parr.

Winter steelhead are not highly abundant in the Willamette. Figure 6 shows the total count of winter steelhead into the Willamette ESU from 1971 through 2003. The counts include hatchery fish, about 30 – 40% of the counts in some years, until 1996 when the counts began to identify wild fish based on the absence of fin marks. All winter steelhead hatchery programs were discontinued in the upper Willamette in the late 1990s so the run is now 100% wild. The entire Willamette steelhead ESU averaged 7,400 wild adult steelhead annually passing Willamette Falls since 1996.
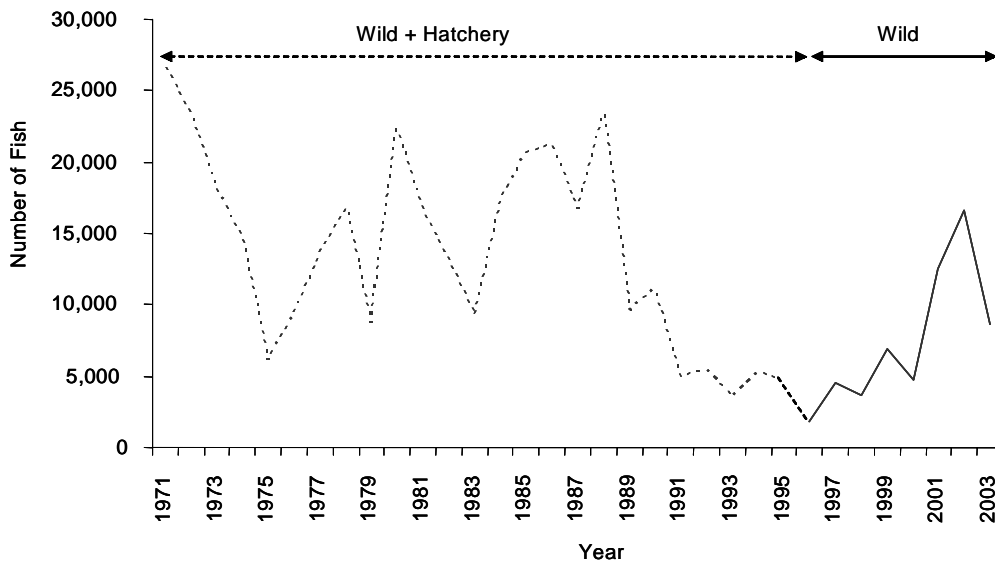

Figure 6. Total winter steelhead abundance entering the Willamette ESU, counted at Willamette Falls from 1971 to 2003.

Lower Columbia ESU

The abundance of steelhead populations in the Lower Columbia ESU are measured in most major subbasins by dam/trap counts or by redd counts. However, trout abundance data are lacking. Trout are present in the ESU, both sympatric with steelhead and in areas above dams in the Sandy, Lewis and Cowlitz basins that block access to historic steelhead habitat. The natural historic distribution of *O. mykiss* trout was probably less than that of steelhead because they appear to be either absent or extremely rare in some parts of the ESU. Coastal cutthroat are the dominant trout in most subbasins.

One *O. mykiss* density data set is available from this ESU, from the Wind River (data provided by P. Connolly USGS). Data are available for two years in the mid-1980s, and from the late 1990s (Table 5). The data are for all fish age 1+ and were a mix of steelhead parr and trout. It is not possible to determine how many of them were trout. There is not enough information to expand these densities to abundance estimates. There appears to have been a slight decrease in *O. mykiss* densities between the two time periods, although based on the bench marks provided by Dambacher and Jones (1995) most abundances were moderate in both time frames. Local biologists believe that trout are a small portion of the *O. mykiss* production in the Wind (P. Connolly USGS).

Out-migrating *O. mykiss* are measured at smolt traps in the Hood, Kalama, Clackamas and Wind rivers. The out-migrants are thought to primarily be smolts, although it is clear in the Hood that some of fish that are being captured in the traps are moving in-basin, and these could include trout (based on data from E. Olsen, ODFW). Age at smolting has been measured from adult scales in the Hood and Kalama. About 7 – 8% of the smolts in the Kalama and 12 – 20% of the smolts in the Hood are age 3. About 1% of the Hood River smolts are age 4 (based on data from C. Sharp, WDFW and E. Olsen, ODFW). The fish are also aged when they are captured and older fish that could only be trout are not being taken in these traps. Adults that are larger than steelhead parr are seen occasionally throughout the ESU but are rare and it is likely that most trout have resident life histories. There are exceptions, for example in the Bull Run reservoirs where the adfluvial trout can grow to large size. Some local biologists have noticed that the occurrence of larger trout has increased in areas where wild trout catch-and-release angling regulations have been adopted (D. Rawding WDFW).

Expert opinion is that resident *O. mykiss* abundance in areas of current or historic steelhead distribution varies from basin to basin:

- *O. mykiss* trout are probably common throughout the Wind River basin, where cutthroat trout are not present.

- Trout are common in the West Fork of the Hood Basin where cutthroat trout are not present. They are rare in the Middle Fork, and possibly absent in the East Fork Hood which is dominated by cutthroat.

- Trout are common in the Collowash subbasin of the Clackamas, but they are rare in the rest of the basin below natural barriers. *O. mykiss* trout are thought to have been more abundant in the lower Clackamas historically (D. Cramer, PGE).

Table 5. Density of age 1+ *O. mykiss* measured as fish/m^2 in tributaries of the Wind River. Data are averaged over all reaches sampled within the tributary each year. The number of sampled reaches varied from year to year. NS = not sampled. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). Data provided by P. Connolly, USGS.

Year	Trout Creek (3 – 8 reaches sampled/year)	Panther Creek (1 – 4 reaches sampled/year)	Upper Wind (1 – 6 reaches sampled/year)
1984	0.13	0.14	0.15
1985	0.18	0.29	0.12
1996	0.06	0.06	NS
1997	0.12	0.18	NS
1998	0.09	0.23	0.09
1999	0.03	NS	0.05

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- Trout are abundant above the Bull Run dams in the Sandy, but are rare or absent elsewhere in the basin which is dominated by cutthroat. The Bull Run reservoirs provide ample rearing habitat for trout and they are not subjected to any hatchery planting or angling because the watershed is closed to public access.

- Trout are probably common above the Cowlitz and Lewis basin dams, but are rare below the dams in these basins.

- Trout are probably common in the upper Kalama and Washougal basins, but are rare in the lower portions of these basins.

- Trout are absent from all the smaller lower Columbia tributaries that have small patches of spawning steelhead.

The major river basins in the Lower Columbia ESU each have several hundred to several thousand adult steelhead in them, in some cases including both winter-run and summer-run fish. An estimate of average wild steelhead abundance since the late 1990s in the basins that monitor adult steelhead is provided in Table 6. Steelhead are also present in some other areas but are not monitored. Total current annual ESU abundance is probably about 10,000 – 12,000 adult steelhead.

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Table 6. Estimated average abundance of adult steelhead in major basins in the Lower Columbia Steelhead ESU. Data for Oregon basins are from E. Olsen, ODFW, D. Cramer, PGE and ODFW unpublished data. Data for Washington basins are from the NMFS Technical Review Team for the Lower Columbia Steelhead ESU, originally provided by D. Rawding, WDFW.

Basin (years averaged)	Estimated average wild steelhead abundance
Cowlitz (Toutle) (1998 – 2002)	735
Coweeman River (1998 – 2002)	245
Kalama (1998 – 2001)	1,180
Lewis (E.Fk.)(1998 – 2002)	500
Clackamas (1999 - 2003)	800
Sandy (2000 - 2003)	890
Washougal (1998 – 2002)	670
Wind (1998 – 2002)	540
Hood (1998-2002)	1,050

Mid-Columbia ESU

The abundances of steelhead populations in the major mid-Columbia basins are measured by either dam or redd counts. The Mid-Columbia ESU is also comparatively rich with data about *O. mykiss* trout. It contains the only long time series data set on adult trout abundance in the Columbia Basin, collected on the lower mainstem Deschutes. Trout have also been studied in the Yakima Basin, and other incidental observations are common throughout this ESU. The following sections break out several of the basins that are relatively data-rich for separate discussion and are followed by a summary of the other basins and the whole ESU.

DESCHUTES BASIN

The Deschutes River is a large tributary of the Columbia. However, only about two-thirds of it was historically accessible to steelhead, and of the historic steelhead range, only about half of it remains. The discussion in this paper takes into consideration only those trout populations below Big Falls on the mainstem Deschutes, which marked the historic upstream boundary of steelhead.

The Deschutes River is unique among large, inland Columbia Basin tributaries in that its lower mainstem is relatively intact, with year-round strong flows and cold water temperatures. Its natural water storage system is underground aquifers that feed the mainstem through numerous springs. In comparison, the John Day River historically relied on extensive headwater beaver meadows for water storage, and these were largely lost in the late 1800s which changed the hydrology of the lower mainstem. The lower Umatilla, Walla Walla and Yakima mainstems are severely modified by irrigation diversions. The Deschutes is also unique in that it still has a large, productive *O. mykiss* trout population in its lower mainstem. These trout are among the most abundant, the largest, the oldest and the most fecund *O. mykiss* trout in the Columbia Basin. Possibly the other major rivers in the Mid-Columbia ESU had similar mainstem trout populations historically, but they are gone now because summer and fall water quality is inhospitable.

The Deschutes trout provide a popular sports fishery and their abundance has been monitored since the early 1970s by measuring trout densities at several index areas along the mainstem. Fish were captured using a boat-mounted electroshocker. Age and maturity of the fish were also measured so the data can be divided into adults and sub-adults. Details about the monitoring program are provided in Schroeder and Smith 1989, with six annual updates (Newton and Nelson, 1995, 1996, 1997, 1998, 1999 and 2000). Over the years, measurements were taken at five index sites. Measurements were not taken each year, nor were all five index sites monitored in any given year. The authors did not expand or summarize their data, but rather reported a fish density per mile (transformed to kilometers), per site, per year. For the purposes of this document their original data were averaged and expanded over the length of the lower mainstem so that the information could be put in the same unit as lower Deschutes River steelhead abundance data.

Over the monitoring period, the authors observed an average of 950 trout per kilometer. On the average, 29% of the fish that were observed were adults, or about 285 adult trout per kilometer. The estimated annual total trout abundance, by age class, expanded over the entire mainstem (about 145 km), is provided in Figure 7.

In order to combine trout abundance with steelhead abundance and obtain an overall estimate of abundance for the whole species it is necessary to focus only on the adult trout, since only adult steelhead are measured. Deschutes River steelhead abundance at Sherar's Falls is presented in Figure 8 (data from M. Chilcote, ODFW). Adult trout abundance and steelhead abundance are presented together in Figure 9. The data demonstrate that steelhead are only about 10% of the total adults present in the lower mainstem. An average of about 4,800 steelhead adults have returned to Sherars Falls each year since 1978. There has been an estimated annual average of over 40,000 adult *O. mykiss* trout in the lower mainstem over the same period. The combined total *O. mykiss* abundance is therefore estimated to be about 45,000 fish. This estimate includes all of the steelhead in the basin but counts only the trout in the lower mainstem. Additional trout are in the lower river tributaries and in subbasins in historic steelhead range above Pelton/Round Butte dams.

A second assessment of trout and steelhead abundance is also possible, using redd counts. Three years of trout and steelhead redd counts are available for the mainstem Deschutes from Zimmerman and Reeves (2000) and annual steelhead redd count monitoring has been conducted in the Warm Springs River and Shitike Creek by the Warm Springs Tribes (unpublished data provided by B. Spateholts, CTWSR). In the three years of the Zimmerman and Reeves study, steelhead produced about 3% of the redds they observed. Steelhead in all three locations produced an average of about 1 redd per km over the monitoring period (Figure 10). Trout in the mainstem produced about 66 redds per km in the three years of the trout study.

The trout in the Deschutes are also well distributed in other areas in the basin, in addition to the mainstem. Below Pelton/Round Butte dams, they also occur throughout Warm Springs River, Shitike Creek and Trout Creek, and in several smaller tributaries. Possibly some of the tributary populations are fluvial, and if so they might be detected during the mainstem density monitoring. However, it is probable that other resident trout are also in the tributaries. Therefore, the adult abundance estimate based on trout data from only the lower mainstem underestimates the total abundance of *O. mykiss* trout below the dams, perhaps by a large amount.

Trout also remain well distributed in the historic steelhead area above Pelton/Round Butte dams and the abundance of these populations would need to be included to obtain a total basin-wide abundance. The largest tributary of the Deschutes, the Crooked River, is above the dams and was probably the major steelhead production area historically. Much of the mainstem Crooked River, and the entire South Fork, are now severely impacted by irrigation and cattle grazing. These activities have lowered water tables, caused passage blockages, dewatered reaches, and decreased water quality. However, many of the headwater areas still have good desert trout habitats, although the best remaining habitats
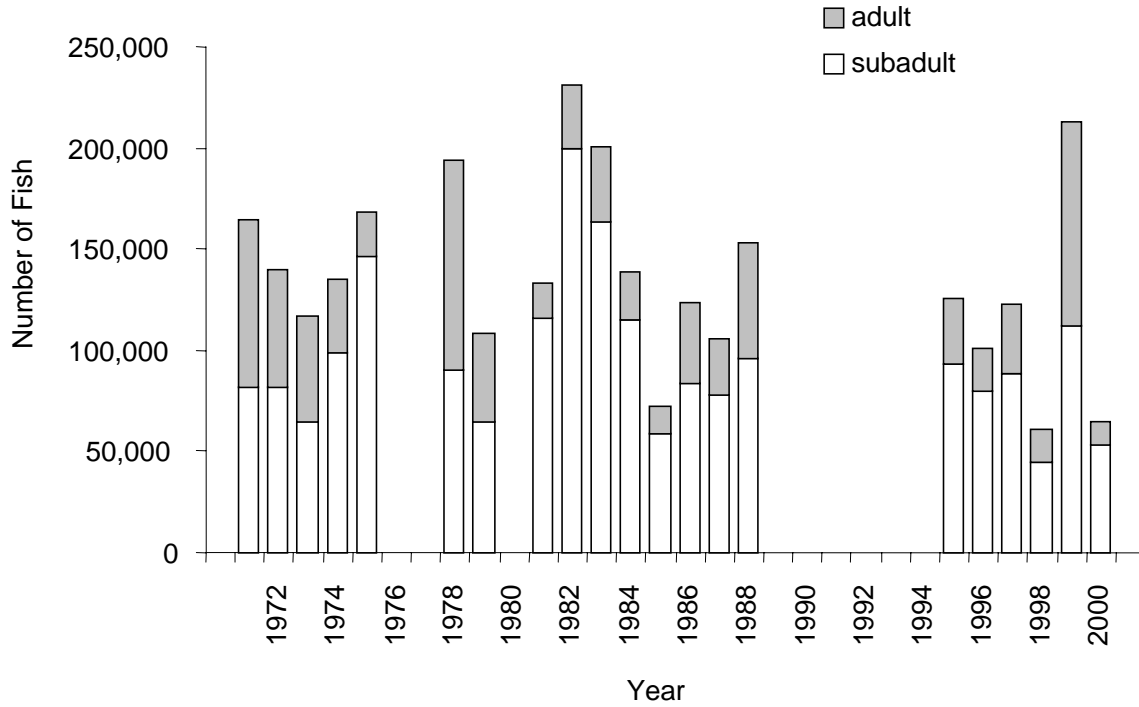
Figure 7. Estimated total abundance of *O. mykiss* trout in the lower Deschutes, based on density data from Schroeder and Smith (1989) and Newton and Nelson (1995 – 2000). Blanks are years with no monitoring.

