Controls on the Distribution and Life History of Fish Populations in the Deschutes River: Geology, Hydrology, and Dams

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In the Deschutes River basin, geology and hydrology exert first-order controls on salmonid fish populations through two broad mechanisms. As studies of the distribution of chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout/steelhead (*O. mykiss*), and bull trout (*Salvelinus confluentus*) illustrate, the geologic history of the Deschutes River basin controls the hydrologic, sediment transport, and temperature regimes of the watershed, establishing the environmental niches and gradients to which fish species have adapted. Geological disturbances, such as floods, volcanism, and tectonism, have generated landforms that define habitat areas and constrain the interactions among fish species and populations. Specific events, such as an exceptionally large flood about 4400 years ago, may have created persistent habitat conditions partly responsible for the robust rainbow trout/steelhead fishery in the lower Deschutes River. Existing blockages to anadromy resulting from specific geologic events are clearly defined for sea-going salmonid species such as chinook salmon, steelhead, and sockeye salmon (*O. nerka*). Evidence for prehistoric blockages by ancient lava flows and landslides is more speculative but consistent with the present distribution of certain life history forms and genetic groups. Dams influence fish populations in manners similar to both types of broad geologic controls. Although changes to environmental gradients, such as temperature, substrate, and flow, often result downstream of impoundments, these habitat characteristics have apparently been little affected by the Pelton-Round Butte dam complex. The major effect of the dams on native fish populations has been to block fish passage, thus limiting anadromy and isolating fish populations above and below the dam complex.

INTRODUCTION

Fish have long been a significant focus of interest and research in the Deschutes River watershed. As early as 1824, explorers with the Hudson's Bay Company reported the presence of Native American salmon weirs on the Crooked River and, in 1855, described abundant salmon in the Metolius River [*Nehlsen*, 1995]. By the late 1800's, the mouth of the Deschutes River was the site of intensive commercial fisheries [*Nehlsen*, 1995], and today, significant recreational and Native American fisheries exist throughout the watershed. Indeed, much of the research reported in this volume was prompted by concerns regarding the effects of the Pelton-Round Butte dam complex on downstream fish

A Peculiar River
Water Science and Application 7

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habitat. In addition, proposals to reinstate fish passage around these facilities have propelled fishery scientists and managers into renewed efforts to understand life histories and interactions among the various fish species in the Deschutes River basin [*Lichatowich,* 1998].

The aim of this paper is to relate aspects of the historic and present distribution of fishes in the Deschutes River basin to geologic and physiographic conditions in the watershed, thus linking a key aspect of the basin's ecology to the geologic and hydrologic understanding described in the other papers in this volume. Furthermore, this perspective is relevant to current issues surrounding human disturbance of fishes in the basin, such as dam construction, which have parallels with geologic events and processes. We first propose a framework for understanding relations between geologic conditions and fish distribution, then support that framework with examples from our research and that of others on fish distribution, community structure, and population dynamics in the basin. We conclude by discussing the similarities and differences between geologic controls on fish distribution and human influences on fishes in the basin, such as dam construction and management, and how this understanding might be pertinent for future management of fish resources in the Deschutes River basin. Our examples derive from studies of fish of the family Salmonidae, by far the best studied species in the basin due to their regional economic and cultural importance.

SALMONIDS OF THE DESCHUTES RIVER BASIN

Available literature, interviews with biologists, and a survey of cataloged specimens show that at least twenty-six species of fish inhabit the Deschutes River basin (Table 1), seven of which are of the family Salmonidae, collectively referred to as "salmonids". These include native salmon and trout: chinook salmon (*Oncorhynchus tshawytscha*), sockeye salmon/kokanee (*O. nerka*), rainbow trout/steelhead (*O. mykiss*), and bull trout (*Salvelinus confluentus*). Salmonid species introduced to the basin from other regions include: brown trout (*Salmo trutta*), Atlantic salmon (*S. salar*), and brook trout (*Salvelinus fontinalis*). Many species of salmonids in the Deschutes River can be further subdivided into distinct stocks or life-history forms based on differences in genetic, morphologic, and ecological characteristics.

Salmonids have a variety of life history characteristics reflecting diverse adaptations to landscape conditions. One characteristic that varies among and within fish species in the Deschutes River basin is migratory behavior. Life history forms include anadromous, fluvial, adfluvial, and resident fish. Anadromous species include chinook salmon, steelhead (a form of rainbow trout), and sockeye salmon. Anadromous species spawn in freshwater, and the juveniles migrate to the ocean before returning to freshwater as mature adults (Figure 1). Fluvial migration, typical of some rainbow trout and bull trout in the Deschutes River, is between larger rivers (such as the mainstem) and smaller tributaries. Migration to lakes for rearing is referred to as adfluvial migration and is observed in bull trout, kokanee (a freshwater form of sockeye salmon), and rainbow trout. Residency is observed in rainbow trout and describes fish that do not migrate between habitat types. Although resident fish do not migrate between habitat types, they often make long-distance movements within the same habitat [*Gowan et al.,* 1994].

All salmonids are substrate spawners. As a result, salmonid spawning and survival is directly related to substrate characteristics and the timing and frequency of bed-mobilizing flows and deposition. The female constructs a nest (or redd) in the gravel substrate by turning on her side and directing flow downward by arching her body. This action dislodges particles into the current and excavates a depression containing larger rocks. She then releases eggs into this depression as the male simultaneously releases sperm. The female then moves slightly upstream and digs another depression, displacing substrate material downstream that covers the previous depression and eggs. Each redd can contain several such egg pockets; the ultimate shape of the redd and its location serve to maximize downwelling and current through the egg pocket [*Chapman,* 1988; *Bjornn and Reiser,* 1991], which serves to bring oxygen to the eggs and remove metabolic wastes (Figure 2). Reduction in permeability following construction of the redd, due to the deposition of fine sediments, leads to decreased downwelling and can lead to lower survival of incubating eggs and embryos [*Chapman,* 1988].

Three species of salmonids, chinook, rainbow trout, and bull trout, have been particularly well studied in the Deschutes River basin because of their cultural significance, historic and modern importance as a food and recreational resource, and regional concerns regarding species preservation.

Chinook Salmon (Oncorhynchus tshawytscha)

Chinook salmon in the Deschutes River basin were and continue to be a mainstay of the cultural identity of Native Americans residing near the Deschutes River, especially in the northern part of the basin. In addition, management of wild chinook salmon in the Deschutes River basin is an important component of regional strategies to maintain viable populations in the Columbia River basin [*Lichatowich,* 1998]. Two separate populations of chinook

Table 1. Fish species present in the Deschutes River Basin.

Common Name	Scientific Name	Origin
Pacific lamprey	*Entosphenus tridentatus*	Native
Steehead/Rainbow trout	*Oncorhynchus mykiss*	Native
Chinook salmon	*Oncorhynchus tshawytscha*	Native
Sockeye salmon/ Kokanee	*Oncorhynchus nerka*	Native
Bull trout	*Salvelinus confluentus*	Native
Mountain whitefish	*Prosopium williamsoni*	Native
Shorthead sculpin	*Cottus confusus*	Native
Torrent sculpin	*Cottus rhotheus*	Native
Slimy sculpin	*Cottus cognatus*	Native
Mottled sculpin	*Cottus bairdi*	Native
Prickly sculpin	*Cottus asper*	Native
Longnose dace	*Rhinichthys cataractae*	Native
Speckled dace	*Rhinichthys osculus*	Native
Chiselmouth	*Acrocheilus alutaceus*	Native
Largescale sucker	*Catostomus macrocheilus*	Native
Bridgelip sucker	*Catostomus columbianus*	Native
Northern pikeminnow	*Ptychocheilus oregonensis*	Native
Redside shiner	*Richardsonius balteatus*	Native
Threespine stickleback	*Gasterosteus aculeatus*	Unknown
Brook trout	*Salvelinus fontinalis*	Introduced
Brown trout	*Salmo trutta*	Introduced
Atlantic salmon	*Salmo salar*	Introduced
Largemouth bass	*Micropterus salmoides*	Introduced
Smallmouth bass	*Micropterus dolomieu*	Introduced
Yellow perch	*Perca flavescens*	Introduced
Brown bullhead	*Ameiurus nebulosis*	Introduced

salmon have been defined in the Deschutes River basin on the basis of timing of adult migration from the ocean, age at out-migration of juveniles, and location of spawning [*Jonasson and Lindsay,* 1988; *Lindsay et al.,* 1989]. Fall chinook salmon (also known as "ocean-type" chinook salmon) typically spawn in mainstem reaches and the resulting progeny migrate to the ocean within a few months after emergence from the gravel [*Jonasson and Lindsay*, 1988; *Healey*, 1991]. Spring chinook salmon (or "stream-type" chinook salmon) spawn in headwater tributaries, and the juveniles remain in these streams for over a year before migrating to the ocean [*Lindsay et al.*, 1989; *Healey*, 1991]. Returning to their natal streams after about two or three years in the ocean, adult spring chinook salmon enter freshwater during the late spring and hold in cold pool habitats until the fall when they spawn. Fall chinook return to freshwater during the late summer or fall and spawn in October or November.