Figure 8. Estimated number of wild adult steelhead passing Sherars Falls on the Deschutes River (data from M. Chilcote, ODFW).
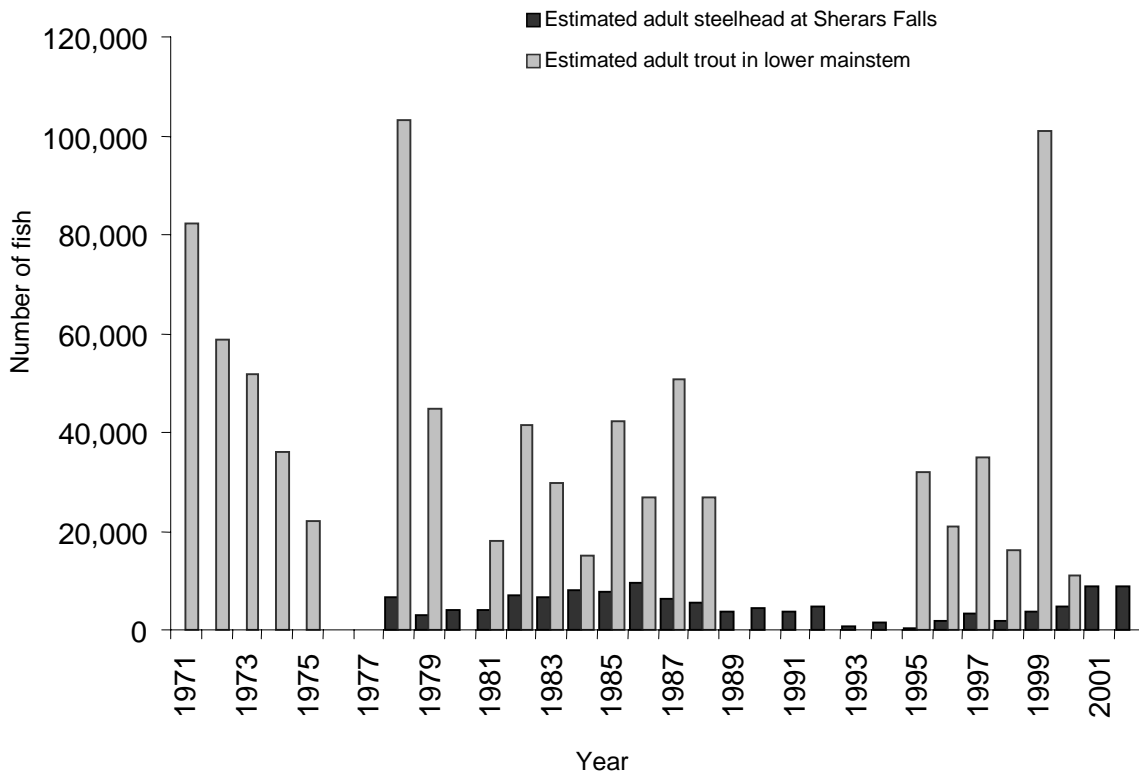
Figure 9. A combined estimate of wild adult trout and wild adult steelhead abundance in the Deschutes River. The steelhead estimate is for the total basin while the trout estimate is only for the mainstem below Pelton/Round Butte dams. Additional trout occur in the lower basin tributaries and above the dam complex.

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are above the historic range of steelhead, above the falls on the North Fork. *O. mykiss* trout, including both resident populations and fluvial fish that migrate into the mainstem and lower North Fork, are still distributed through much of the Crooked River basin, although their abundance and status are variable depending on local conditions.

Trout abundance was estimated by Dambacher and Jones (1995) in three Crooked River tributaries. They found abundances of 1+ fish ranging from less than 1,000 fish to over 8,000 fish per tributary. Adult abundances would have been perhaps one third to half of these estimates, or from lows of 300 to highs of 4,000 adults per tributary. The range of abundance per tributary was high and depended on local conditions. Therefore, further surveys would be needed before a Crooked River basin-wide abundance estimate could be attempted.

The other two major tributaries within historic steelhead range above Pelton/Round Butte dams are Squaw Creek and the Metolius River. Steelhead redds were historically counted in Squaw Creek (Figure 11). Some people have questioned whether steelhead
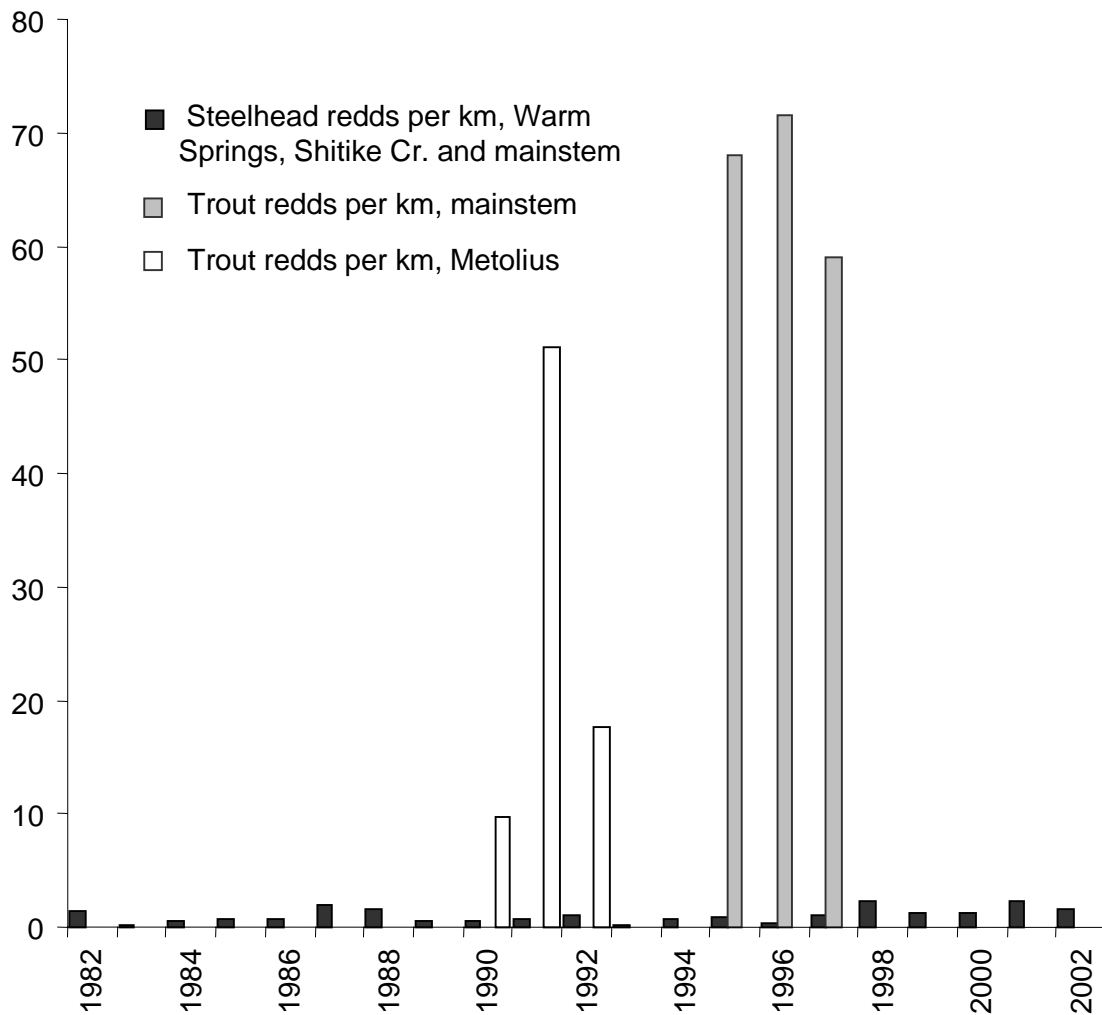
Figure 10. Annual steelhead redd counts (redds per km) presented along with three years of trout redd counts on the mainstem Deschutes, and three years of trout redd counts on the Metolius River, above Pelton/Round Butte dam complex. Data from B. Spateholts, CTWSR, Zimmerman and Reeves 2000, and Hemmingsen et al. 1994.
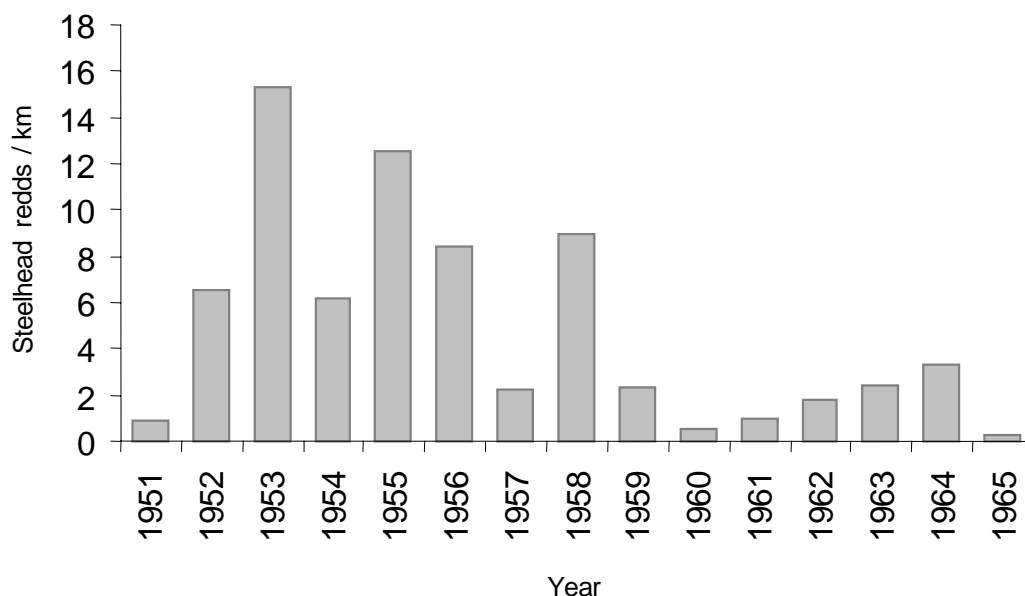
Figure 11. Historic steelhead redd counts (redds/km) in Squaw Creek, a tributary of the Deschutes above Pelton/Round Butte dams. Data from ODFW (1996).

was present in the Metolius, which had both the upper Deschutes spring chinook and sockeye production areas. However, the Metolius River would have provided good steelhead habitat and it is likely they were overlooked among the other species rather than absent (S. Marx, ODFW). Trout are still present in both systems. Some parts of upper Squaw Creek are severely impacted, including seasonal dewatering. Recent surveys of lower Squaw Creek found several hundred 1+ *O. mykiss* per index site. Several surveys of the short reach of Deschutes mainstem between the inlet of Lake Billy Chinook and Big Falls have detected several thousand 1+ fish per index site.

The Metolius River is spring fed and provides good habitat for trout. *O. mykiss* trout were studied on the Metolius from 1990 to 1993. During that period, trout redds and adults were monitored in the upper Metolius, between the source of the river and the Metolius Gorge (Hemmingsen et al. 1994). Trout redds were counted on a 6.4 km index reach of the Metoluis River from fall 1990 through spring 1993. The annual redd counts are included in Figure 10 along with the trout and steelhead data from below the dams. An average of 26 redds/km were counted over the three years. Adult abundance was also monitored over the same period. Adult trout densities averaged 1.26 fish/m^2, which can be classified as very abundant (Dambacher and Jones 1995). The abundance is even higher than the benchmark indicates (where >0.2 = abundant) since the estimate is specifically of adults whereas the benchmark is for a sample that includes sub-adults.

It is not possible to conclude some overall trout abundance for the part of the Deschutes Basin within historic steelhead range above the dams. However, given that abundances of several thousand adults have been observed in some individual tributaries, one can

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estimate that total abundance above Pelton/Round Butte dams must be in the range of tens of thousands of adult trout.

Adding the trout in the upper and lower basins together, the total abundance of *O. mykiss* in the portion of the Deschutes Basin within current and historic steelhead range includes about 5,000 steelhead plus perhaps 100,000 adult trout.

JOHN DAY BASIN

The John Day is also a large basin with over 4,000 km of *O. mykiss* spawning and rearing habitat, now located primarily in tributaries and the upper subbasins. Hydrological changes in the basin following the loss in the late 1800s of extensive beaver meadows that had provided natural water storage have rendered most mainstem habitats useful only for migrations. Historic *O. mykiss* trout populations probably included fluvial fish which used the mainstem habitats for rearing. Recent length frequency measurements of *O. mykiss* demonstrated that over 98% of the fish sampled were less than 6 inches (14 cm) (ODFW 2001) suggesting that the current trout life history in the basin is resident.

Density of 1+ *O. mykiss* has been measured at 43 locations in the three major subbasins that produce steelhead in the John Day (the North Fork, Middle Fork and upper mainstem), summarized by subbasin in Table 7. These measurements were intended to target steelhead parr, but also include some unknown number of *O. mykiss* trout. According to abundance benchmarks developed by Dambacher and Jones (1995), most 1+ *O. mykiss* abundances ranged from moderate (0.06 – 0.19) to high (>0.2) across the John Day basin and from year-to-year within the same subbasin. These density measurements could be expanded to local abundance measurements if habitat areas were measured, but the necessary information is not currently available. The John Day steelhead are primarily 2-year old smolts. Age data measured from scales and collected

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Table 7. Density of 1+ *O. mykiss* in the John Day Basin, based on sampling in 43 locations. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). (unpublished data, T. Unterwegner, ODFW)

Year	North Fork fish/m^2	Middle Fork fish/m^2	Upper Mainstem fish/m^2
1990	0.05	0.15	0.19
1991	0.13	0.20	0.22
1992	0.28	NS	NS
1994	0.19	NS	NS
1996	0.23	NS	NS
2000	NS	0.23	NS

Figure 12. Estimated abundance of adult steelhead in the John Day Basin since 1958, expanded from redd counts using data and methods provided by M. Chilcote and T. Unterwegner, ODFW.

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during the summer after the age 2 smolts have out-migrated would reveal how many age 2 or older fish, which would include breeding age trout, remain in the tributaries. Based on the available size data (ODFW 2001), possibly about 2% of the fish present might be adult trout (those >14 cm). Given the densities observed in the John Day, the trout population could be very large.

Redd counts at index areas throughout the three John Day subbasins are used to monitor adult steelhead abundance (Figure 12).   An average of 6 redds/km have been counted since 1958, and an average of 3.5 redds/km have been counted since 1990.   Adult steelhead abundance is relatively robust in the John Day, estimated to average over 14,700 fish since 1958, and over 8,500 fish since 1990 (expansion from redds by M. Chilcote, ODFW).   Trout redds are also observed during the counts although they are small and easily missed, especially when survey conditions are poor. The trout redds are not currently enumerated although it may be possible to count them at least in some years and locations when survey conditions are optimal.   This effort could provide some information about the relative number of trout and steelhead redds in some areas.

The mainstem of the Umatilla River is heavily impacted by irrigation diversions and is inhospitable during most of the year. Summer steelhead is the only remaining native anadromous salmonid species in the Umatilla Basin, although reintroductions of several other species are underway. However, many headwater tributaries are relatively intact and continue to support the production of both steelhead and trout.

The Umatilla Tribes measured the natural production of *O. mykiss* in the upper Umatilla Basin in the early 1990s as part of an extensive basin recovery program (Umatilla Tribes 1994, Contor et al. 1995, 1996 and 1997). Densities of *O. mykiss* were measured in 13 upper basin streams during the summers of 1993-95. Habitat parameters were also measured to produce an estimated habitat area and the density measures were expanded to tributary abundance estimates (Table 8).

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Table 8. Estimated abundance of 0+ and 2+ *O. mykiss* in tributaries in the upper Umatilla, measured in the summers of 1993, 1994 and 1995. Each tributary was measured once. Data from Umatilla Tribes 1994, Contor et al. 1995 and 1996.