Spring chinook salmon historically spawned in the west side tributaries to the Deschutes River including the Warm Springs River, Shitike Creek, and the Metolius River (Figure 3). In the Deschutes River, Big Falls at River Mile (RM)[1] 132.2 was the upstream extent of spring chinook salmon [*Nehlsen*, 1995] (Figure 4). Anecdotal reports suggest that spring chinook salmon might have spawned in the Crooked River [*Nehlsen*, 1995]. At maturity, spring chinook are typically 60 to 90 cm long and attain weights of approximately 7 kg.

Fall chinook salmon are the largest salmonids in the Deschutes River basin, attaining lengths of 70 to 110 cm and

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[1] Units given are metric except for locations, which are given as river miles (RM), or miles upstream from the river mouth as marked on USGS topographic maps. These values are close to, but not necessarily the same as, actual distances along the present channel. Fractional river miles given herein are based on interpolations between these published river miles.

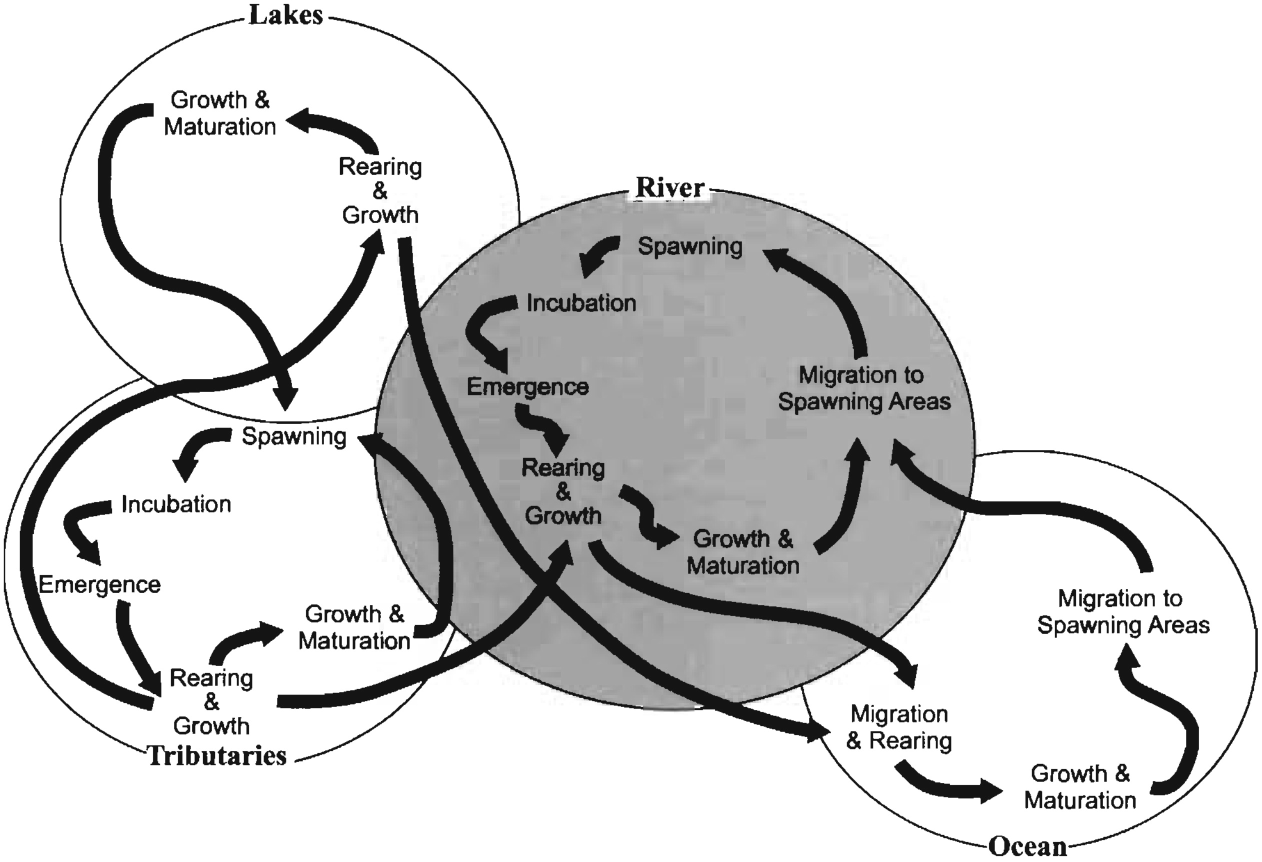

Figure 1. Conceptual model of life history events and migration across habitats by salmonids in the Deschutes River basin.

weights up to 14 kg. Fall chinook were historically found only downstream of Sherars Falls at RM 44 (Figure 5). A fish ladder was constructed at Sherars Falls in the 1920s and improved in the 1940s that allowed passage of fall chinook salmon at the relatively lower autumn flows [*Jonasson and Lindsay*, 1988; *Nehlsen*, 1995], which expanded the distribution of fall chinook salmon throughout the lower mainstem river to near the confluence of the Crooked, Deschutes, and Metolius Rivers [*Jonasson and Lindsay*, 1988; *Nehlsen*, 1995]. The Reregulating Dam at RM 100.1 is now the upstream boundary for both types of chinook salmon.

Rainbow Trout / Steelhead (Oncorhynchus mykiss)

Rainbow trout in the Deschutes River have two distinct life history forms. Anadromous rainbow trout, referred to as steelhead, spawn in the lower Deschutes River, and migrate as juveniles to the ocean, returning to natal streams after one to two years. At maturity, they are typically 60 to 70 cm long and attain weights of approximately 7 kg. Steelhead historically occupied the Deschutes River mainstem and tributaries upstream to Big Falls, and much of the Crooked River and its principal tributaries (Figure 6). Presently, upstream passage is blocked by the Pelton-Round Butte dam complex and steelhead are only found in the mainstem and tributaries downstream of the Reregulating Dam. Resident and fluvial rainbow trout spend their life in fresh water and are present throughout the Deschutes River basin in forty-six separate wild populations divided into three "gene conservation groups" [*ODFW*, 1995]. Resident rainbow trout are typically smaller than steelhead, attaining lengths of 20 to 40 cm and weights typically between 0.7 and 3 kg. Presently, resident and fluvial rainbow trout are sympatric with steelhead throughout the lower river, meaning that they spawn and rear in close proximity. Populations of resident rainbow trout are particularly strong in the lower mainstem Deschutes River, below the Pelton-Round Butte dam complex, where they are the basis of a robust recreational fishery [*Lichatowich,* 1998]

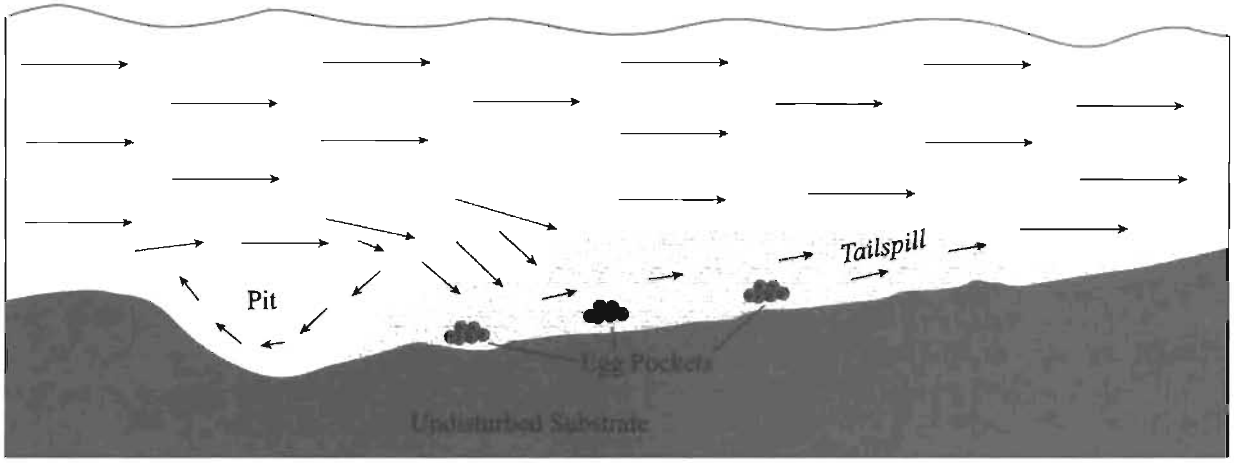

Figure 2. Longitudinal section of an idealized salmonid redd. Arrows indicate direction of water flow (after figures in *Chapman* [1988] and *Bjornn and Reiser* [1991]).

Bull Trout (Salvelinus confluentus)

Bull trout spend their lives in fresh water, migrating between small cold-water streams and larger rivers. At maturity, they are typically 40 to 70 cm long and attain weights of up to 14 kg. Bull trout were historically distributed along much of the mainstem Deschutes River, Metolius River, and lower Crooked River as well as in several high elevation tributaries to the lower Deschutes River in the Cascade Range (Figure 7). Their current distribution is restricted to the western portion of the basin. Formerly considered a "trash" fish and subject to bounties in the early part of the 20th century, the marked contraction of their distribution throughout their historic range has triggered significant concern regarding bull trout viability and has resulted in an "threatened" designation under the Endangered Species Act for much of the species' range in the intermountain west and Pacific Northwest.

GEOLOGIC CONTROLS ON FISH DISTRIBUTION AND POPULATION DYNAMICS

Geologic processes and conditions affect fish distribution and population dynamics in two distinct manners. Geologic events, the sequence of which constitutes the geologic history of a basin, affect fish by producing connections or barriers between watercourses and landscapes, shaping channel- and valley-bottom morphology, and by directly disturbing fish populations. In the Pacific Northwest, tectonic activity, volcanism, glaciation, and floods have likely played an important role in structuring fish communities throughout the Cenozoic Era [*McPhail and Lindsey*, 1986; *Reeves et al.*, 1998]. In addition to discrete geologic events, the present-day physical environment or "regime" of a watershed, which is ultimately a product of geologic history and climate, also controls the distribution, composition, and structure of fish communities and populations by forming environmental gradients of habitat conditions [*Li et al.*, 1987; *Mathews*, 1998]. Aspects of the physical regime important to fish include conditions of water flow (discharge, velocity, and daily, seasonal, annual, and longer-time-scale discharge fluctuations), water temperature, water chemistry, and the size distribution of the channel-bottom sediment and frequency of sediment transport. Understanding the present-day structure of fish communities, therefore, requires an appreciation of both the geologic history of a basin and the current conditions and geologic processes affecting the aquatic environment.

In the Deschutes River basin, as elsewhere, there are clear relations between fish and current habitat conditions such as flow, temperature and substrate composition. These relations can be readily analyzed in controlled field and laboratory experiments, and involve timescales conducive to human observation. Less apparent are relations between geologic history and modern fish distribution and behavior (aside from the role of modern and historic channel blockages), which are site specific, involve long timescales, and commonly depend on incomplete knowledge of regional and local geologic history. However, increased understanding of the role of geologic history in controlling fish distribution has emerged in recent years, as a result of the increased ability to track fish groups with genetic methods as well as from increased communication between geoscientists and biologists. The remainder of this paper describes

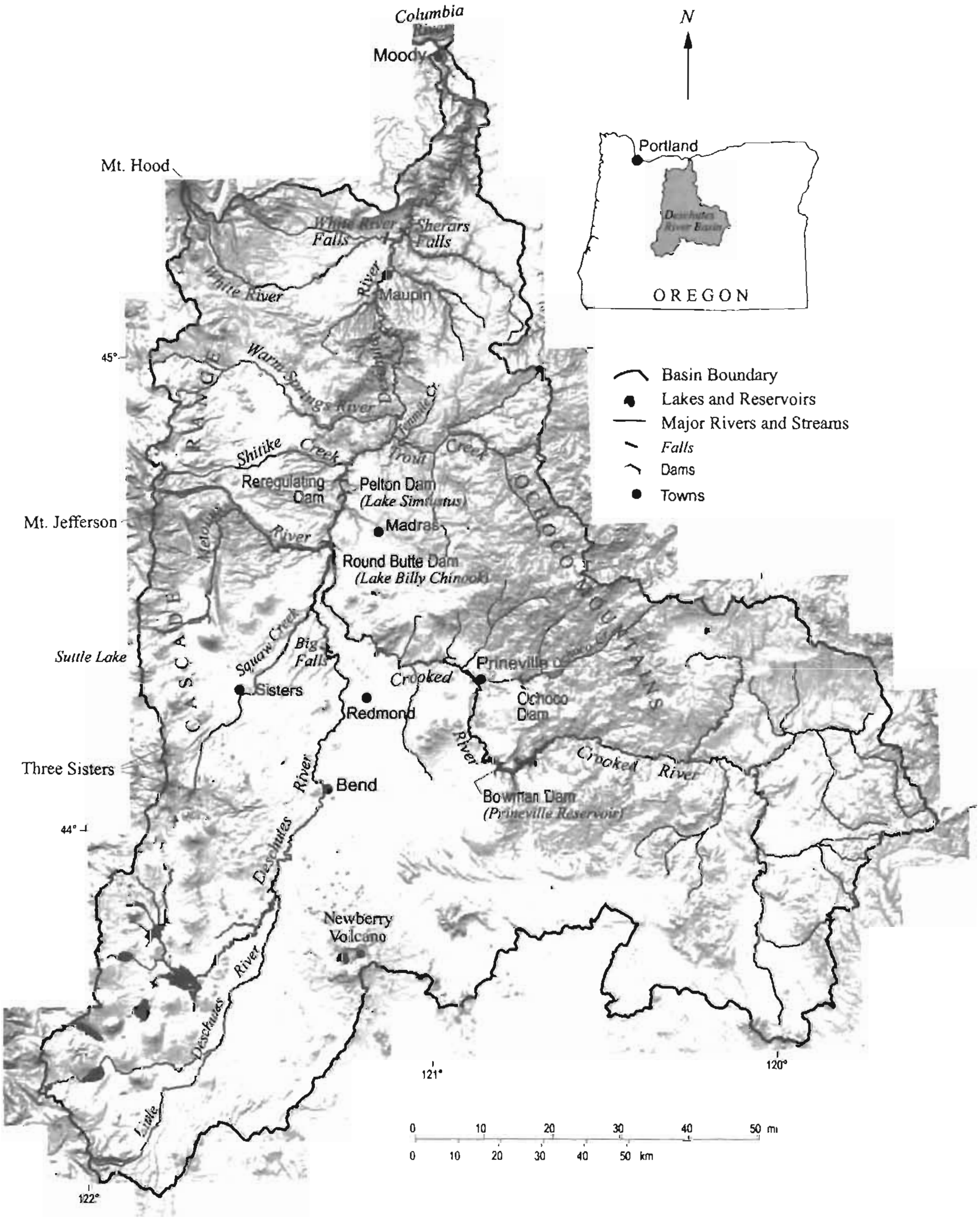

Figure 3. Map of Deschutes River basin, Oregon, with locations mentioned in the text.