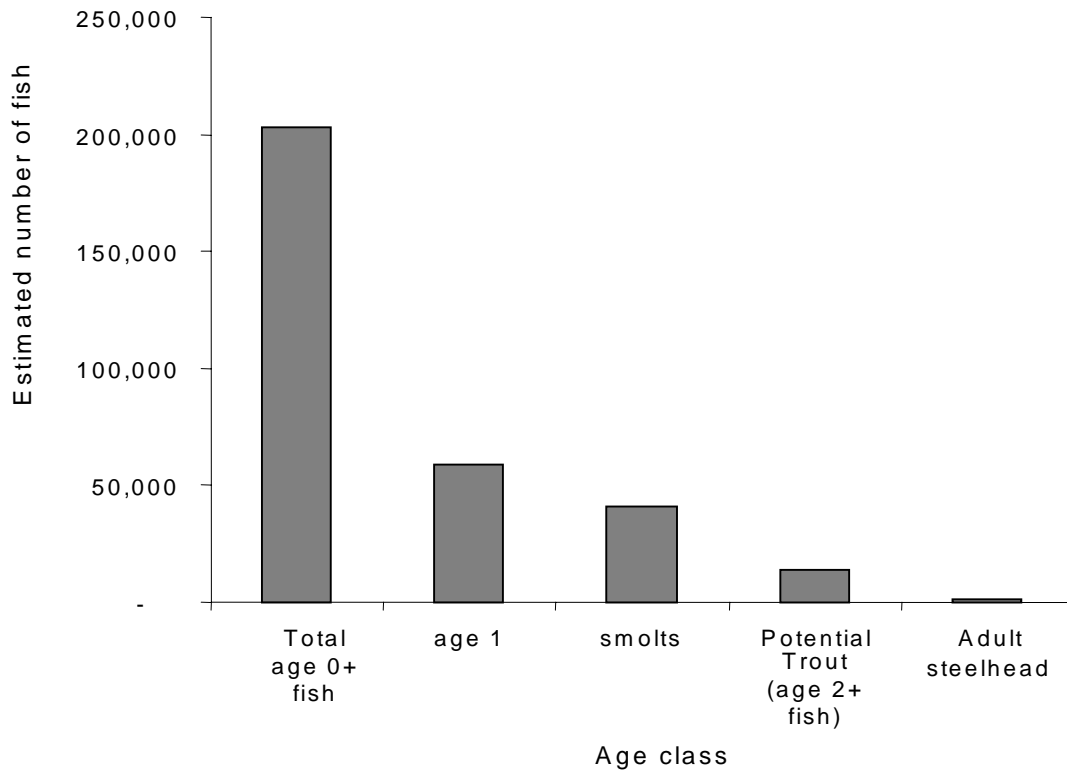| Tributary (year estimated)	Estimated abundance of 0+ *O. mykiss*	Estimated abundance of 2+ *O. mykiss*
Buckaroo Cr (1993)	3,961	277
Boston Canyon Cr (1993)	5,550	389
Boston Canyon trib (1993)	39	3
Line Cr (1993)	3,260	228
Meacham Cr (1993)	71,937	5,036
MS RM 56.1 to 81.8 (1994)	16,878	1,181
Squaw Cr (1994)	36,453	2,552
Camp Cr (1994)	6,646	465
MS RM 81.8-89.6 (1995)	54,258	3,798
Moonshine Cr (1995)	1,138	80
Mission Cr (1995)	839	59
Cottonwood Cr (1995)	489	34
Coonskin Cr (1995)	1,426	100

Figure 13. Estimated abundances of juvenile *O. mykiss* and potential adult trout in 13 tributaries in the Umatilla and the average adult steelhead count at Threemile Dam from 1993-95.
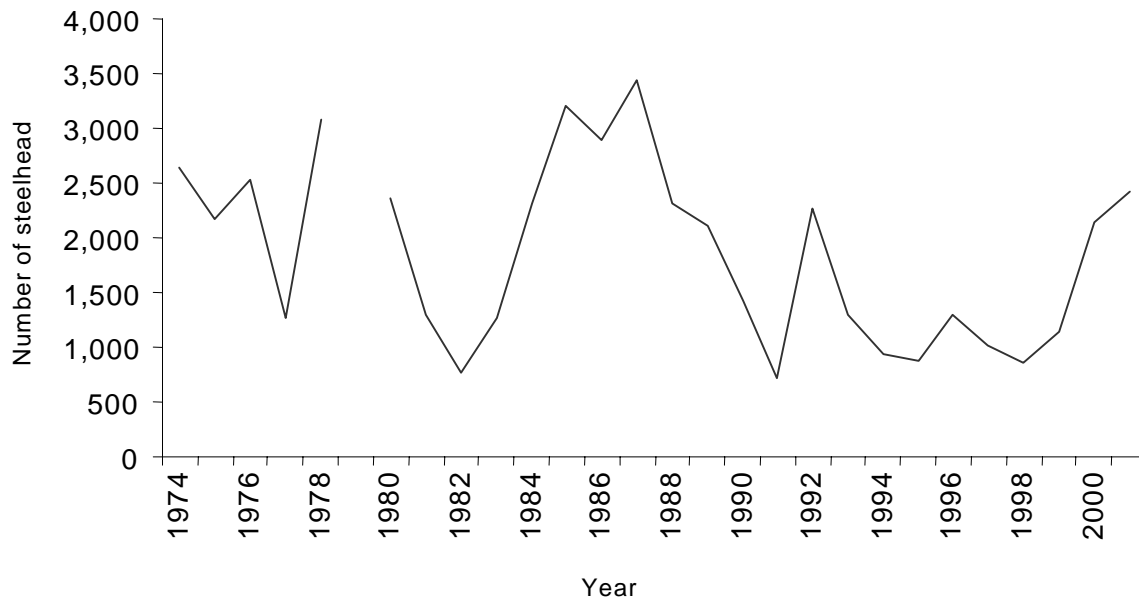
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Figure 14. Number of wild summer steelhead adults counted at Threemile Dam on the Umatilla (1974-2001).

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The ages of the fish captured were determined in all streams from a sub-sample of scales and length frequency measurements. The majority of the fish were found to be age 0 (65%). Most of the remaining fish were age 1 (29%). Nearly all Umatilla smolts are age 2, therefore the age 1 fish captured in the summer would be out-migrating the following spring if they were steelhead. Steelhead smolt production from the upper basin was measured in the winter and spring of 1993-94, 1994-95 and 1995-96, using smolt traps and mark/recapture methods. An average of 40,910 smolts was produced from the upper Umatilla Basin each year (Umatilla Tribes 1994, Contor et al. 1995 and 1996). Only about 6% of the fish captured in the summer were age 2 fish that had not out-migrated the previous spring. Only about 1% of the fish captured were ages 3 or 4. These 2+ fish were probably trout. Neither older *O. mykiss*, nor many large trout were observed during the sampling. This included sampling in mainstem reaches where one might expect to find larger, fluvial trout. Sampling in the lower Umatilla mainstem in the summer of 1996 captured very few *O. mykiss*. It appears that the primary life history in the Umatilla is resident trout

A combination of the density and smolt data provides a rough idea of the portion of the fish observed in the monitoring areas that might be trout. As shown in Figure 13, most of the *O. mykiss* observed during tributary density monitoring were 0+ fish that could be either life history. The number of smolts exceeded the estimated number of adult trout indicating that most of the juveniles produced in the Umatilla are destined to become steelhead. However, the adult steelhead population size in the Umatilla is relatively small. All steelhead adults in the Umatilla are counted at Threemile Dam in the lower basin (Figure 14). An average of 1,853 wild adult steelhead returned annually to the Umatilla Basin since 1974; about 1,000 returned in each of the three years that *O. mykiss* densities were measured in the upper basin tributaries. Although the relative number of age 2+ fish was low compared to the numbers of parr and smolts, the estimate in terms of potential breeding age trout was about 15,000 fish, or about 93% of the known or potential adults each year (Figure 13).

These estimates were only of the number of fish in the 13 tributaries. Further, these density measurements were made in areas where steelhead production was expected to occur and intentionally targeted suspected steelhead. Trout may be relatively more abundant further up the tributaries. There are also three major tributaries in the Umatilla Basin, Willow, Butter and McKay creeks, from which steelhead are excluded by artificial barriers. All *O. mykiss* production in these blocked areas is probably of resident trout, although tribal biologists have expressed an interest in setting smolt traps below the blockages to determine if the fish in the blocked areas are still producing smolts (C. Contor, Umatilla Tribes). Density measurements have not occurred in the blocked areas. But from the available information, it can be estimated that there are several tens of thousands of adult trout in the entire Umatilla Basin.

YAKIMA BASIN

The distribution of sympatry between trout and steelhead varies in the Yakima Basin (Berg 2001). The mainstem Yakima River has been severely impacted by irrigation development. It is inhospitable during summer months and is now only used by *O. mykiss*

as a migration corridor. Only, or primarily, steelhead are present in Toppenish and Satus creeks, the two major tributaries in the lower basin, based on an absence of 2+ *O. mykiss* in these tributaries. Yakima smolts are nearly all 2-year olds.   Historically the upper Yakima above Roza Dam was probably the most productive area for steelhead; however, steelhead passage at Roza Dam was very poor for about 18 years (see Figure 4). Although steelhead passage and abundance has now improved above the dam, the upper Yakima is still dominated by *O. mykiss* trout. Steelhead and trout are also sympatric in the Naches subbasin. Trout distribution extends into headwater areas above current steelhead distribution. The trout have resident and fluvial life histories. Trout in tributaries are smaller than the trout in the mainstem (Pearsons et al. 1994).

The Yakima Basin has been the location of one of the most extensive studies of *O. mykiss* trout in the Columbia Basin. One ongoing question in the study has been the relationship between natural populations of trout and steelhead. Some of the best genetics work targeting this question has been conducted in the Yakima and demonstrated that gene flow occurs between steelhead and trout life histories (Pearsons et al. 1998). In addition, trout abundance was measured annually from 1991 through 1996 in a 25.1 km section of the mainstem Yakima above Roza Dam. The monitoring area was divided into five segments. Trout were sampled from a boat electroshocker and abundance estimates were made using mark-recapture methods. Only trout larger than 8 cm were counted. This size is probably the minimum size of sexually mature fish (Pearsons et al. 1994). Details about the sampling methods and data are available in Ham et al. (1998). Trout were not evenly distributed through the study reach. As shown in Figure 15, the average density of trout was higher in the uppermost reach. An average density of just over 300 fish per km was observed over all five reaches for all years combined. The annual abundance of trout greater than 8 cm in the 25 km of the Yakima mainstem above Roza Dam can be estimated by expanding the average number of fish per km across the entire study reach. Over the six years, an average of 7,725 adult trout was present in the Yakima mainstem above Roza Dam each year.

Annual steelhead abundance data is available for the same area as the trout data (upper Yakima steelhead population), as well as for the entire Yakima Basin, measured since 1985. Total steelhead abundance for the Yakima Basin is presented in Figure 16. An average of 1,430 adult steelhead per year have entered the Yakima since 1985, although the run dropped below 1,000 fish several years during the 1990s. The upper Yakima steelhead population is the smallest population in the basin, averaging only 90 fish per year. Figure 17 presents the size of the upper Yakima steelhead population and the total steelhead abundance for the entire Yakima, as well as the abundance of trout in the 25 km of the mainstem Yakima above Roza Dam. Similar to other basins in the Mid-Columbia ESU, trout strongly dominate the Yakima. Trout comprised about 99% of the adult fish observed in the upper Yakima. Further, the trout in this single reach of the Yakima were about 85% of the adult fish observed if the total Yakima Basin steelhead run is taken into consideration.
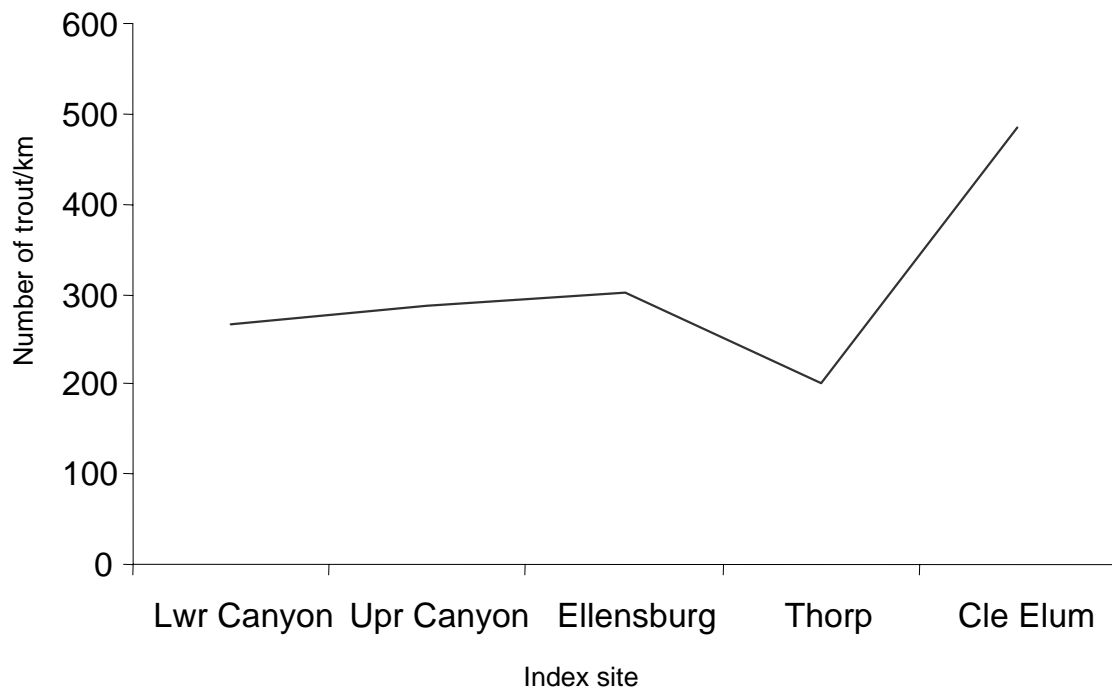
Figure 15. Average density of resident *O. mykiss* in five index reaches above Roza Dam in the upper Yakima Basin (data from Ham et al. 1998, Table 2).
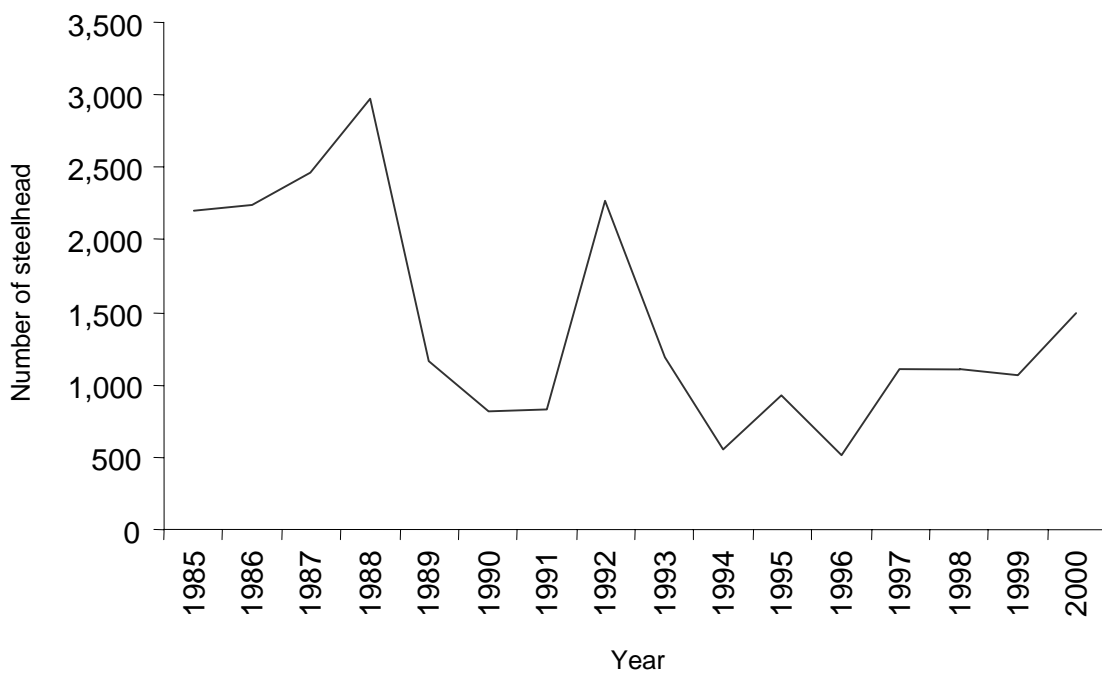