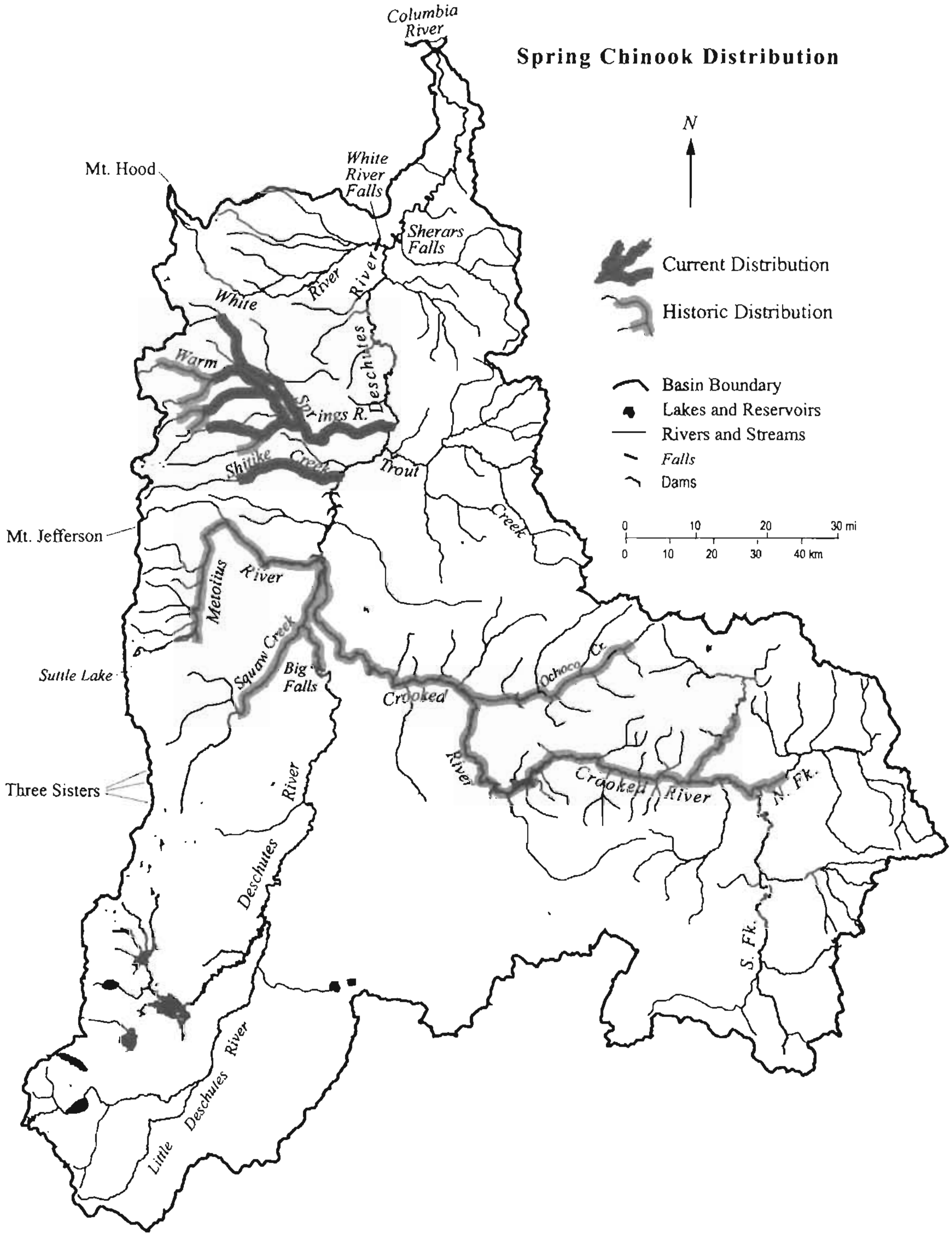

Figure 4. Present and historic distribution of spring chinook salmon (*Oncorhynchus tshawytscha*) in the Deschutes River basin, Oregon.

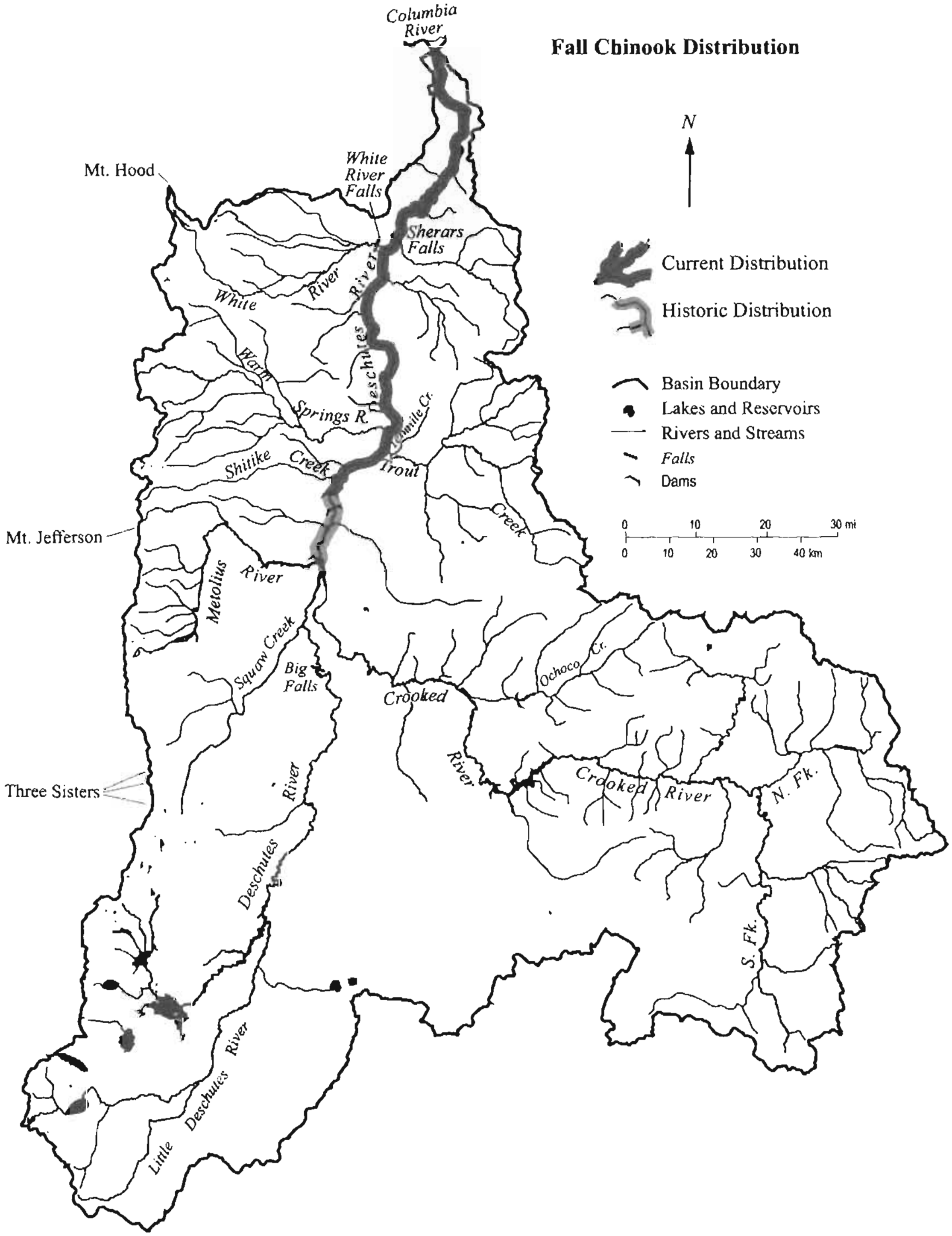

Figure 5. Present and historic distribution of fall chinook salmon (*Oncorhynchus tshawytscha*) in the Deschutes River basin, Oregon.

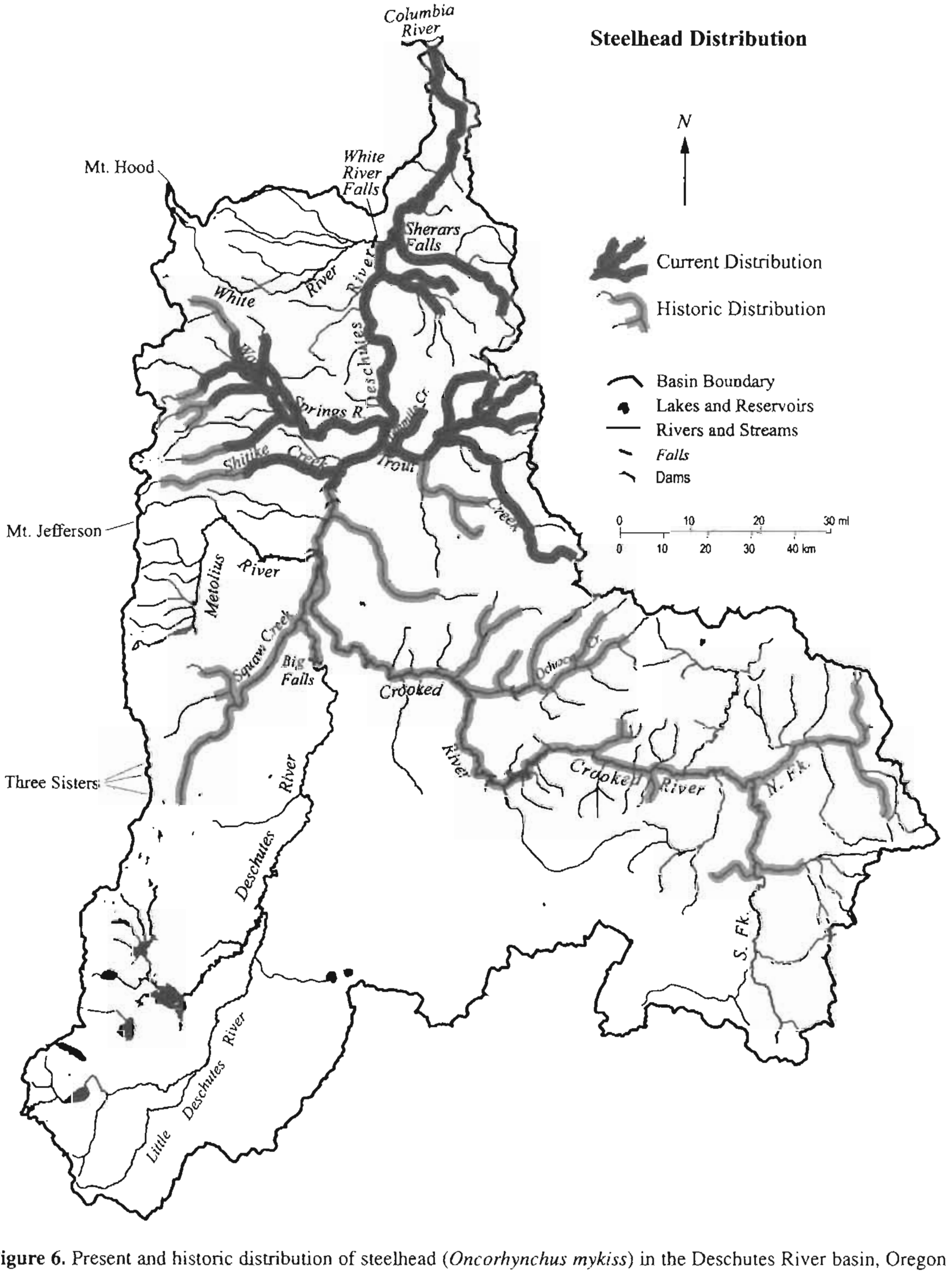

Figure 6. Present and historic distribution of steelhead (*Oncorhynchus mykiss*) in the Deschutes River basin, Oregon.