Figure 16. Total abundance of adult steelhead in the Yakima Basin between 1985 and 2000 (data from Berg 2001).
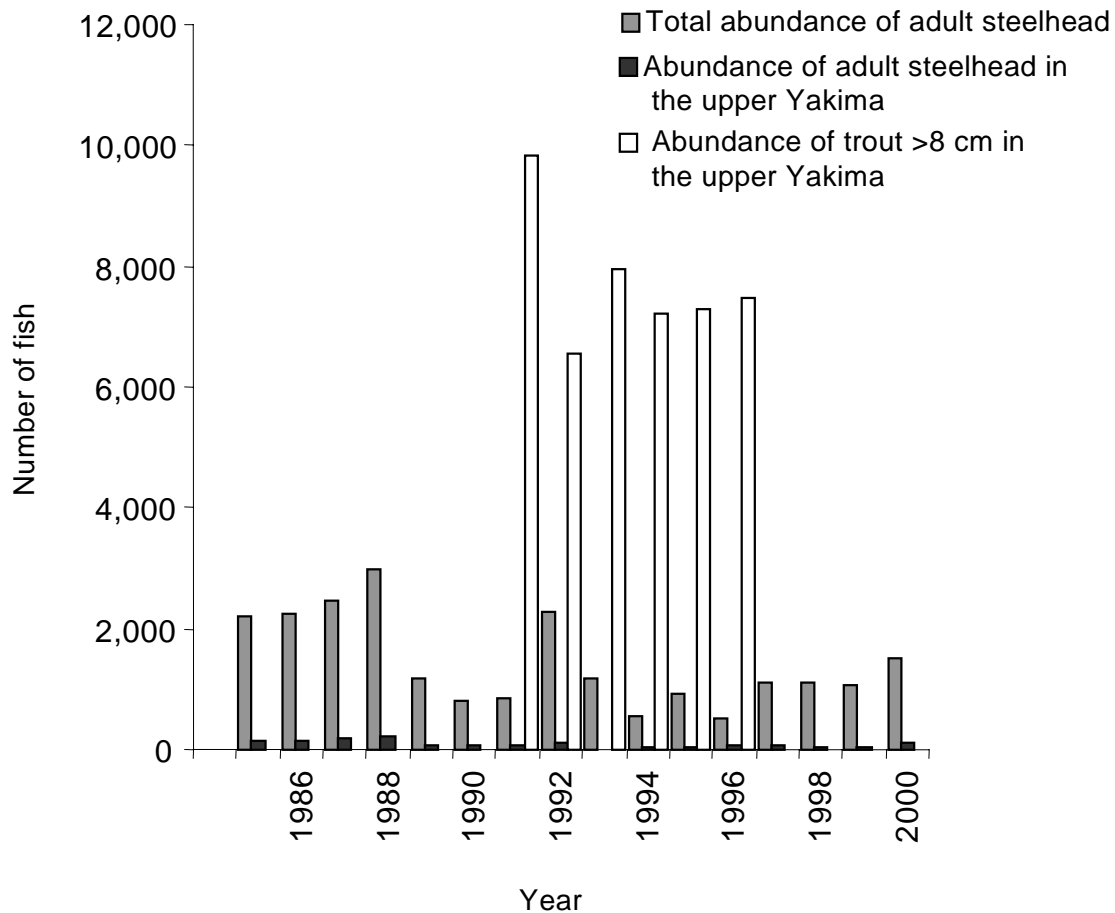
Figure 17. Steelhead and trout abundance data from the Yakima Basin. Two steelhead data sets are shown: one for the entire Yakima Basin, and the second for the upper Yakima population that occupies the trout index area (data from Berg 2001, Figure 33.). Trout abundance is only for the index area and was estimated from the average number of trout / km over all five index areas per year, expanded over the 25 km index area (data from Ham et al. 1998, Table 2).

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The trout abundance measurements were only of trout in a small part of the Yakima Basin. Although trout do not appear to occur in the large lower basin tributaries (Toppenish and Satus) or in the lower mainstem Yakima, they are well distributed throughout the rest of the basin, including into headwater areas where their densities are probably high. Therefore the abundance estimate from the upper Yakima study vastly under represents the total trout abundance in the Yakima Basin, which probably is several tens of thousands of trout.

OTHER BASINS

Steelhead and resident *O. mykiss* are also sympatric in several other basins in the Mid-Columbia ESU, including Fifteenmile Creek, and the Klickitat and Walla Walla rivers. Trout also remain in the historic steelhead range above Condit Dam on the Big White Salmon River. The estimated annual abundance of steelhead in these basins during the 1990s is provided in Table 8. Trout abundances have not been measured in these basins.

Biologists estimate that resident *O. mykiss* are abundant in the Klickitat (B. Sharp, YN) and in the upper Walla Walla (C. Contor, Umatilla Tribes). Trout and trout redds are commonly observed in both basins, although the redds have not been enumerated. *O. mykiss* density measurements have been made in the Klickitat, but similar to other basins, the proportion of these that are trout versus steelhead is uncertain. Trout are reported to be present throughout the Klickitat including in the mainstem (Sharp 2001). However, the mainstem Walla Walla is heavily impacted by irrigation development and is only used as a migration corridor by *O. mykiss.* Trout and steelhead production occurs in the upper Touchet and in the upper North and South forks of the Walla Walla (James 2001). The upper forks drain from Blue Mountain wilderness areas where habitat is in good condition. Several tens of thousands of trout are likely present in these two basins with distributions and densities similar to those seen in the larger Mid-Columbia ESU basins.

O. mykiss trout are less common in Fifteenmile Creek, which also has populations of native coastal cutthroat trout. Resident *O. mykiss* are known to be present throughout Eightmile Creek, but cutthroat occur in other tributaries such as Threemile Creek. While steelhead have been blocked from Big White Salmon River by Condit Dam, *O. mykiss* trout are still present in historic steelhead range above the dam, and local biologists estimate that they are common in the basin (P. Connolly, USGS, USFWS and WDFW unpublished data).

ESU-WIDE SUMMARY

There have been about 17,500 adult steelhead in the Mid-Columbia ESU annually during the 1990s. It appears that fish with non-anadromous life histories consistently make up 90% or more of the adult *O. mykiss* in most basins in this ESU. The estimated total abundance of adult *O. mykiss* in the Mid-Columbia ESU is probably on the order of 175,000 to 200,000 fish, counting both life histories. The majority of these are sympatric steelhead and trout populations, although the estimate includes several tens of thousands of trout above Pelton/Round Butte dams and Condit Dam.

Table 8. Estimated abundance of wild steelhead in other Mid-Columbia ESU basins.

Basin	Estimated number of wild steelhead
Fifteenmile Cr. (winters)	~ 200 - 300
Klickitat (winters and summers)	260 (average 1996-2000)
Walla Walla (summers)	450 (average 1993-2000)

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Snake ESU

The Snake ESU covers a very large geographic area with substantial, but varied, information about *O. mykiss*. Wild steelhead abundance for the entire Snake River ESU is available from dam counts on the Snake River. Data on *O. mykiss* trout abundance in the part of the Snake Basin currently occupied by steelhead are variable. Most monitoring efforts have been focused on measuring densities of juvenile steelhead and observations of trout are incidental. The Snake ESU, as originally described by NMFS, terminated at the Hells Canyon dam complex. However, the NMFS is now reassessing their original ESU boundary decision. Therefore this report also includes information about trout abundance in basins above Hells Canyon Dam that were historically occupied by steelhead. The sections below provide a total abundance estimate for the Snake River steelhead, then breaks out trout information for several basins where the two life histories are sympatric, and then concludes with a review of the information available about the basins above Hells Canyon Dam

SNAKE RIVER STEELHEAD ABUNDANCE

The abundance of wild Snake River steelhead has been monitored at the lower Snake River dams since the 1962 run year. The counts since 1975 have been at Lower Granite Dam and so exclude one Snake River subbasin that has a steelhead population, the Tucannon in southeast Washington. The number of wild steelhead observed over the monitoring period is shown in Figure 18. The counts were quite low in the 1990s, but increased recently. The 5-year average run size since the 1998 run year was 26,900 steelhead.

Figure 18. The number of Snake River wild steelhead counted at the uppermost dam between 1962 and 2003. The counts after 1975 are at Lower Granite Dam and exclude the steelhead population that is in the Tucannon. Data provided by S. Keifer, IDFG.

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SALMON BASIN

The Salmon River Basin is a very large system with over 15,300 stream km. It is probably the largest producer of steelhead in the Snake ESU. Although large tracks of the basin are in wilderness and could be considered pristine, much of the system is relatively sterile because of granite substrates and high elevations. *O. mykiss* trout share the basin with westslope cutthroat trout and are not present in all areas. In recent presence/absence surveys in the upper Salmon Basin by IDFG, *O. mykiss* were found in about 48% of the streams surveyed (Brimmer et al. 2002). Some of the major subbasins that are occupied by *O. mykiss* trout include the Little Salmon, Lemhi and Pahsimeroi rivers, and the South, Middle and East forks of the Salmon. *O. mykiss* of either life history appear to be less common in most head water areas, including in the Stanley Basin. The *O. mykiss* trout can be large as adults, reaching 50 cm, often with fluvial life histories (Bjornn 1978). But the trout in many tributaries are resident fish and are small in size.

Table 9. The distribution of three species of native trout among 16 reaches in Sulphur Creek, a tributary of the Middle Fork, Salmon River. Data from Allen et al. (1996), Tables 12-14.

Reach	Density of westslope cutthroat (fish/m^2)	Density of *O. mykiss* (fish/m^2)	Density of mountain whitefish (fish/m^2)
1	0.0034	0.0118	0.0017
2	0.0031	0.0063	0.0063
3	0.0028	0.0014	0.0112
4	0.0016	0.0016	0.0256
5	0.0028	0	0
6	0.0025	0	0
7	0.0023	0	0
8	0.0018	0	0
9	0	0.0089	0
10	0	0.003	0.0557
11	0	0.0139	0.0035
12	0	0.012	0.0051
13	0	0.0032	0.0049
14	0	0	0.184
15	0	0	0.0022
16	0	0	0

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A 1993 snorkel survey of Sulphur Creek, a tributary of the Middle Fork Salmon, demonstrated how sympatric westslope cutthroat, *O. mykiss*, and mountain whitefish (*Prosopium williamsoni*), all native trout species in the basin, partitioned themselves in a single creek (Allen et al. 1996). The survey included 16 reaches and the data were partitioned by species, reach and size class (0-7.6 cm, 7.7 - 15.3 cm, 15.4-22.8 cm, 22.9-30.4 cm and >30.5 cm). The total densities of each species by reach are shown in Table 9. Cutthroat was the only species present in half of the reaches it occupied, while *O. mykiss* and mountain whitefish were more often sympatric. Further, the fish were partitioned by size, which suggest different life histories and micro-habitat use even where they were all sympatric in a reach. All of the *O. mykiss* trout were smaller than 22.8 cm, while all of the cutthroat were larger than 22.9 cm. The cutthroat trout must have been fluvial with the smaller fish in the population rearing elsewhere. The mountain whitefish fell into all size classes.

Bjornn (1978) studied the ecological relationship between trout and steelhead in Big Springs Creek in the Lemhi subbasin. He noted that steelhead, while historically native to the basin, were rare or absent in the study area until they were reintroduced in the early 1960s. He also noted that westslope cutthroat were absent from the study area. *O.*
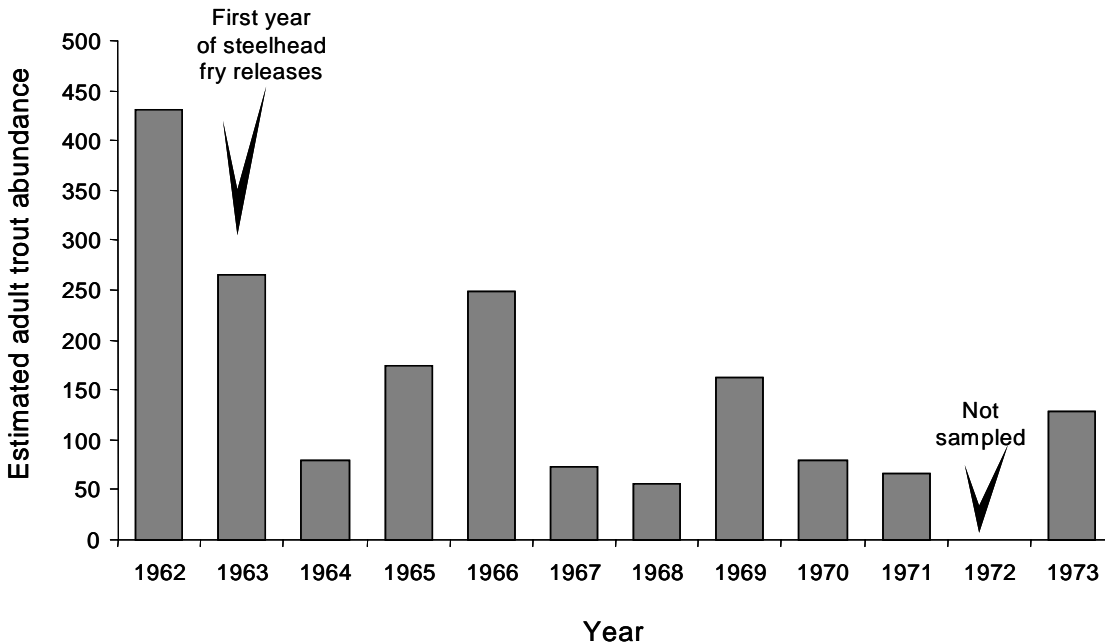
Figure 19. Estimated abundance of adult, fluvial *O. mykiss* trout, >30 cm, in Big Springs Creek in the Lemhi Basin from 1962 to 1973. Data from Bjornn (1978), Table 30.

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mykiss trout was the dominant species present prior to the introduction of steelhead, making up 75% of the fish sampled. The other species present were native spring chinook (*O. tshawytscha*), native mountain whitefish and exotic brook trout. The trout were fluvial with breeding adults that were 20 to 45 cm in size and two to four years old. After several years of steelhead hatchery fry releases, the total number of *O. mykiss* in the study area did not change, but fish with trout life histories dropped to only 10 to 20% of the mixture of trout and juvenile steelhead (Bjornn 1978). This result suggests that trout and steelhead can compete with each other and that trout populations may be smaller if steelhead are also present. The estimated annual abundance of wild, fluvial adult trout in Big Springs Creek from 1962 through 1973 is shown in Figure 19. The hatchery fish releases over the study period returned between 14 and 75 adult steelhead per year but wild steelhead adults were rare or absent (Bjornn 1978).

More recently, since 1991, adult fluvial trout have been counted at a weir on the Pahsimeroi River as they migrate between rearing areas and spawning areas. Naturally-produced steelhead returning to the Pahsimeroi subbasin have also been counted at the weir since 1997. Total counts of both life histories are shown in Figure 20. The total abundance of adult *O. mykiss* passing above the weir ranged from a low of 33 fish to a high of 439 fish, including similar numbers of trout and steelhead until the last couple of years when steelhead abundance increased. However, this number probably does not represent the entire adult *O. mykiss* abundance in the Pahsimeroi, rather the trout abundance is probably underestimated. The counts occurred during the steelhead run-time. It is not known whether trout pass the area of the weir at other times, but they may
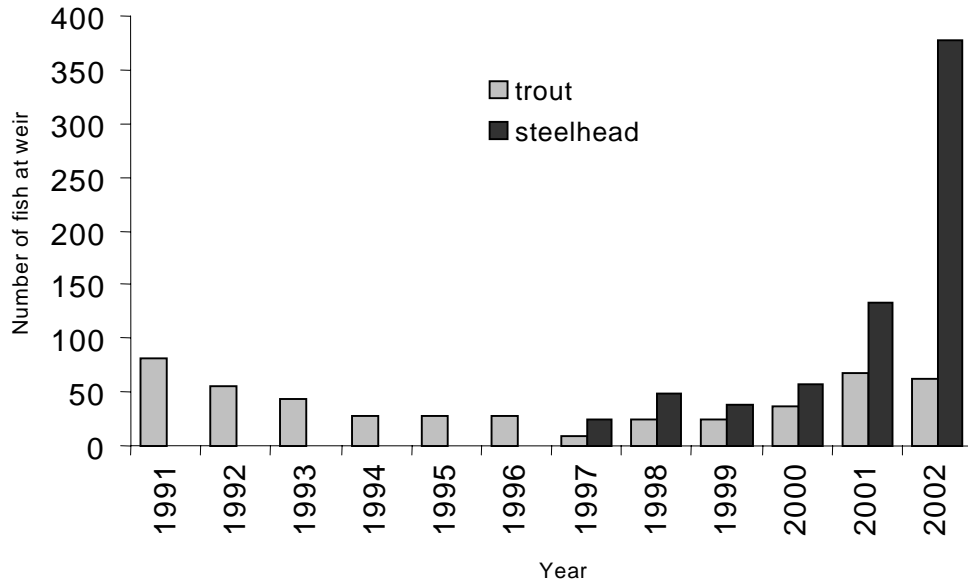
Figure 20. The number of adult steelhead and fluvial trout counted at a weir on the Pahsimeroi. Unpublished data from D. Engemann, IDFG.