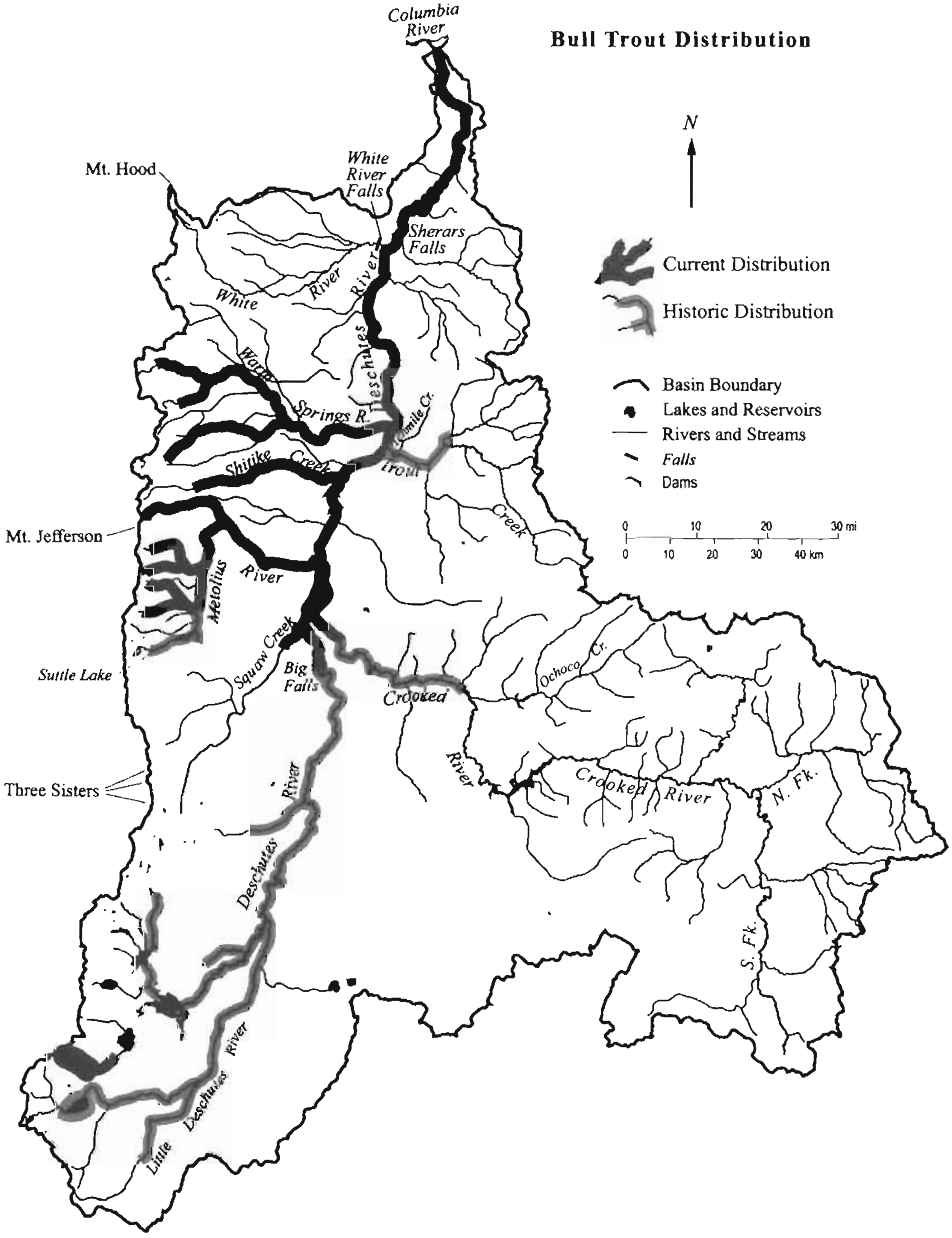

Figure 7. Present and historic distribution of bull trout (*Salvelinus confluentus*) in the Deschutes River basin, Oregon.

examples of geologic influences on Deschutes River basin fish distribution and population dynamics, illustrated with cases of both "regime" and "history" controls. For the reasons noted above, the geologic history aspects are more speculative than are the factors relating to modern conditions. Nevertheless, such speculation is relevant because it increasingly pertains to issues confronting modern fish management, in which modern human perturbations to the river system, such as dam construction and subsequent reconnecting of habitats, mimic geologic events as well as alter environmental gradients.

Watershed Regime Controls

Climate, physiography, and geology exert "regime-type" controls on fish distribution in the Deschutes River basin through their effects on environmental variables such as water temperature, flow conditions, and sediment transport and substrate conditions. Water temperature is a critical factor in structuring fish communities, and changes in temperature regime can cause changes in fish community structure and distribution [*Li et al.*, 1987]. For example, *Reeves et al.* [1987] found that behavioral interactions between competing juvenile steelhead and redside shiner (*Richardsonius balteatus*) were mediated by temperature. When water temperature was >15°C, the production of steelhead decreased by up to 54% when redside shiner were present. *Ebersole et al.* [2001] found that warm stream temperatures effectively limited the distribution and abundance of salmonids in streams due to mortality associated with higher water temperatures.

Bull trout distribution. The effects of water temperature are most evident in the distribution of bull trout. The present day (and presumably historic) distribution of spawning and rearing locations used by bull trout is highly related to water temperature. In the Metolius River, bull trout spawning and initial rearing of juveniles is limited to tributaries with water temperatures below 5°C [*Ratliff*, 1992]. This relationship is driven by physiological requirements of bull trout. Intergravel survival of the eggs and alevins is temperature dependent with egg to fry survival of 0-20% at 8-10°C, 60-90% at 6°C, and 80-95% at 2-4°C [*McPhail and Murray*, 1979]. An additional but related aspect is flow stability. For bull trout, which spawn during summer and early fall, the eggs and resulting embryos incubate and remain in the redd for approximately 160 to 190 days before they emerge from the gravel as free-swimming fry [*Pratt*, 1992], thus requiring that the redds are neither scoured nor dewatered for nearly half a year. In contrast, rainbow trout that spawn during late spring and early summer in water temperatures of 12°C may emerge in less than 60 days [*Zimmerman*, 2000]. The narrow range of temperatures selected by spawning adults and the temperature-dependent survival of emerging juveniles form the primary constraints on bull trout distribution within the Deschutes River basin. Therefore, the coldwater habitats preferred by bull trout correspond to spring-fed streams and rivers, most of which emerge from the High Cascade geologic province of young volcanic rocks.

Similarly, spring chinook require cool pools for refuges during the holding period between entering freshwater in the spring and spawning in the fall [*Torgersen et al.*, 1999]. Consequently, historic spring chinook habitat in the Deschutes River basin was primarily in the tributaries draining the High Cascade geologic province and in the spring-fed Deschutes River. It is unlikely that the anecdotal observations of spring chinook in the warmer Crooked River reflect large populations of spring chinook salmon, although it cannot be completely ruled out. Spring chinook in the Yakima River, Washington and John Day River, Oregon behaviorally thermoregulate to maintain internal temperatures by seeking patches of cooler water [*Berman and Quinn*, 1991; *Torgersen et al.*, 1999], and such behavior might have allowed spring chinook salmon to exist in the Crooked River.

Local species composition in relation to environmental gradients. In addition to controlling distributions of individual species, environmental gradients controlled by overall geologic, hydrologic, and climatologic conditions likely influence fish community structure. Although a detailed analysis of fish community structure has not been conducted in the Deschutes Basin, our surveys provide an anecdotal demonstration of large variations in fish assemblage composition among five locations in the Deschutes River basin downstream of the Pelton-Round Butte dam complex. At each of these sites, all fish present were identified to species and counted by electrofishing. The area sampled at each site ranged from 239 m^2 to 346 m^2. The mainstem Deschutes River sites included side-channels associated with islands on the east bank of the river at RM 9.9, RM 82.6, and RM 98.8 (Figure 8). Mainstem sites were sampled in August 1997 with the exception of the site at RM 82.6, which was sampled in July 1996. The study site on Shitike Creek was located approximately 3.5 km upstream from the Deschutes River (Figure 8), and was sampled by dive counting rather than electrofishing in August 1997. Tenmile Creek was sampled by electrofishing in July 1998, and the sampled area included approximately 600 m of stream beginning approximately 200 m upstream of the confluence with Trout Creek (Figure 8).

These surveys identified twelve species of fish during tabulation of 1,059 individuals. Rainbow trout (resident and

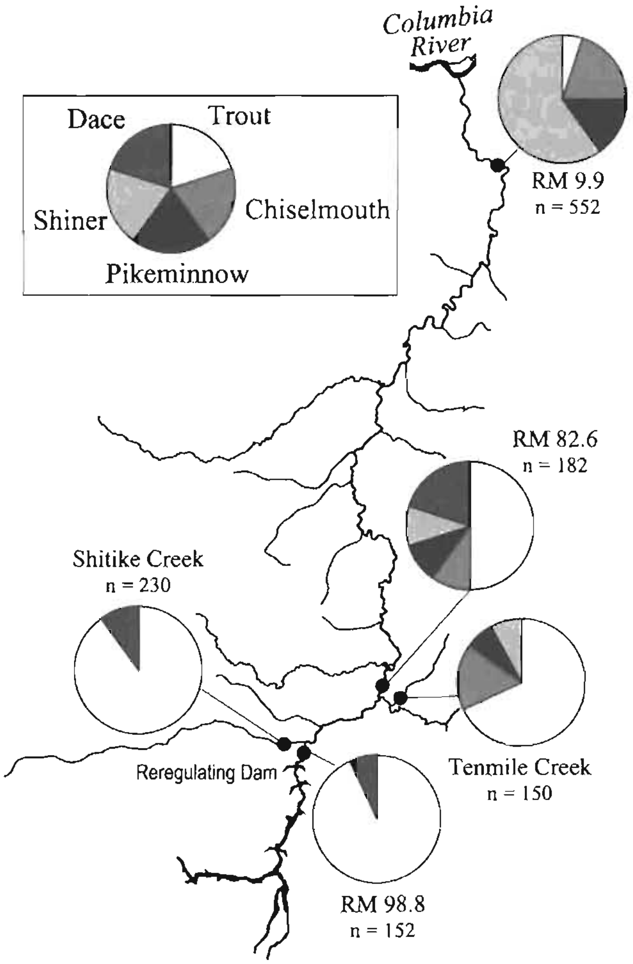

Figure 8. Percent composition of the dominant fish species at five locations in the lower Deschutes River, Oregon.

steelhead combined), speckled dace (*Rhinichthys osculus*), longnose dace (*R. cataractae*), redside shiner, northern pikeminnow (*Ptychocheilus oregonensis*), and chiselmouth (*Acrocheilus alutaceus*) were the dominant species, but bull trout, chinook salmon, mountain whitefish (*Prosopium williamsoni*), threespine stickleback (*Gasterosteus aculeatus*), and sculpins (*Cottus* spp.) were also encountered. Bull trout, chinook salmon, whitefish, and sculpins were excluded from this analysis because, in most cases, only one or two individuals were encountered. Sculpins were present in much greater numbers, but because they are benthic and live within the gravel substrate, they are difficult to count accurately.

Rigorous statistical comparisons among the survey sites are inappropriate because the sampling was conducted by different methods and at different times, but the results show distinct differences in fish assemblages among locations within the lower Deschutes River (Figure 8). The various proportions of fish species are similar to the longitudinal distribution of fish species presented by *Li et al.* [1987], which they attributed to longitudinal variation in temperature. Other studies have demonstrated temperature dependent variation in fish community structure or distribution [*Reeves et al.*, 1987; *Ebersole et al.*, 2001]. For example, *Rosenfeld et al.* [2001] found that chiselmouth in British Columbia rivers were typically absent from sites with maximum temperatures below 20°C. This is consistent with the variation in abundance of chiselmouth in the lower Deschutes River sites (Figure 8). Chiselmouth are more abundant at Tenmile Creek and the island side-channel sites at RM 82.6 and RM 9.9, which are characterized by warmer water temperatures, than they are at the cooler sites in Shitike Creek and the island side-channel site at RM 98.8.

Geologic Events and Fish Distribution

Individual geologic events and geologic processes also control patterns of fish distribution and community structure by establishing the physical template for modern habitats and environmental gradients, including features such as migration barriers, channel and valley-bottom morphology and substrate, and channel network geometry. Geologic events have also caused substantial changes to watershed and habitat conditions (such as ancient blockages and interbasin connections) that have a continuing legacy for fish distribution and population dynamics. The understanding of the geologic history for the Deschutes River basin, summarized in the other contributions to this volume, allows us to hypothesize about how the history of geologic processes and events contributed to the control of certain aspects of fish distribution within the basin.

Lower Deschutes River valley-bottom morphology. Within the lower Deschutes River, downstream of the Pelton-Round Butte dam complex, side channels associated with islands provide important spawning and rearing habitats for salmonids and other species. For example, in 1995, 68% of all steelhead spawning between the Reregulating Dam and the mouth of Trout Creek occurred in side channels between islands and channel margins, despite the fact that such side channels comprise less than 10% of the channel length within that reach [*Zimmerman*, 2000]. The remaining steelhead spawning occurred in areas associated with edge habitats (along river margins) not associated with islands.

Systematic snorkeling counts on the lower Deschutes River also indicate the importance of edge habitats as rearing sites for juvenile fishes. We identified and counted fish distribution within 3-m lanes in 100 line transects snorkeled from the bank to middle of the river. Juvenile salmonids were observed from the bank to a maximum of 30 m from the bank, but their distribution was highly influenced by stream depth and velocity. In some transects, juvenile salmonids were not observed beyond 1 m from the bank, especially where water depth exceed one meter.

The islands and channel margins in the lower Deschutes River reflect specific geologic events that may make the Deschutes River channel environment unique among Pacific Northwest rivers. Downstream of the Pelton-Round Butte dam complex, the Deschutes River flows in a channel averaging about 71 m wide within a valley bottom averaging about 165 m wide [*Curran and O'Connor*, this volume]. This channel has been exceptionally stable compared to typical alluvial channels: nowhere has the channel migrated more than a few tens of meters since the first historic surveys of the late 1800s and early 1900s [*Curran and O'Connor*, this volume]. Of the 153 existing and historic (since 1911) islands within the lower Deschutes River, 75% percent are alluvial and the remainder are formed of bedrock, reflecting long term incision of the Deschutes River into basalt flows of the Columbia River Basalt Group [*Curran and O'Connor*, this volume]. Historically, the bedrock islands have changed little, but the alluvial islands have been more dynamic, with a very general pattern of growth between large floods and erosion during the largest historic floods, such as those in 1964 and 1996. Nevertheless, most alluvial islands (and associated side channels) have maintained very similar areas and locations for the past century [*Curran and O'Connor*, this volume]. All islands between the Reregulating Dam and Trout Creek, the reach sampled in the spawning surveys, are alluvial.

The stability of the side channels and channel margins, key fish habitat features, may be attributed to a large flood that affected the lower Deschutes River about 4400 years ago. Termed the "Outhouse flood" [*Curran and O'Connor*, this volume; *Beebee and O'Connor*, this volume], this event probably exceeded the magnitude of the largest historic floods by a factor of at least two, and left boulder bars that now form many of the channel margins and islands of the lower Deschutes River [*Curran and O'Connor*, this volume]. Large landslides are another process contributing to the stability of the Deschutes River channel, as debris from the landslides themselves or coarse flood deposits from the breaching of landslide dams forms the channel margins between RM 60 and 85. We suspect that the stability of the channel and islands of the lower Deschutes River, which is attributable to specific geologic events, is an important factor (along with the stable flow regime) in maintaining the relatively strong populations of resident rainbow trout in the lower mainstem. This channel and flow stability is also likely a factor in the survival of a fall chinook population, which spawns in the lower Deschutes River and is the single remaining population of a gene conservation group of chinook salmon that probably once included now-extinct populations in the John Day, Umatilla, and Walla Walla Rivers [*Lichatowich*, 1998].

Existing geologic barriers. Barriers to fish migration, such as waterfalls and rapids, basin divides, and reaches of insufficient flow, are geologic and hydrologic factors that strongly control fish distribution and migration patterns. These patterns are most evident in the historic distributions of anadromous fish such as chinook salmon, steelhead, and sockeye salmon, which navigate from the ocean to accessible spawning grounds within the basin. Blockages at the upstream limits of anadromy, including falls and reaches of insufficient flow, likely influence the distribution of resident, fluvial, and adfluvial populations, as well as the gene flow of bull trout and resident rainbow trout, although these latter effects are more difficult to document.