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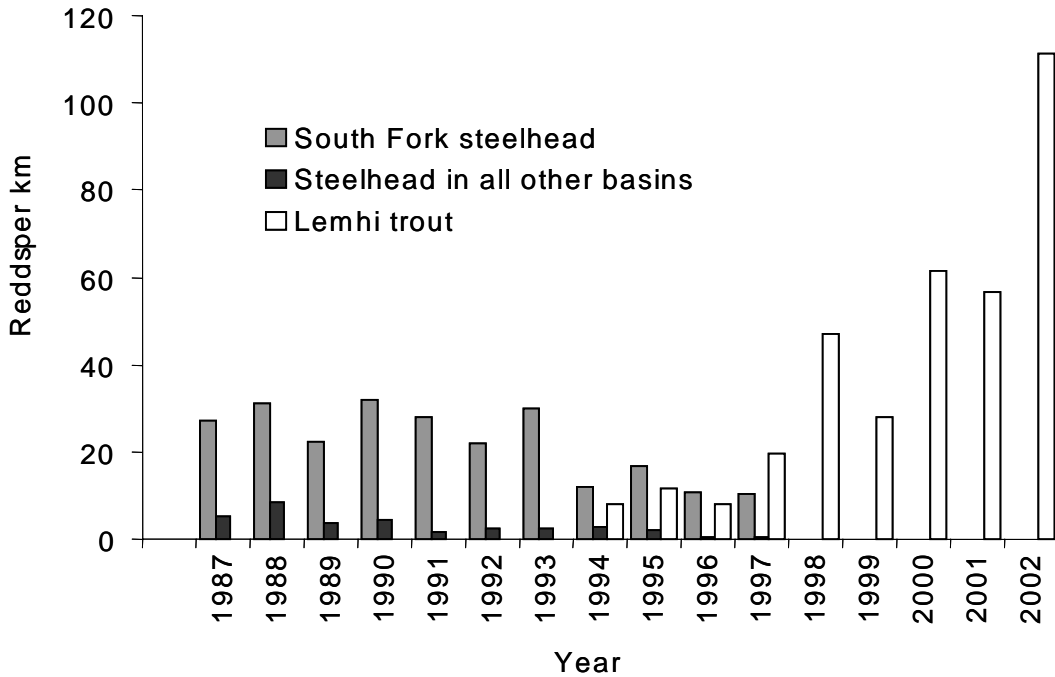
Figure 21. Redd counts for steelhead in the South Fork Salmon subbasin and for steelhead in all other subbasins combined, 1987 through 1997 (data from Streamnet). Steelhead spawning ground surveys have not been conducted in more recent years. Redd counts for the Lemhi *O. mykiss* trout index areas, 1994 – 2002, are also shown (data from Brimmer et al. 2002).

do so. Also, resident fish are probably present, particularly resident males as suggested by the skewed sex ratios observed. The trout were 70% female and both genders averaged about 40 cm in length while the steelhead were 59% female and both genders averaged about 65 cm in length (data provided by D. Engemann, IDFG).

IDFG conducted steelhead redd counts throughout the Salmon Basin between 1987 and 1997. The counts on the South Fork Salmon were much higher than in other subbasins, so for this document they were summarized separately while data for all other basins were combined. Over the ten year period, an average of 21.9 steelhead redds/km were counted in the South Fork Salmon subbasin, and an average of 4.9 steelhead redds/km were counted over all other areas in the Salmon Basin (data from Streamnet). IDFG also counted trout redds in three index reaches in the Lemhi subbasin since 1994. IDFG report the total number of trout redds observed annually rather than a density of redds. An annual average of 195 redds have been counted since 1994. More recently the counts have increased and the average since 1998 has been 304 redds (Brimmer et al. 2002). In order to obtain some information about total *O. mykiss* abundance in the Salmon Basin using these redd counts, it is necessary to place both data sets into a similar metric and context. For this document IDFG staff estimated that their index areas total about 5 km (A. Brimmer, IDFG) which provides an average density of 38.9 trout redds/km in the Lemhi between 1994 and 2001.

The annual Salmon Basin steelhead redd counts and Lemhi subbasin trout redd counts are presented together in Figure 21. While this information demonstrates that the *O. mykiss* species in the Salmon River is much more abundant when trout are counted along with steelhead, it is not possible to expand these data to estimate the total abundance of the species in the Salmon Basin. Abundance of steelhead is clearly irregular across the basin as demonstrated by the different redd densities in the South Fork as compared to other areas. IDFG biologists also believe that the Lemhi is an exceptionally productive basin for *O. mykiss* trout and does not represent redd densities or trout abundances elsewhere in the Salmon Basin (T. Curet, A. Brimmer, IDFG). The high-altitude tributaries are much less productive and many areas have different trout species including both native cutthroat and exotic trout.

IDFG also conducted index surveys of *O. mykiss* densities during the summer in the Salmon Basin in 1994 and 1996. The surveys were conducted by electroshocking. Although the purpose of the program was to measure juvenile steelhead production, fish that were large enough to be adult trout are also recorded. While some researchers have used the presence of 2+ *O. mykiss* to represent trout in the Salmon (Bjornn 1978), some steelhead smolts in the Snake River may be 3 years old (S. Yundt, IDFG) making the distinction between trout and steelhead smolts difficult. The density data were compiled by age/size classes. Fish identified as age 1+ ranged in size from 8 to 15 cm, while fish identified as age 2+ ranged in size from 16 to 23 cm (Hall-Griswold et al. 1995, Hall-Griswold and Petrosky 1998). Based on observations of trout maturation elsewhere in the Columbia Basin as well as in the Salmon (Bjornn 1978), both size classes may have included some adult trout.

Table 10. Average density of 1+ and 2+ *O. mykiss* in IDFG Salmon River parr index survey areas in 1994. Averages were calculated using only those index areas that contained fish. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). Data from Hall-Griswold et al. (1995).

Tributary	Total index areas	Number of index areas with 1+ fish	Average density 1+ (fish/m^2)	Number of index areas with 2+ fish	Average density 2+ (fish/m^2)
Lower Salmon	7	7	0.067	7	0.022
Little Salmon R	2	2	0.034	2	0.031
Lwr Salmon R. Canyon	9	9	0.035	9	0.018
SFk Salmon R	32	26	0.010	17	0.009
MFk Salmon	51	28	0.010	15	0.006
Upr Salmon R. Canyon	20	19	0.031	18	0.009
Lemhi R	5	3	0.092	3	0.011
Pahsimeroi R	2	1	0.016	2	0.002
EFk Salmon	4	2	0.003	3	0.004
Upper mainstem Salmon	29	12	0.007	8	0.013
Headwater tributaries	52	22	0.018	17	0.006

Table 11. Average density of 1+ and 2+ *O. mykiss* in IDFG Salmon River parr index survey areas in 1996. Averages were calculated using only those index areas that contained fish. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). Data from Hall-Griswold and Petrosky (1998).

Tributary	Total index areas	Number of index areas with 1+ fish	Average density 1+ (fish/m^2)	Number of index areas with 2+ fish	Average density 2+ (fish/m^2)
Lower Salmon	8	8	0.077	7	0.028
Little Salmon R	4	4	0.053	4	0.038
Lwr Salmon R. Canyon	11	11	0.050	11	0.015
SFk Salmon R	30	21	0.010	17	0.009
MFk Salmon	27	10	0.006	11	0.005
Upr Salmon R. Canyon	8	5	0.008	3	0.006
Lemhi R	7	5	0.082	6	0.011
Pahsimeroi R	4	4	0.011	4	0.024
EFk Salmon	3	1	0.001	1	0.008
Upper mainstem Salmon	17	6	0.002	8	0.001
Headwater tributaries	12	2	0.003	3	0.003

Table 12. Densities of *O. mykiss* between 9 cm and 17 cm in the Salmon Basin. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). (Unpublished data, T. Curet, IDFG).

Tributary	No. of index areas	Tributary-wide density of *O. mykiss* (fish/m^2)
MFk Salmon River	19	0.041
NFk Salmon River	55	0.050
Lemhi River	67	0.049
Pahsimeroi River	15	0.028
EFk Salmon River	21	0.020
Yankee Fork River	1	0.040
Horse Creek	1	0.19
Main Salmon (Below MFk)	9	0.070
Main Salmon (MFk to NFk)	53	0.073
Main Salmon (NFk to Lemhi)	8	0.076
Main Salmon (Lemhi to Pahsimeroi)	15	0.031
Main Salmon (Pahsimeroi to EFk)	38	0.069
Main Salmon (EFk to Yankee Fk)	23	0.032
Main Salmon (Yankee Fk to Headwaters)	34	0.017

Surveys were conducted at 213 index areas in 1994. Age 1+ *O. mykiss* were found in 62% of the areas and age 2+ *O. mykiss* were found in 47% of the areas (Hall-Griswold et al. 1995). Surveys were again conducted at 131 index areas in 1996. Age 1+ *O. mykiss* were found at 59% of the areas and age 2+ *O. mykiss* were found in 57% of the areas (Hall-Griswold and Petrosky 1998). Density data from these surveys are presented in Tables 10 and 11. Densities of 1+ *O. mykiss* were low to moderate, according to the benchmarks provided by Dambacher and Jones (1995), while densities of 2+ fish were low. The "low" measure of 2+ fish was expected since the benchmarks were established for a population that included younger fish, which tend to be much more abundant.

In some basins, including the Little Salmon River, the South and East Forks Salmon River and the Pahsimeroi River, the densities of 2+ fish were quite similar to the densities of 1+ fish. This relationship was observed in both years of sampling. In most density measurements (e.g. Dambacher and Jones 1995, also see the Umatilla data, Table 8 and Figure 13), the densities of younger fish, ages 0+ and 1+, are much higher than the densities of older fish in the population. This seems to be especially the case where production is predominately of steelhead and the most abundant age class is 0+ young of the year followed by 1+ parr who out-migrate the following spring as age 2 smolts. An age distribution where older, 2+ fish occur at similar densities as younger ones is more likely to be seen in a trout population. Adult trout may be long-lived so that several year classes are seen. Adults may be relatively abundant but they may not be breeding each year so that some juvenile classes can be underrepresented. Also, trout may have fluvial life histories such that adults and juveniles are partitioned into different habitats, and the sampling may have occurred in a reach dominated by adults, simlar to what was seen in the Sulpher Creek cutthroat (Allen et al. 1996). Bjornn (1978) noted that adult trout made up 44% of the fluvial Lemhi trout population prior to the reintroduction of steelhead. Therefore, the basins in Tables 10 and 11 where age 2+ densities approached those of age 1+ fish may represent areas where trout were abundant. *O. mykiss* in general, and the 2+ fish in particular, tended to be more abundant in the lower Salmon Basin through the tributaries of the Salmon River Canyon and into the Lemhi and Pahsimeroi rivers. Above the confluence of the Pahsimeroi, and also in the much of the Middle Fork, *O. mykiss* densities dropped and the species was absent from many index areas.

Additional density data are available from IDFG for the upper Salmon Basin. These data are from 359 index areas in 14 major tributaries or mainstem sections of the Salmon Basin. Only fish that were between 9 cm and 17 cm were measured, which could include both large smolts and small mature trout. Larger *O. mykiss* trout were present but were not included in the measurements, which were intending to target steelhead parr. These data, presented in Table 12, also demonstrate that 1+ *O. mykiss* densities in the mid to upper Salmon Basin reflect a moderate to low abundance (data from T. Curet, IDFG).

The data that are available from the Salmon Basin cannot be expanded to produce a basin-wide estimate of *O. mykiss* abundance that counts both the steelhead and trout partly because the distribution and density of the species varies across the basin. The available information, particularly the relatively high densities of 2+ fish in some areas,

indicate that trout are locally very abundant in some subbasins. However, their distribution is patchy since they appear to be absent from other locations. The trout also display an interesting variety of life history strategies. The irregular distribution and abundance of *O. mykiss* trout is probably a result of the occurrence of native westslope cutthroat in the basin, which dominate the higher elevation tributaries and headwaters. The total abundance of *O. mykiss* trout in the Salmon River Basin is probably less than what was observed in most Mid-Columbia ESU basins, but adult trout are still likely very abundant, perhaps on the order of several tens of thousands of fish.

CLEARWATER BASIN

The Clearwater is also a major producer of steelhead in the Snake River. However, the dominant trout species in the basin is thought to be cutthroat trout. Two dams, Lewiston and Stites dams both since removed, historically blocked much of the Clearwater Basin, although Lewiston Dam passed some steelhead. The passage impediments caused by these dams may have increased the relative abundance of resident *O. mykiss* throughout the Clearwater, similar to the continuing effect of Dworshak Dam on the North Fork.

Index surveys of *O. mykiss* densities in the Clearwater Basin were made in 1994 and 1996, similar to those conducted in the Salmon Basin. The surveys were conducted by electroshocking. The same age/size criteria were used: fish identified as age 1+ ranged in size from 8 to 15 cm, while fish identified as age 2+ ranged in size from 16 to 23 cm (Hall-Griswold et al. 1995, Hall-Griswold and Petrosky 1998). Again, both size categories were large enough to include adult trout.

In 1994, 1+ *O. mykiss* were found in 93% of the 115 index areas surveyed, while 2+ *O. mykiss* were found in 67% of them (Hall-Griswold et al. 1995). In 1996, 1+ *O. mykiss* were found in 85% of the 103 index areas surveyed, while 2+ *O. mykiss* were found in 67% of the index areas (Hall-Griswold and Petrosky 1998). The average densities observed in the Clearwater are presented in Tables 13 and 14. The densities all subbasins fell in the low abundance category according to the Dambacher and Jones (1995) benchmarks. Although the densities of 2+ fish were less than that of the 1+ fish, they were relatively high enough that they may indicate fairly abundant trout populations in some areas, particularly in the Selway and Lochsa rivers. IDFG has not expanded these densities to abundance estimates.

IDFG also conducted steelhead redd counts in the Clearwater Basin between 1990 and 1998 (data from Streamnet). They counted an average of 2.4 redds/km over the eight year period (Figure 22). This is a lower density of steelhead redds than was observed in the Salmon Basin. Trout redds have not been counted in the Clearwater.

It is not possible to expand the available information and estimate the abundance of either trout or steelhead where they are sympatric in the Clearwater. However, the available information suggests that abundance of steelhead is lower in the Clearwater than in the Salmon Basin. Steelhead redd densities in the Clearwater are about half of what was observed in the Salmon. However, the densities and distribution of 2+ *O. mykiss* appear to be similar in the two basins, even though it is generally recognized by local biologists

that cutthroat trout dominate the Clearwater to a greater extent than they do in the Salmon.

The total abundance of *O. mykiss* in the Clearwater Basin needs to take into consideration the steelhead, the trout that are sympatric with steelhead and the trout population that remains within historic steelhead range above Dworshak Dam on the North Fork. There are no abundance data for the trout population above the dam. However, local biologists believe trout are common in that subbasin (C. Corsi, IDFG).

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Table 13. Average density of 1+ and 2+ *O. mykiss* in IDFG Clearwater River parr index survey areas in 1994. Averages were calculated using only those basins that contained fish. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). Data from Hall-Griswold et al. (1995).

Tributary	Total index areas	No. index areas with 1+ fish	Average density 1+ (fish/m^2)	No. index areas with 2+ fish	Average density 2+ (fish/m^2)
Mainstem / MFk Clearwater	14	14	0.011	8	0.003
SFk Clearwater	30	25	0.027	20	0.014
Crooked R	26	26	0.016	17	0.007
Selway R	24	24	0.044	20	0.024
Lochsa R	21	18	0.049	12	0.026

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Table 14. Average density of 1+ and 2+ *O. mykiss* in IDFG Clearwater River parr index survey areas in 1996. Data from Hall-Griswold and Petrosky (1998).

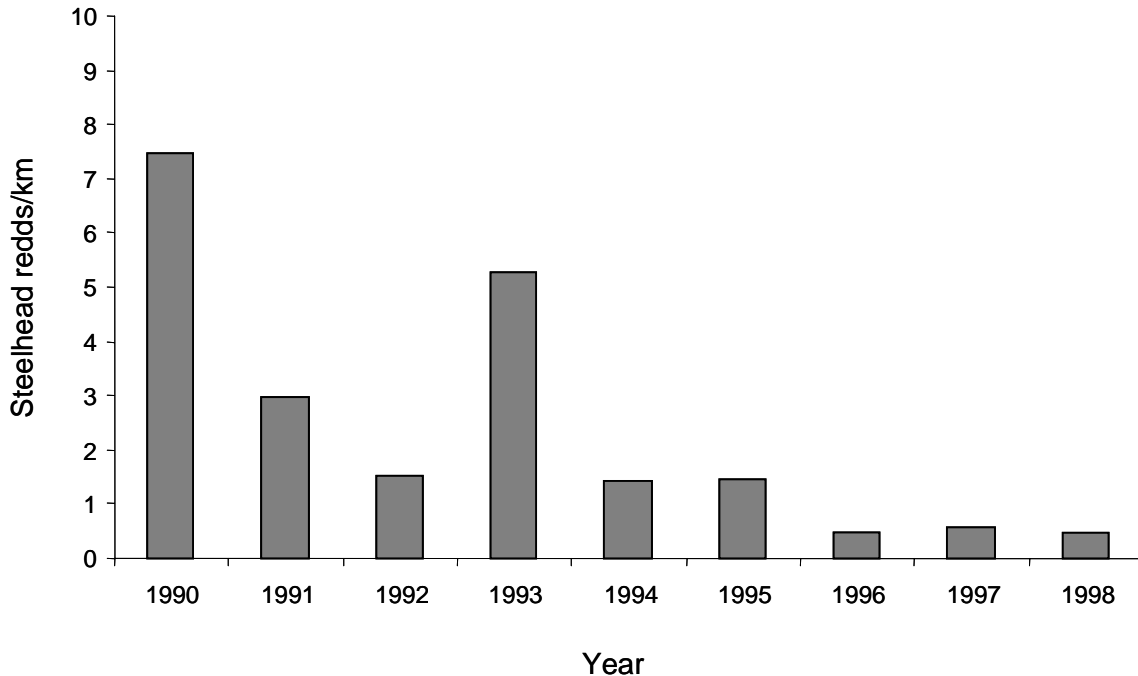| Tributary	Total index areas	No. index areas with 1+ fish	Average density 1+ (fish/m^2)	No. index areas with 2+ fish	Average density 2+ (fish/m^2)
Mainstem / MFk Clearwater	11	6	0.014	6	0.006
SFk Clearwater	24	20	0.012	15	0.010
Crooked R	26	25	0.012	14	0.005
Selway R	24	21	0.012	22	0.013
Lochsa R	18	16	0.037	12	0.019

Figure 22. Average steelhead redd counts per year in the Clearwater Basin, 1990-98. Data from Streamnet.

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JOSEPH CREEK, GRANDE RONDE BASIN

Joseph Creek is a tributary of the lower Grande Ronde Basin. It is dominated by *O. mykiss*, including a wild steelhead population. Adult steelhead abundance since 1974, expanded from redd counts, is presented in Figure 23. Since 1990, an annual average of 1,225 steelhead spawned in the basin.

In 1994, ODFW estimated the total abundance of 0+ *O. mykiss* in Joseph Creek by measuring fish densities at 25 locations in the subbasin. Densities were measured by electroshocking with blocknets. The estimates were divided into two size groups: fish smaller than 12 cm and fish larger than 12 cm. Although all of the fish larger than 12 cm were called "1+" fish, actual ages were not measured from scales, and some fish in that size range may have been older. Since trout may mature and spawn as small as 10 cm, the larger size range may have included some adult trout. This effort produced an abundance estimate of 155,503 fish (0.32 fish/m^2) that were smaller than 12 cm, and 67,429 fish (0.14 fish/m^2) that were larger than 12 cm (ODFW unpublished data from B. Knox, ODFW).

The question is, how many of the larger fish might have been trout rather than steelhead smolts that would have out-migrated in the spring of 1995. All of the fish may have been smolts. The 1997 adult return to Joseph Creek was relatively small, only 574 fish. However, with a parr-to-adult survival rate of 0.9%, all of the fish >12 cm in the summer

of 1994 may be accounted for as steelhead. In a separate study of Joseph Creek *O. mykiss* in 1989-90, cooperatively conducted by IDFG and ODFW, a strong correlation was found between 1989 steelhead redd counts and 1990 parr densities ($R^2 = 0.75$). Parr densities in that study varied by location and ranged from 0.07 to 0.20 fish/m^2 (unpublished data from B. Knox, ODFW). Both of these results suggest that most of the parr observed were juvenile steelhead rather than trout.

However, it is likely that some of the fish observed during the density sampling were trout. It may be possible to make an estimate of potential adult trout by considering only the largest fish in the 1994 samples. Only 2% of the total fish observed were larger than 14 cm. However, these expand to a population estimate of 13,255 fish. The remaining "1+" fish (those between 12 and 14 cm), with a parr-to-adult survival of 1.1%, could still produce the adult steelhead population seen in 1997. Even if only half of the fish larger than 14 cm were adult trout, the trout population would be over 6,700 fish, or about 85% of the adult *O. mykiss* in the basin. Most of the *O. mykiss* parr observed in Joseph Creek may well be steelhead, yet the population size of adult trout could still be greater than 10,000 fish.
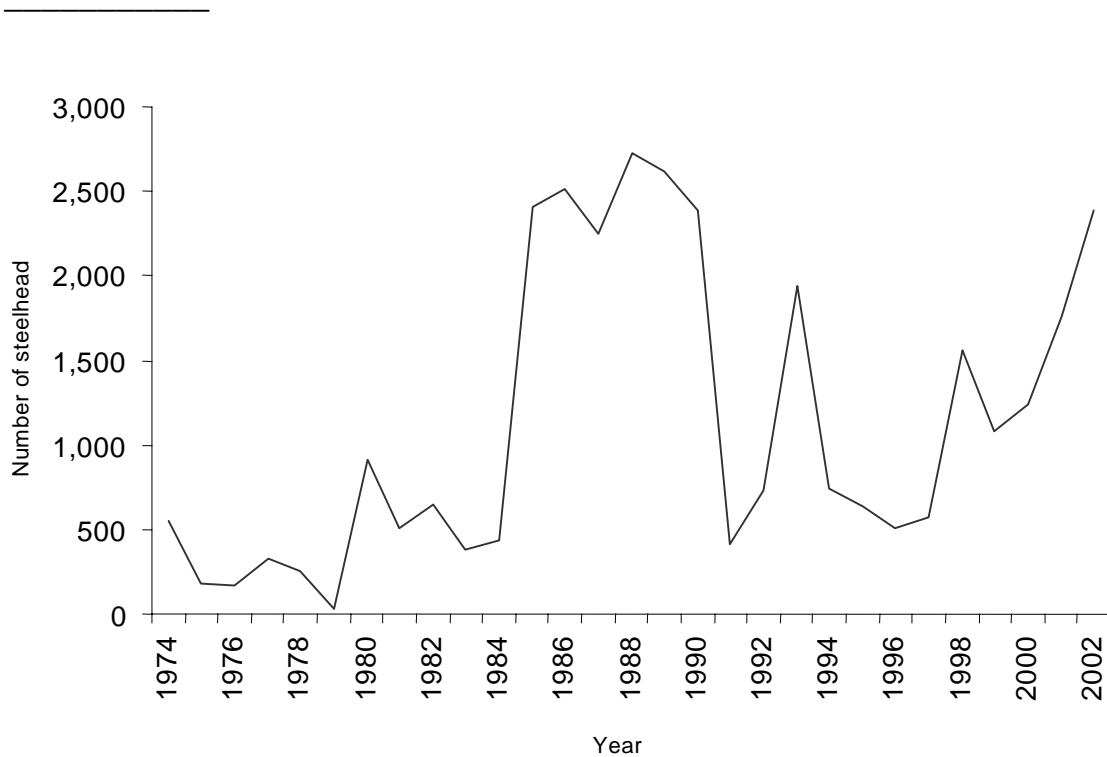
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Figure 23. Abundance of wild adult steelhead in Joseph Creek, a tributary of the lower Grande Ronde Basin. Data from M. Chilcote, ODFW, expanded from redd counts.

OTHER BASINS CURRENTLY OCCUPIED BY STEELHEAD

Other basins in the Snake ESU that are currently occupied by steelhead include the Tucannon River and Asotin Creek in Washington and the Imnaha River and the rest of the Grande Ronde River in Oregon. Steelhead parr density data are available from some locations in these basins but the relationships and necessary assumptions to estimate trout abundance are similar to those already reported here.

O. mykiss trout abundance appears to be low in the Tucannon, based on incidental observations. Occasional mature trout are seen that are about 30 cm. Some trout redds are seen during steelhead spawning ground surveys, but they are only about 1-2% of the redds observed (M. Schuck, WDFW). However, smaller mature trout and very small redds may be present that would be difficult to detect by incidental observation.

Trout densities or abundances have not been measured in the Imnaha, but the results of a genetics pedigree study in upper Little Sheep Creek suggests that trout may be abundant in this basin. In the study, 100% of the adult steelhead entering Little Sheep Creek have been sampled. However, when *O. mykiss* parr above the weir were compared with the adults passed over the weir, a substantial proportion (approximately one half to two thirds) of the parr could not be matched to an anadromous parent-pair. Forty adult trout and residualized steelhead were also assayed, however, no parents were found in that group. These data suggest that the resident *O. mykiss* population in Little Sheep Creek is much larger than previously thought, and that their juvenile offspring intermingle with the progeny of anadromous fish. Although the "orphans" are certainly the progeny of resident fish (other potential explanations have largely been rule out), it is not yet clear if they result entirely from resident by resident crosses or from some resident by anadromous crosses similar to what has been seen in the Hood River. A larger sample of several hundred resident adults was collected in 2002. Those data should help identify parents of the parr, and also provide information about the degree (and direction) of genetic exchange between resident and anadromous components of this *O. mykiss* population (P. Moran, NMFS).

BASINS ABOVE HELLS CANYON DAM

In 1995, the USFWS was petitioned to list the resident *O. mykiss* trout between Brownlee Dam and Shoshone Falls under the ESA. The Service found that the petition did not present substantial information that listing was warranted because the proposed unit was not demonstrated to represent a distinct population segment (DPS) (60 FR 49819). Therefore a status review of the trout did not occur. However, partially in response to the action, the states of Idaho and Oregon, and the Burns/Paiute Tribes in eastern Oregon increased their efforts to collect information about trout densities and abundance in the basins above Hells Canyon Dam.

Information about resident *O. mykiss* densities and/or abundance is available from the Weiser, Payette, Boise, Owyhee and Malheur basins. Multiple years of data are available from a few locations. The lower mainstems and some larger tributaries in all of these basins are heavily impacted by irrigation development, including some diversion dams

Table 15. Densities of *O. mykiss* trout by size in the Middle Fork Boise River, measured in two different years. Abundance benchmarks for density data: low (< 0.05), moderate (0.06 – 0.19), high (>0.2) according to Dambacher and Jones (1995). Data from Allen et al. (1996), Table 9.

Size Class	1988 *O. mykiss* densities fish/m^2	1993 *O. mykiss* densities fish/m^2
0 - 10.1 cm	0.0006	0.0025
10.2 – 20.3 cm	0.0042	0.0046
20.4 – 30.4 cm	0.0043	0.0022
> 30.4 cm	0.0001	0.0005
Total	0.0092	0.0169

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that form complete fish passage barriers. Many of these reaches are not hospitable to resident fish. However, the headwater areas of most basins have relatively good habitat for trout. Parts of the Payette and Boise drain from wilderness areas. The Owyhee is a desert basin and is ecologically quite different from the other systems for which data are available.

IDFG surveyed 14 index areas in the Middle Fork Boise River in 1988 and again in 1993 (Allen et al. 1996). Total densities were at low abundance in both years based on the benchmarks provided by Dambacher and Jones (1995) (Table 15). Densities were highest for mid-sized fish (10 to 30 cm), which were probably young breeding-aged adults. This seems like an unexpected result since typically the smallest age-classes are the most abundant. The observed size distribution can be explained by a period of depressed reproduction associated with drought conditions in the early 1990s.

IDFG also surveyed three tributaries of the Owyhee Basin in the late 1970s and again in the early 1990s (Allen et al. 1996). Based on the sizes of fish sampled, which ranged from 4 to 24 cm, the samples included both sub-adults and adults. These data indicate that fish density was very high in some local reaches (Table 16). Some reaches had high abundances according to the Dambacher and Jones (1995) benchmarks. However the abundances estimated by IDFG (Table 16) were not very large because only small areas within the basin were occupied. The distribution was highly patchy with fish concentrated in some reaches, but rare or absent from others. Occupation of tributaries varied from year-to-year. For example, in Deep Creek fish were present, but in low numbers, in the single reach that was surveyed in 1977. Fish were absent from 8 out of 9 reaches surveyed in 1993, but were at a very high density in the one occupied reach (Table 16, also Allen et al. 1996). No fish were found in Deep Creek in 1999 (see Table 17, K. Meyer, IDFG). This kind of patchy and variable distribution, which is also commonly seen in eastern Oregon desert streams (Dambacher et al. 2001),

Table 16. Average densities and estimated abundances of trout in three tributaries of the Owyhee Basin in eastern Idaho, including comparison between measurements in the late 1970s and the early 1990s. Data from Allen et al. (1996).

Tributary	Years sampled	Number of reaches sampled	Number of reaches occupied	Range of estimated abundances per reach	Total estimated abundance	Average density (fish/m^2) in occupied reaches
Jordan Creek	1976-77	8	8	5 to 86	275	0.12
	1993	8	8	1 to 70	153	0.09
Red Canyon Creek	1991	3	3	1 to 69	83	0.11
	1993	3	2	0 to 91	92	0.10
Deep Creek	1977	1	1	10	10	0.23
	1993	9	1	0 to 112	112	1.02

Table 17. Number of trout/km and densities (fish/m^2) of *O. mykiss* trout >10 cm in four Idaho tributaries above Hells Canyon dam complex. Smaller fish were also observed in most areas. All data collected in 1999 except as noted. (unpublished data, K. Meyer, IDFG; also Meyer 1999).

Tributary	Streams	Number of index areas (*)	Average fish/km	Average density (fish/m^2)
Weiser (No *O. mykiss* seen in Anderson, Johnson and King Hill creeks. Most reaches had other trout species)	Weiser River, 1998	16	--	0.16
	Beaver Creek	3	280	0.08
	Cottonwood Creek	3(1)	253	0.05
	Grizzly Creek	1	80	0.07
	Little Weiser River	1	145	0.02
	Weiser River EFk	3	150	0.02
	Weiser River WFk	3(1)	369	0.09
North Fork Payette (No *O. mykiss* seen in Fisher, Powelson, SFk Lake Fork, and SFk Kennally creeks. Most reaches had other trout species.)	NFk Payette River, 1998	26	--	0.20
	Brush Creek	2	25	0.005
	Fawn Creek SF	1	374	0.117
	Kennally Creek EFk	3(2)	12	0.002
	Lake Fork EFk	3(1)	134	0.05
	Rapid Creek	3(1)	81	0.02
	Twah Creek	1	51	0.02
	Twenty Mile Creek	3(1)	15	0.004

* Number among the index areas in the stream that had no *O. mykiss*. Many of these had other trout species, including exotic species. These reaches are not included in the averages.

Table 17. *Cont. O. mykiss* trout in Idaho tributaries above Hells Canyon dam.