Historic chinook salmon distribution on the mainstem Deschutes River basin was controlled by geologic barriers to upstream migration. Big Falls at RM 132.2 was the upstream limit for all anadromous fish on the Deschutes River, including spring chinook and steelhead [*Nehlsen*, 1995] (Figure 3). Big Falls likely formed sometime between 700,000 and 300,000 years ago when lava flows from the vicinity of Newberry Volcano repeatedly filled the Deschutes River canyon from near Bend to as far downstream as Round Butte Dam at RM 110.1 [*Sherrod et al.*, in press]. Near the vicinity of Big Falls, the Deschutes River was apparently diverted about 5 km westward from a channel near Redmond [*Sherrod et al.*, 2002], resulting in incision of a younger canyon along the present course of the Deschutes River. This incision is recent enough that the river has not yet attained a graded profile, resulting in rapids and falls where it intercepts more resistant strata, such as the basalt flow that composes Big Falls. An important hydrologic factor enhancing the blockage at Big Falls is that the Deschutes River descends below the level of the regional water table near this location, and discharge increases substantially downstream of Big Falls [*Gannett et al.*, this volume]. The rapidly diminishing flow encountered by fish migrating upstream likely compounded the difficulty in navigating Big Falls.

The larger fall chinook salmon may have been blocked most years by the 4.7-m-high Sherars Falls at RM 44 [*Jonasson and Lindsay*, 1988; *Nehlsen*, 1995] (Figure 3), where the Deschutes River intercepts resistant basalt flows of the Columbia River Basalt Group [*O'Connor et al.*, this volume]. Sherars Falls is probably at least partly the result of incision during the last 10,000-100,000 years, judging from the distribution of Quaternary deposits within the Deschutes River canyon [*O'Connor et al.*, this volume] and, thus, may not be as old as the upstream blockage at Big Falls. In addition, during periods of increased flow and sediment transport, such as during the Pleistocene ice ages, channel aggradation may have decreased the severity of the blockage, allowing passage of fall chinook. Recently, passage facilities constructed and improved between the 1920s and 1940s at Sherars Falls allowed annual migration of fall chinook as far upstream as the location of Pelton Dam at RM 102.6. At present, anadromous fish are prevented from upstream passage at the downstream end of the Pelton-Round Butte dam complex at RM 100.1.

Ancient geologic barriers. The effects of ancient geologic barriers that have since been removed are more speculative than those of existing barriers. Ancient barriers are presumably reflected in the present distribution of distinct populations of genetic subgroups and life history types. Within the Deschutes River basin, several recent studies evaluating genetic variation within individual salmonid species indicate patterns of genetic variation potentially attributable to geologic events and conditions.

The coexistence of alternate life-history forms of rainbow trout in the lower Deschutes River likely reflects past formation and removal of geologic barriers. *Zimmerman and Reeves* [2000] examined the relationship between steelhead and resident rainbow trout in the lower Deschutes River through analysis of the timing and location of spawning, and by investigating population structure using the analysis of otolith microchemistry. The timing studies showed that steelhead and resident rainbow trout spawning was spatially and temporally isolated, with only a small amount of temporal overlap, suggesting that significant interbreeding was not likely.

The otolith microchemistry studies were used to identify the maternal origin of adult steelhead and rainbow trout from the Deschutes River, in order to determine if interbreeding occurred between the two life history forms. Comparison of strontium to calcium ratios (Sr/Ca) in the primordia (the part of the otolith that forms first) with those from the region of the otolith formed during the period of time the fish was rearing as a juvenile can be used to identify whether the mother of that fish was a steelhead or a resident rainbow trout (Figure 9). Based on these analyses, the adult populations of steelhead and resident rainbow trout in the Deschutes River did not include progeny of the alternate life history form. That is, there was no evidence of steelhead of resident rainbow trout maternal origin, or of resident rainbow trout of steelhead maternal origin. Both the timing of spawning and otolith results allowed *Zimmerman and Reeves* [2000] to surmise that steelhead and resident rainbow trout in the Deschutes River were reproductively isolated, and hence constituted potentially distinct populations.

To explain the presence of both life history forms using the same reach of river, *Zimmerman* [2000] suggested that this population structure could be the result of allopatric (during separation) divergence caused by the large Pleistocene landslide dams between RM 60 and RM 85 described by *O'Connor et al.* [this volume]. One or more of these landslide dams may have created a physical blockage of the river, forcing divergence of a downstream group of anadromous steelhead from an upstream group of resident rainbow trout for a sufficient duration to allow the behavioral characteristic of spawning timing to become distinct enough to persist even after breaching of the landslide dam(s). A similar case was reported by *Morita et al.* [2000] in conjunction with a constructed dam, for which they demonstrated that anadromous white spotted char (*Salvelinus leucomaenis*) populations separated from the sea showed substantial changes in behavioral characteristics within thirty years. Above the dam, there was a decrease in the production of smolts and an increase in the rate of residency. Likewise, *Kurenkov* (1978) described a similar scenario leading to the development of reproductively isolated populations of kokanee in Kamchatka, Russia. Consistent with these rapid changes in life history strategy, *Hendry et al.* [2000] demonstrated that genetic divergence and reproductive isolation in salmonids can occur within thirteen generations.

The genetic variation of resident rainbow trout within the Deschutes River basin provides evidence of longer-term blockages and exchanges of genetic material. *Currens et al.* [1990] determined the genetic structure of resident rainbow trout in the Deschutes River basin by analysis of genetic and morphologic variation among several distinct populations. A primary finding was that resident rainbow trout above White River Falls (Figure 3) shared similar genetic characteristics with rainbow trout populations in now-isolated drainages of the northern Great Basin, including the Fort Rock Basin and Catlow Valley, but were distinctly different from other populations in the Deschutes River basin. *Currens et al.* [1990] concluded that a common ancestral rainbow trout was present in the northern Great Basin and Deschutes River, thus indicating connections between these now-separate basins. The Fort Rock population was probably separated by late Pleistocene lava flows from the vicinity of Newberry Volcano that separated the Deschutes River

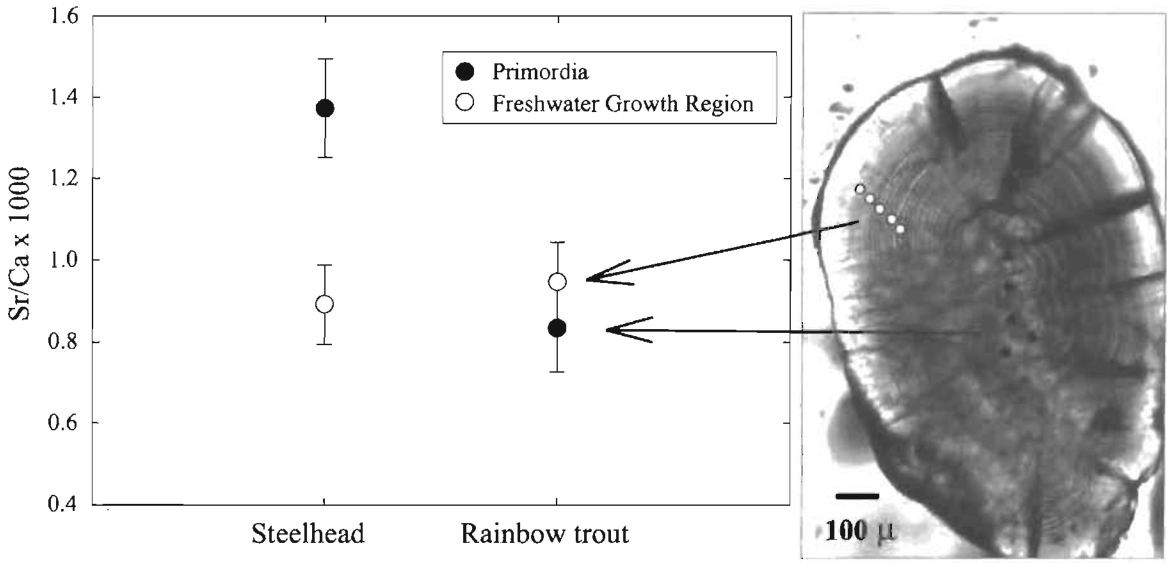

Figure 9. Determination of maternal origin in steelhead and resident rainbow trout (*Oncorhynchus mykiss*) progeny based on otolith microchemistry. Strontium to calcium ratios (Sr/Ca) are determined in points sampled within the primordia and freshwater growth region of sectioned otoliths. This otolith is from a young-of-year steelhead.

basin and the Fort Rock basin. Subsequent divergence or colonization of resident rainbow trout in the Deschutes River led to the present genetic differences between the rainbow trout above White River Falls and those in the rest of the Deschutes River basin.