Tributary	Streams	Number of index areas (*)	Average fish/km	Average density (fish/m^2)
South Fork Boise	Big Smokey Creek NF	3	281	0.08
	Big Smokey WF	3(2)	125	0.02
(No *O. mykiss* seen in EFk Big, Peak and Grouse creeks. Most reaches had other trout species)	Blackhorse Creek	3	61	0.04
	Boardman Creek	3	251	0.04
	Cayuse Creek	3(1)	394	0.15
	Dog Creek	3(1)	208	0.07
	Elk Creek	3	325	0.07
	Emma Creek	3(1)	37	0.01
	Green Creek	3(2)	140	0.05
	Grindstone Creek	3	178	0.11
	Kelly Creek EF	3(1)	176	0.07
	Little Smokey Creek	2	94	0.04
	Loggy Creek	2(1)	20	0.01
	Ross Fork Creek	3(1)	104	0.03
	Ross Fork Creek NF	3	185	0.06
	Ross Fork Creek SF	3	192	0.05
	Skeleton Creek	1	531	0.09
	Skunk Creek	3	119	0.04
	Snowslide Creek	3(2)	185	0.07
	Spring Creek	3	227	0.14
	Wagontown Creek	2(1)	280	0.11
	Whiskey Jack Creek	3	227	0.07
	Worswick Creek	3	123	0.09
Upper Owyhee	Corral Creek	3	810	0.36
	Hurry Back Creek	3 (1)	17	0.01
(No fish seen in Trout, Camas and Deep creeks)	Indian Creek	2(1)	2,324	1.00
	Juniper Creek	1	170	0.05
	Nip & Tuck Creek	3	450	0.23
	Owyhee River NF	4(1)	523	0.22
	Pete's Creek	2	403	0.14
	Rail Creek	2(1)	30	0.01
	Red Canyon WF	3	361	0.15
	S Boulder Creek	1	1,042	0.34
	Smith Creek	3	124	0.10
	Squaw Creek	3	154	0.07

makes the fish populations very vulnerable if the few densely occupied patches undergo some catastrophic event.

IDFG surveyed 42 sites for trout densities in the Weiser and North Fork Payette rivers in 1998, then continued the surveys with 152 new sites in the Weiser, North Fork Payette, South Fork Boise and Owyhee basins in 1999 (Meyer 1999, K. Meyer, IDFG). 100 of the index sites surveyed in 1999 (65%) in 48 streams (80% of those surveyed) had *O. mykiss* trout present. Although a few of the sites without *O. mykiss* were completely vacant, most notably in the Owyhee, most of them had other trout species present. Other native trout species in these tributaries were bull trout and mountain white fish. However, the most common other species present was eastern brook trout. This exotic species dominated many of the streams surveyed, especially in the Payette and Weiser rivers. Introduced cutthroat trout also were present at some of the survey sites.

Density estimates of *O. mykiss* trout in the basins surveyed by IDFG are presented in Table 17. The measurements presented are of trout larger than 10 cm, which are probably adults. Densities of smaller fish were also measured, but are not included in the table. Although the benchmarks provided by Dambacher and Jones (1995) range from low to high abundances depending on location, the information presented here is specifically for adult-sized trout while their benchmarks include juvenile fish. The average number of fish/km could expand to good population sizes depending on the amount of habitat available in the basins. The average linear densities were 99 fish/km in the North Fork Payette, 194 fish/km in the South Fork Boise, 213 fish/km in the Weiser and 534 fish/km in the Owyhee. The linear densities in the Weiser and Owyhee were comparable to those seen in the upper Yakima for similar-sized fish. It is likely there are several tens of thousands of adult trout in each of the four basins. IDFG biologists believe that the trout populations in most of these basins are at carrying capacity (K. Meyer, IDFG).

O. mykiss trout densities and abundance have also been measured in the Malheur Basin by Burns/Paiute tribal biologists and ODFW. The focus has been on the trout populations in the upper mainstem and North forks of the Malheur. ODFW determined that most of the trout in the upper basins are small, resident fish between 10 and 25 cm as adults, and spawn between 2 and 5 years of age. They are well distributed in the upper North Fork, but have a patchy distribution in the upper mainstem (Buckman et al. 1991, Pribyl and Hosford 1985).

Staff from the Burns/Paiute tribes have subsequently measured the densities and abundance of 1+ trout in two tributaries of the Middle Fork Malheur. They found densities of 0.095 fish/m^2 in Bosenberg Creek, which expanded to a population estimate of 615 fish in their index area. They found densities of 0.36 fish/m^2 in Crooked Creek, which expanded to a population estimate of 3,544 fish in their index area. These measurements correspond to moderate and high abundances according to Dambacher and Jones (1995). Brook trout were also observed at both index sites, and were particularly abundant in Bosenberg Creek (Namitz 2000).

The tribes have also measured the abundance of *O. mykiss* trout in a portion of the North Fork Malheur, using a rotary screw trap. In 1998, a total of 3,208 *O. mykiss* trout, primarily age 0, were captured. However, in that year the trap efficiency was not measured. In 1999, the tribes were able to expand their data to a population estimate of 2,597 age 1+ fish, plus approximately the same number of age 0 fish (Tiley 2000).

The area above Hells Canyon that is occupied by resident *O. mykiss* is very large and it is impossible to expand the information from the sites that have been monitored to any estimate of abundance for the individual tributaries, much less for the entire area. However the available information suggests that ten thousand-plus adult trout are likely present in each of the major subbasins. The trout are likely very abundant in local areas, but often with a patchy distribution and with complete reproductive isolation between most patches, especially in the more desert basins. The trout production has been lost from most mainstem reaches.

ESU-WIDE SUMMARY

Steelhead abundance in the Snake ESU is currently about 20,000 to 25,000 adults annually. The available data about trout densities and abundance suggests that similar numbers of adult trout are likely present in each of the major Snake subbasins, or roughly 50,000 to 100,000 trout in the area where they are currently sympatric with steelhead. Another 100,000 adult trout are likely present within historic steelhead range above Dworshak and Hells Canyon dams.

Upper Columbia ESU

The cold, high elevation, high latitude tributaries that form most of the Upper Columbia Steelhead ESU have been called among the least productive basins for salmonids in western North America (Mullen et al. 1992). Although the anadromous fish populations in the upper Columbia have been severely impacted by downstream factors, including dams and historic harvest, Mullen et al. (1992) argued that steelhead productivity in these areas has decreased very little since historic times. Like many Columbia Basin tributaries, the lower mainstem rivers in this ESU are impacted by irrigation development, but the headwaters still have good habitat for trout and steelhead.

Steelhead abundance is quite low in the Upper Columbia ESU; however, *O. mykiss* trout appear to be quite abundant, particularly if trout above Chief Joseph Dam are included in the measurement. Similar to the Snake ESU, the NMFS originally drew the boundary of the Upper Columbia ESU at Chief Joseph Dam. However, unlike the Snake ESU, the amount of area above Chief Joseph/Grand Coulee dams that was historically used by steelhead and is in the United States is quite limited. Most of the large tributaries above the dams and in the United State were naturally blocked to steelhead passage by waterfalls and have westslope cutthroat trout above them. The major steelhead production area above Grand Coulee Dam was in Canada where steelhead distribution
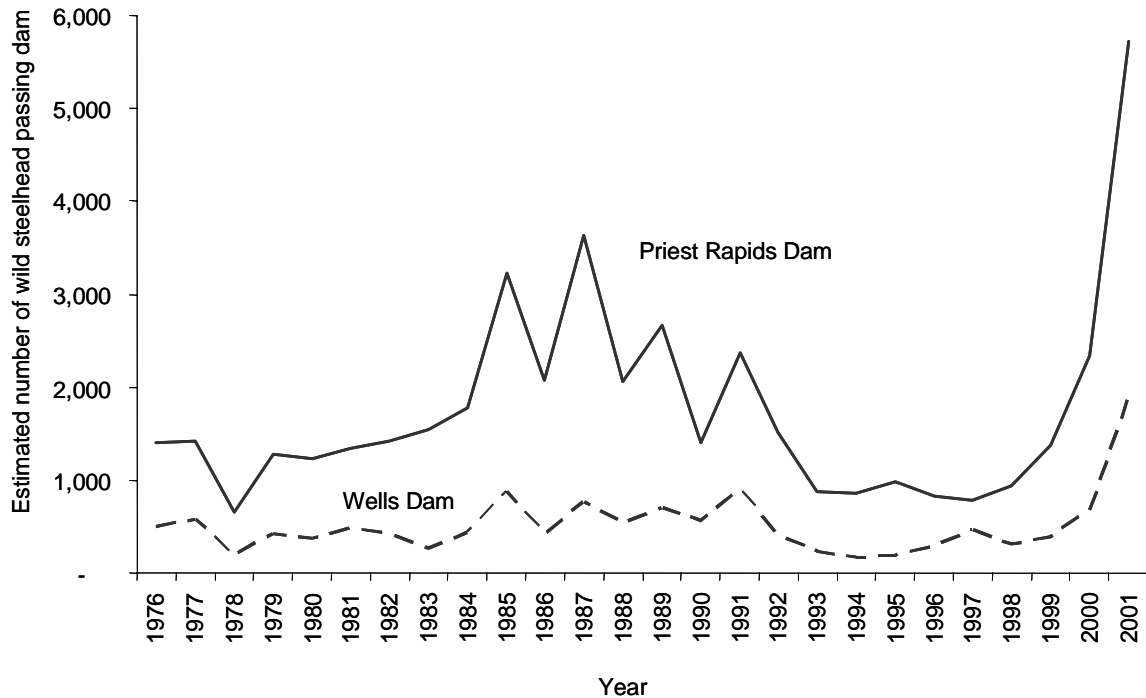
Figure 24. Estimated number of wild steelhead passing Priest Rapids and Wells dams on the mainstem Columbia River. Data provided by T. Cooney, NMFS.

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extended into the Columbia River headwater lakes. Possibly the historic biological boundary of the ESU was not dissimilar to the political one if Kettle Falls formed a natural boundary between historic upper Columbia ESUs. Resident *O. mykiss* trout are present throughout the historic steelhead range in both the U.S. and Canada. Information for this report is only provided up to the U.S./Canada border since the jurisdiction of ESA is the United States.

STEELHEAD ABUNDANCE

Current steelhead abundance in the Upper Columbia ESU is very low. This is the only Columbia Basin steelhead ESU with an "endangered" ESA listing. Total current wild steelhead abundance between Priest Rapids and Chief Joseph dams can be estimated from dam counts on the mainstem Columbia River. Priest Rapids Dam is near the lower boundary of the ESU and counts of wild fish at that location can be used to estimate the total number of steelhead entering the ESU. Wells Dam separates the upper ESU production areas (Methow and Okanogan) from the lower ESU production areas (Wenatchee and Entiat). Wild steelhead abundances at Priest Rapids and Wells dams, from 1976 to 2001 are shown in Figure 24 (data provided by T. Cooney, NMFS). An average of 2,226 wild steelhead have been counted at Priest Rapids Dam and an average of 745 wild steelhead have been counted at Wells Dam, both since 1997.

O. mykiss trout and steelhead production in the Wenatchee, Entiat and Methow was studied by the USFWS during the mid-1980s. Mullen et al. (1992) believed that there was a strong affinity between the trout and steelhead life histories in these basins, including the production of resident fish by steelhead when water temperatures and other factors triggered episodes of very slow growth. Trout apparently occur through most of the steelhead range, although they become more common further up the basins and they extend into headwater areas above steelhead production areas (A. Viola, WDFW). Trout with fluvial life histories are present in some areas and can reach sizes of 50cm (H. Bartlett, WDFW). Adfluvial trout are likely present in Lake Osoyoos in the Okanogan and Lake Wenatchee in the Wenatchee. However, small resident trout are also present, especially in colder, headwater areas.

The densities of *O. mykiss* were measured by the USFWS in 181 index areas in the Wenatchee, Entiat and Methow during the mid-1980s. No information is available for the Okanogan. The surveys used a combination of electroshocking and chemical sampling methods. The results, averaged over major streams, are shown in Table 18 (from Mullen et al. 1992, tables 6 and 8). The data are for combined trout and steelhead in all areas except for the upper Methow headwater areas, where only trout were observed. *O. mykiss* were observed in 94% of the index areas surveyed that were suspected to have combined steelhead and trout production, but the species was seen in only 38% of the Methow headwater areas that had only trout. Abundances of 1+ fish, based on the benchmarks from Dambacher and Jones, were low (<0.05) throughout the Entiat. Abundance was also low through most of the Methow, except for in the smaller streams with steelhead and in the headwaters where abundance was moderate (0.06-0.19). Abundance was also low through much of the Wenatchee, except in two creeks where abundance was high (>0.20). These density estimates have not been expanded to abundance estimates.

Adult trout, specifically identified as fish larger than 20cm, were seen in all basins, except the mainstem Entiat, although not at all index sites. In basins occupied by steelhead, trout larger than 20 cm were from 0.3% to 10.4% of the fish observed during the density surveys. This is a very high proportion compared to Mid-Columbia Basin tributaries, where only 1-2% of the fish observed during density sampling were generally thought to be adult trout. Also, these trout were identified as such based on relatively large size criteria. Smaller mature trout were likely also present, especially since the authors believed that growth rates in these basins were relatively low.

While the actual adult trout population abundance is not known for the four basins that currently contain steelhead in the Upper Columbia ESU, it would be reasonable to estimate that several tens of thousands of trout were present during the 1980s based on the large proportion of adult trout-sized fish seen during the density surveys. More recent density data is not available.

Table 18. Densities of *O. mykiss* (fish/m^2) in the Wenatchee, Entiat and Methow basins, measured in the mid-1980s. Data from Mullen et al. (1992) Tables 6 and 8. The authors considered the fish larger than 20 cm to be adult trout, although smaller adults may also have been present. Steelhead are included among the age 0 and 1+ fish. Only trout were observed in the Methow headwaters. Benchmarks from Dambacher and Jones (1995) are best applied to the Age 1+ column.

Tributary	Number of Index Areas		Stream	Density of *O. mykiss* (fish/m^2)			Percent described as "adult trout"
	Total	with *O. mykiss*		Age 0	Age 1+	> 20 cm	
Wenatchee Basin	78	71	Wenatchee River MS	0.053	0.027	0.002	2.8%
			Peshastin Cr	0.233	0.346	0.047	7.6%
			Ingalls Cr	0.198	0.798	0.021	2.1%
			Icicle Cr	0.316	0.024	0.001	0.3%
			Chiwaukum Cr	0.355	0.063	0.003	0.7%
			Nason Cr	0.090	0.012	0.002	1.6%
			Other tributaries	0.037	0.006	0.003	7.0%
Entiat Basin	14	14	Entiat River MS	0.100	0.009	0.000	0.0%
			Mad R	0.056	0.032	0.003	3.3%
Methow Basin (anadromous fish reaches)	47	45	Methow River MS	0.034	0.041	0.003	3.5%
			Twisp R	0.071	0.057	0.015	10.4%
			Chewack R	0.086	0.024	0.001	0.9%
			Early Winters Cr	0.052	0.038	0.006	5.7%
			Other tributaries	0.098	0.181	0.004	1.4%
Methow Basin (headwaters)	42	16	All tributaries	0.173			100%

The tributaries above Chief Joseph Dam are further blocked by numerous dams and contain a large diversity of exotic fish species. Warm water species, such as crappie and bass occupy many of the reservoir habitats, while exotic trouts, such as brown and brook trout, are common in many streams. Hatchery rainbow trout are present outside of their native range above natural barriers in tributaries that historically contained native westslope cutthroat. These exotic species, many of which are important game fish, have been the focus of much of the work on resident fish above Chief Joseph Dam (e.g. McLellan 2001).

However, native *O. mykiss* trout are also present in historic steelhead tributaries like the lower Spokane River, the Sanpoil River, and many of the other smaller streams that now enter Lake Roosevelt. The fish have been identified as belonging to inland *O. mykiss* by genetic analysis but they have not been compared to steelhead below Chief Joseph Dam (J. Whalen, WDFW). Many of the native trout have adfluvial life histories, migrating between rearing areas in Lake Roosevelt and spawning areas in the tributaries. Mullen et al. (1992) argued that native steelhead lineages in the upper Columbia were preserved in the trout that are still present above Chief Joseph Dam. There is evidence of further biodiversity among the resident trout in that different life histories and other characteristics are observed among the trout around Lake Roosevelt compared to those above the Kettle Falls area (J. Whalen, WDFW).

Neither densities nor abundances of the *O. mykiss* trout above Chief Joseph Dam have been measured. However, in the expert judgment of local biologists, they are common in these basins (C. Vail, WDFW).

Selected Risk Factors that Impact Native Trout

It is beyond the scope of this document to thoroughly review risk factors that influence the status of *O. mykiss* trout. Instead, this report briefly summarizes some of the risk factors that may be more specific to trout rather than to steelhead. Much greater detail is available about steelhead risk factors, some of which are also important to trout, in the status review by Busby et al. (1996), which is currently being updated by NMFS.

Influence of exotic trout species on native trout

Exotic species of trout, including eastern brook trout, European brown trout, and non-native cutthroat trout have been widely planted in the range of native *O. mykiss* in the Columbia Basin, and have established natural spawning populations in many areas. Exotic trout species are generally not emphasized as a primary source of impact to steelhead (see steelhead status reviews by Chilcote 1998, Busby et al. 1996, Kostow 1995). Most exotic trout populations in the Columbia Basin are established in upper basin areas, often above most anadromous fish distributions. However they are within trout ranges and they can have a significant impact on native *O. mykiss* trout in many basins. Exotic trout can ecologically displace native trout, especially where habitat is
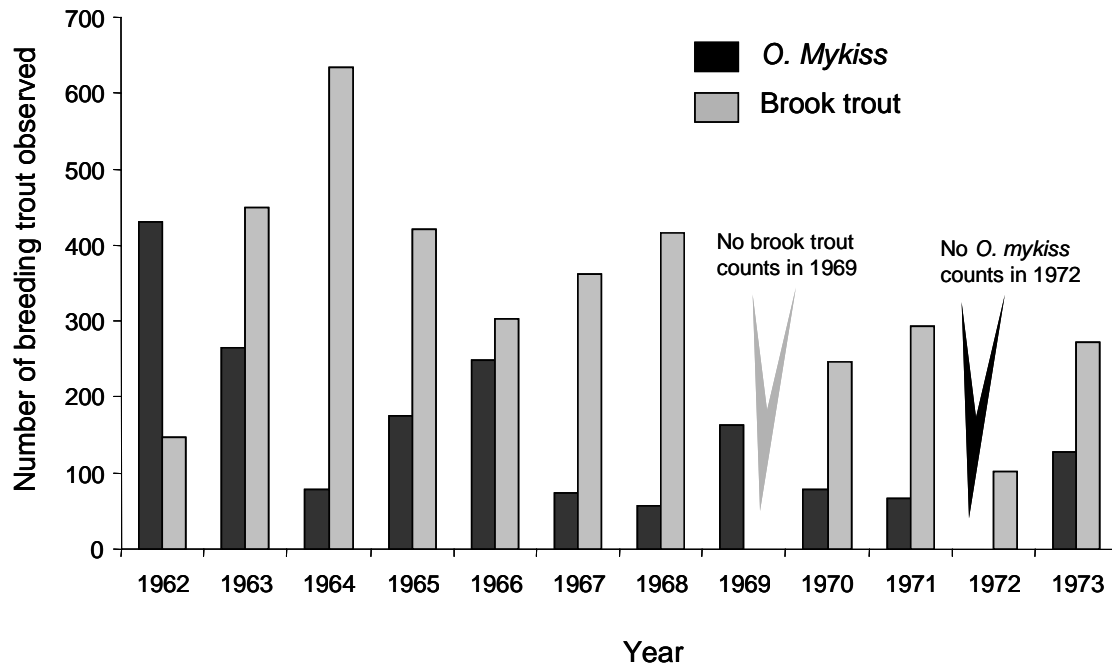
Figure 25. Estimated abundance of adult *O. mykiss* trout and brook trout in Big Springs Creek, Lemhi subbasin of the Salmon River. Data from Bjornn (1978) Table 30.

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also degraded. Where the exotic trout are cutthroat trout, such as in some eastern Washington and southwestern Idaho rivers, they may also hybridize with native *O. mykiss* trout.

Risks due to exotic trout appear to be most notable in the Snake and Upper Columbia ESUs. For example, in the density surveys conducted by IDFG, brook trout or exotic cutthroat dominated 30% to 40% of the reaches surveyed in the Weiser and North Fork Payette rivers where they made up more than 70% of the fish observed. Exotic trout were the only species in 9 index areas out of 27 surveyed in North Fork Payette, and in 6 index areas out of 22 surveyed in the Weiser (based on data provided by K. Meyer, IDFG). Brook trout were also noted by Bjornn (1978) in the Lemhi, where they out-numbered spawning *O. mykiss* trout in most years (Figure 25). Bjornn (1978) also noted that while the *O. mykiss* trout population declined following the reintroduction of steelhead, the brook trout population did not change. Ecological displacement by exotic species, especially by eastern brook trout, is also considered to be a high risk factor for the native trout above Grand Coulee Dam (C. Vail, WDFW). Exotic trout are also present in the upper Yakima Basin in the Mid-Columbia ESU. However, established populations of exotic trout are less common within current or historic steelhead range in

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most other Mid-Columbia ESU basins, or within historic steelhead range in the Lower Columbia or Willamette ESUs.

States continue to plant exotic trout species in some Columbia Basin waters, primarily in lakes and reservoirs. All of the currently planted areas are outside of current steelhead range, but some are within historic steelhead range and current *O. mykiss* trout range.

Risks due to conspecific hatchery trout

The risks to wild fish due to hatchery programs, and particularly due to stock transfers, were a major consideration in the NMFS original status review of steelhead (Busby et al. 1996). The risks also apply to trout. Hatchery trout have been planted throughout the Columbia Basin to provide sports fisheries, primarily using non-native stocks such as the "McCloud" stock from northern California. Hatchery stocking of trout has been both extensive and long-term (Taylor 1999).

The impact of hatchery trout stocking across the Columbia Basin appears to vary, but generally seems less than what might be expected based on the history of hatchery stocking. For example, genetics data demonstrates that native trouts have persisted with little evidence of introgression in the areas of extensive hatchery stocking in the upper Willamette (unpublished data from D. Teel, NMFS), in much of eastern Oregon (Currens 1997, Phelps et al. 1998), in many basins above Grand Coulee Dam (Knudsen et al. 2002, J. Whalen, WDFW) and in many basins in the Snake (Currens 1997, Leary 2001, Wishard et al. 1984). Trout have maintained very high variation between populations, as opposed to the homogenous pattern over the entire area that would result if most wild fish had been replaced by the "McCloud" hatchery fish. Oregon can also show several examples, such as the Chewaucan and Goose Lake basins (ODFW, unpublished data), where native *O. mykiss* trout in previously heavily stocked basins quickly reestablished resilient populations with complex life histories upon elimination of hatchery stocking and with some habitat restoration.

Several recent studies have used genetic admixture analysis to demonstrate that local lineages can persist in stocked areas, even while large numbers of hatchery fish are present (e.g. Marshall et al. 2000, Kostow et al. 2003). In some cases differences in life histories or special local adaptations may have contributed to the lack of interbreeding and to the failure of hatchery lineages to persist more than a few generations (Kostow et al. 2003, Leider et al. 1994). Utter (2001) noted that generally trout populations may more readily introgress with hatchery fish, as compared to anadromous populations, because trout life histories are less complex. However trout may also be adapted to unique features of their local environments that insulate them from introgression. For example, inland *O. mykiss* are often uniquely adapted to warm water temperatures and severe desert environments which seems to have protected them from introgression (Wishard et al. 1984). Many *O. mykiss* hatchery trout stocks are quite old, originating from the "McCloud" stock, a Sacramento River stock from northern California which was founded in the 1800s (Taylor 1999). Further, most trout hatchery stocks are propagated from captive broodstocks which have been captive for their entire life cycle

since the original founding and they carry a very high genetic load as evidenced by the high frequency of lethal traits such as albinism, melaninism, Siamese twinning and other deformities among them (ODFW unpublished data). Some trout stocks have also undergone intentional artificial selection for behavioral and morphological traits (ODFW unpublished data). This management history is further likely to decrease the fitness of the hatchery trout in natural stream environments (Lynch and O'Hely 2001). Evidence of introgression may be temporary if the fitness of the hatchery fish in the wild is poor (Utter 2001).

Evidence for apparent introgression between hatchery and wild trout also exists (Leary 2001, Knudsen et al. 2002, Williams et al. 1997, Campton and Johnson 1985, Phelps et al. 1998) although some of the markers used to detect evidence of hatchery introgression in these studies may in fact be natural variation in the populations (Utter 2001). For example Phelps et al. (1998) identified alleged hatchery alleles in several very remote, isolated trout populations in the upper Deschutes for which ODFW could reliably document no history of hatchery stocking.

There have been few studies of the fitness implications of hatchery/wild *O. mykiss* trout interbreeding other than the demonstrations of apparent introgression. However, one study on the Metolius River, Deschutes Basin, Mid-Columbia ESU, demonstrated that interbreeding between wild trout and "McCloud" hatchery stocks occurred (Williams et al. 1997) and that it increased the wild population's susceptibility to disease and therefore decreased its fitness (Currens et al. 1997).

Stocking of hatchery rainbow trout in Columbia Basin streams occupied by listed steelhead was sharply curtailed by all three Northwestern states after the steelhead were listed (T. Curet, IDFG; G. Mendel, WDFW; G. Nandor, ODFW). These curtailments were implemented to decrease the impact of trout fisheries on juvenile steelhead and other listed salmonids, and also to improve protection of native trouts. Most stocking now occurs in lakes, ponds and reservoirs outside of current steelhead range, although still within historic range in some cases.

Risks due to harvest

Although the magnitude of harvest pressure on trout is very low compared to a species like chinook that has sport, commercial and tribal fisheries, the risks of consumptive angling on local wild populations may be quite high. Some wild populations may be very susceptible to harvest impacts because they are highly accessible, while remote populations may experience little to no angling. The population structure of trout in some basins, where they are highly concentrated in relatively few locations, may also make them vulnerable if those few locations are also in areas of high recreation use. Some consumptive trout fisheries target larger fish, either by angling regulations (ODFW 2003) or by the preference of anglers, and these fisheries can remove the older fish, including the most fecund female fish in the populations. Several northwest biologists have commented that the occurrence of large trout, especially of large females, noticeably increased when angling regulations required catch-and-release of wild trout (D. Rawding,

WDFW; G. Mendel, WDFW). It is very difficult to generalize about harvest impacts across the whole Columbia Basin because the effects are local and variable. However, impacts to wild trout due to fisheries can be readily controlled as needed by catch-and-release and gear regulations, provided that monitoring is sufficient to detect when problems occur.

Risks due to habitat modifications

Habitat modifications have been extensive in the Columbia Basin and have been generally summarized in previous status reviews and subbasin plans. Busby et al. (1996) includes a discussion about habitat risk factors for steelhead. The Northwest Power Planning Council is currently conducting an extensive subbasin planning effort which focuses largely on habitat issues in individual subbasins through out the Columbia Basin, including in rivers outside of current steelhead range. This report cannot attempt to review this extensive issue as it pertains to *O. mykiss* trout. However, it is important to acknowledge that habitat modifications pose risks to trout, as well as to anadromous fish, and that there are some differences in how the risks are realized by each life history.

Trout, unlike steelhead, spend their entire life cycle in a basin and are completely dependant on local habitat conditions. They are relatively unaffected by the mainstem hydropower development on the Columbia and Snake rivers, although some local impacts to fluvial populations may have occurred. They are completely unaffected by marine conditions. They are also probably less impacted by urban development in the Columbia Basin, which is generally more extensive in lower basins, although trout may have historically used these areas. The following bullets very briefly summarize several Columbia Basin habitat modifications that specifically affect trout:

- Artificial passage barriers that impede trout passage are present in most Columbia Basin tributaries, ranging from impassible dams to small features like road culverts. Passage barriers fragment and isolate trout populations and impede migrations of fish with fluvial and adfluvial life histories, in some cases to the point that migratory life histories are lost.

- Unscreened or poorly screened irrigation diversions are present in many Columbia Basin tributaries, including in areas above anadromous fish distributions. The diversions can divert trout onto agricultural lands.

- Water withdrawals for irrigation or urban uses seasonally lower flows. Water temperatures can increase and some reaches can be completely dewatered, especially during drought conditions. While migratory fish may be able to escape these conditions, resident trout are very susceptible to them. The lower mainstems of many of the more arid inland basins, including the Umatilla, Yakima, lower John Day, Walla Walla, Malheur, Owyhee, lower Payette, lower Boise, and Bruneau, have become largely inhospitable to resident trout.

- Irrigation impacts are coupled with grazing impacts and channelization in some inland basins that have further decreased stream complexity, lowered water tables and removed riparian vegetation, thus increasing the affects of water withdrawals.

- Resource uses that affect small headwater tributaries particularly impact trout populations, which often have distributions that extend further upstream than anadromous fish. Such uses historically included road construction, logging and mining.

- Trout populations that assume fluvial or adfluvial life histories and migrate into some reservoirs and associated rivers may be impacted by the accumulation of contaminants. The contaminants include mercury, PCBs, dioxins, and other organic contaminants and come from industrial, mining and agricultural runoff, as well as from natural sources. The contaminants can accumulate in reservoirs which interrupt natural flows and sediment movement. Listings of contaminated reservoirs and associated rivers in the Columbia Basin are available from the Idaho Division of Health, Washington State Department of Health, and Oregon Department of Human Services. Some of the listed reservoirs notably occupied by *O. mykiss* trout that have been impacted to the extent that warnings about the consumption of trout have been issued include Lake Roosevelt, Owyhee Reservoir and associated creeks, and Brownlee Reservoir.

Conclusions

The original NMFS review of Columbia Basin *O. mykiss* ESUs evaluated status only using information about steelhead, and considered the risk of extinction only from the perspective of the risk to steelhead (Busby et al. 1996). This report evaluates status using information about both trout and steelhead and considers the risk of extinction to the entire ESU. By counting trout, along with steelhead, a number of status indicators change, including:

- *Current and historic distribution:* Steelhead have become extinct above impassible dams in every ESU in the Columbia Basin; however, trout are still present in all areas. Therefore, as a result of counting the trout, the ESUs are still extant throughout most of their historic distribution and the previously apparent broad-scale extinctions are no longer valid.

- *Productivity:* Trout and steelhead use different strategies to balance survival and reproduction. While the strategies are quite different, each has advantages and both are successful. The ESUs are more resilient as a result of having all of these alternative strategies available to them.

- *Population structure:* Trout are more prone to population fragmentation than steelhead. As lower mainstem habitats have become inhospitable to resident trout in many Columbia River subbasins, trout populations have withdrawn into headwater areas. These populations can become isolated and vulnerable to local extinctions and natural recolonization can be difficult. Migratory life histories, including both fluvial trout and steelhead, provide important connectivity between populations and may

significantly lower extinction risk, even if they do not comprise large numbers of individuals.

- *Diversity:* By counting trout as well as steelhead, the ESUs are significantly more diverse. This increase in diversity is evident in morphology, physiology, life history strategies, molecular genetic diversity and likely other factors that have not been measured. This increase in diversity offers the ESU a greater ability to adapt to a wider range of environments, habitat changes and disruptions.

- *Abundance:* By counting the trout that are sympatric with steelhead, the abundances increase by an order of magnitude in the Mid-Columbia, Snake and Upper Columbia ESUs, from a couple tens of thousands of steelhead to hundreds of thousands of *O. mykiss.* The abundance increases in the Lower Columbia and Willamette ESUs are more moderate because *O. mykiss* trout are less common in these coastal basins, which are dominated by coastal cutthroat trout. By also counting the trout that are within historic steelhead range above artificial barriers, abundance increases further in all ESUs, with the largest increase in the Snake ESU.

The status of trout populations has declined from historic conditions. Most notably, their distribution within basins has decreased due to local habitat impacts in lower subbasin mainstems. Trout populations are prone to fragmentation and isolation that make them vulnerable to local extinctions that are not readily mitigated by natural recolonization. They have probably suffered some loss of life history diversity, particularly of migratory life histories.

However, it is highly probable that the *O. mykiss* species in three of the five Columbia Basin ESUs (the Mid and Upper Columbia and Snake ESUs) would persist into the foreseeable future without steelhead. The species has already persisted as trout above impassible dams in these ESUs where steelhead have already been lost. Trout are also the majority of the species in terms of numbers where they are sympatric with steelhead in the inland ESUs. However, steelhead may still represent a significant part of the ESUs, and they are both distinctive and culturally valued.

Oncorhynchus mykiss is a substantially more complex species than most of the ones that previously have been reviewed under the Endangered Species Act. The same extraordinary level of polymorphism does not usually occur within species of mammals or birds. Anadromy is a complicated phenotype in *O. mykiss*. It appears to have some genetic basis, yet the species seems capable of considerable phenotypic plasticity. It is apparent that trout and steelhead within a basin are closely related in an evolutionary sense, and that they are capable of interbreeding and of producing offspring with the alternate life history. Yet trout and steelhead retain their own strong identities even while in full sympatry. While the ESUs are likely to persist, it is highly uncertain that steelhead in the ESUs would persist into the future without the protections provided by ESA.

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