Genetically distinct populations of bull trout in the Deschutes River basin may also be the legacy of former geologic blockages. *Spruell and Allendorf* [1997] examined the genetic structure of bull trout throughout Oregon, including samples from the Warm Springs River, Shitike Creek, and the Metolius River. Their results indicated that populations from the lower Deschutes River tributaries Shitike Creek and the Warm Springs River were markedly different from the population in the Metolius River, and that the Metolius River bull trout were more similar to bull trout in the Klamath River basin in southern Oregon. *Spruell and Allendorf* [1997] suggested geologic changes in connectivity within and adjacent to the Deschutes River basin as one explanation for this difference. To explain the observed genetic correlations, there would need to be connections between the upper Klamath River and the Metolius River, coincident with a blockage of gene flow between the lower Deschutes River and the Metolius River. While there is no specific evidence of a connection between the Deschutes and Klamath River basins, abundant basin-and-range faulting during the Quaternary may have locally shifted the drainage divide, thus making connections between the basins plausible (David Sherrod, U.S. Geological Survey, personal communication, 2002). However, a persistent late Quaternary blockage between the Metolius and lower Deschutes River is quite likely. Repeated basalt flows from Newberry Volcano and nearby vents between 1.2 and <0.4 million years ago flowed into and partly filled the Deschutes River, Crooked River and lower Metolius River [*Bishop and Smith,* 1990; *Sherrod et al.,* in press]. Such flows filled the Deschutes River canyon to a depth of more than 200 m near the present location of Round Butte Dam at RM 110.1, at the confluence of the Deschutes and Metolius Rivers. The falls formed at that time would undoubtedly have blocked migration from the lower Deschutes River to the Metolius River, probably for several tens of thousand of years, until incision around and through the basalt flows returned the Deschutes and Metolius Rivers to near their previous grades.

MODERN IMPOUNDMENTS AND EFFECTS ON FISH

Just as geologic events and conditions have profoundly affected fish populations, humans have also exerted a profound influence on fish distribution and population dynamics in the Deschutes River basin. Human influences on fish species in the Deschutes River basin have taken many forms, ranging from activities focused on fish management (harvest, hatchery programs, fish planting, and construction of fish ladders to improve passage over natural barriers) to reasoned tradeoffs aimed at other societal objectives (dam construction and water diversions), to actions that inadvertently affect fish (upland landuse actions that adversely affect fish habitat). Most of the human actions that have affected salmonids in the Deschutes River basin are summarized in *Nehlsen* [1995] and *Lichatowich* [1998].

The human actions most similar to geologic controls on fish distribution and population dynamics are dam construction and water diversion; these are also the human activities that have arguably had the greatest impact on aquatic ecosystems and habitat [*Stanford and Ward*, 1979; *Li et al.*, 1987]. In the Deschutes River basin, seven large dams, many small reservoirs, and numerous diversion structures have been constructed over the past 100 years, starting with construction of an irrigation diversion on Squaw Creek in 1871 [*Nehlsen*, 1995] (Figure 3). These projects were built for various purposes and objectives, and have had varying impacts on fish communities.

In this section, we consider how these modern impoundments may have affected the distribution and composition of fish communities, using a framework similar to that developed for analyzing geological controls and focusing on the effects of the Pelton-Round Butte dam complex. Like geological controls, dams can influence the physical environment of rivers by directly changing the water flow regime, sediment flux, and temperature regime throughout the system, with potentially serious consequences for aquatic habitat. In much the same way as natural blockages, dams can also be viewed as physical barriers limiting fish migration or interbreeding of populations. In this way, dam construction could be viewed as a singular type of anthropogenic "event" or disturbance. But dams also introduce new processes into a river system, and here we examine the complex relationship between fish and the temperature, blockage, and circulation patterns of water in the reservoir created by Round Butte Dam that have created problems for restoring fish runs in the Deschutes River basin.

Regime Effects of Dams

To assess the ecological effects of changes in streamflow and sediment transport downstream from dams, *Ligon et al.* [1995] proposed a five-step procedure: (1) Characterize the stream and watershed using quantitative measures such as stream type, bar morphology, degree of confinement, and vegetation; (2) Monitor water and sediment discharge; (3) Estimate pre- and post-dam sediment budgets and hydrology; (4) Model dam effects on streambed elevation and grain size; and (5) Predict channel response to the dam. Following this approach, little impact in the lower Deschutes River from the Pelton-Round Butte dam complex might be expected, since geomorphic studies reported in this volume show little change in flow frequency or hydrograph characteristics, bedload transport, channel morphology, and channel bed texture [*Fassnacht et al.*, this volume], or in sediment budgets [*O'Connor, Grant and Haluska*, this volume] attributable to the dam. All of these physical measures directly affect habitat variables that influence biotic communities [*Ligon et al.*, 1995].

The physical variables that were studied do not represent an exhaustive list of all potentially ecologically relevant physical changes introduced by the dams, however, nor are all dam effects necessarily negative. Changes in suspended sediment flux due to reservoir trapping of fine sediment, for example, were not directly evaluated, but may have biological implications. As has occurred with other dams, reduced suspended sediment loads following dam construction on the Deschutes River may have lowered turbidity below the dams. Biological consequences of increased water clarity can include enhanced primary production, decreased impacts of fine sediment on incubating salmonid eggs and embryos, and improved foraging efficiency [*Barrett et al.*, 1992; *Kinoshita et al.*, 2001].

Water temperature is critical to biological communities, because reproduction and growth is frequently temperature dependent [*Bjornn and Reiser*, 1991]. Changes in temperature have been documented downstream of many dams, and frequently lead to dramatic changes in fish communities and their reproductive success [*Stanford and Ward*, 1979]. These changes typically result from withdrawal of water from deep stratified reservoirs, resulting in colder water temperatures and a low-amplitude thermal regime downstream [*Hagen and Roberts*, 1973], as has occurred in the Colorado and Green Rivers in Utah [*Stanford and Ward*, 1979; *Tyus and Saunders*, 2000]. Corresponding shifts from warmwater to coldwater fish communities have been observed in many of these cases.

Huntington et al. [1999] conducted a detailed analysis of pre- and post-dam temperature profiles in the Deschutes River and addressed four primary questions: (1) Are changes in temperature evident; (2) What is the magnitude of change; (3) How far downstream are changes evident; and (4) What effects have those changes had on the biota downstream of the dam? Changes in annual maximum and minimum temperatures downstream of the dams on the Deschutes River are small and not significant [*Huntington et al.*, 1999]. There are shifts in the timing of temperature cycles just downstream of the dam, but these impacts are dampened further downstream. *Huntington et al.* [1999] suggested that shifts in temperature are likely to have delayed the emergence of incubating steelhead embryos by about ten to fourteen days immediately below the dam, but have had no significant impact on the emergence timing of fall chinook salmon. In summary, although there has been some alteration in temperature regime below the Pelton-Round Butte dam complex, these changes are small compared to those below other dams elsewhere.

Migration Barrier Effects

Construction of the Pelton-Round Butte dam complex altered distributions of spring chinook salmon and steelhead (Figures 4 and 6), because these dams form a physical barrier to their former migration. Fish passage facilities initially included a fish ladder from the Reregulating Dam to Pelton Dam, a fish lift over Round Butte Dam, and juvenile collection facilities at both Pelton and Round Butte Dams, which were operated from 1956 to 1968. During this period, a total of 6,933 adult chinook salmon and 6,248 adult steelhead were passed upstream and over Round Butte Dam [*Ratliff and Schulz*, 1999]. Downstream passage of juvenile chinook and steelhead was less successful, and in 1968 upstream and downstream passage of fish was abandoned in favor of hatchery mitigation. Spring chinook salmon and steelhead are produced at the Round Butte Hatchery to replace production in the area of the watershed blocked by dams. In addition to loss of chinook salmon and steelhead production upstream of Round Butte Dam, population dynamics of other migratory species including rainbow trout and bull trout were altered. As a result, blockage of fish passage is probably one of the greatest impacts of the modern dams constructed in the mainstem of the Deschutes River.

Complex Interactions Due to Dams and Management Response

The decision to cease fish passage in 1968 was primarily due to the perceived failure of juvenile fish production and lack of downstream passage of juvenile steelhead and chinook salmon [*Ratliff and Schulz*, 1999]. This failure was likely due to temperature and current conditions in the reservoir at Round Butte Dam, Lake Billy Chinook (Figure 3). In contrast with natural barriers where *upstream* passage is blocked, this large reservoir with its three major tributaries and a deep outlet (73 m below full pool) for hydropower generation created a *downstream* passage barrier. Because of the hydraulic stability (low variation in discharge) at this location [*Gannett et al.*, this volume], Round Butte Dam only spills water from the surface during extremely rare flood events. Thus, essentially all flow exits the reservoir through the power intake at depth. Of the three tributaries, the Crooked River has the warmest inflow and tends to fill the upper portion of the reservoir, whereas the Metolius River is significantly colder and its denser water tends to fill the bottom of the reservoir up to the intake level. The temperature of the Deschutes River is intermediate between the other two tributaries. Downstream migration of juvenile salmonids occurs during spring with peak numbers in April and May. Typically, juvenile steelhead and chinook salmon are surface oriented when passing through deep waters and travel with the prevailing currents [*Smith*, 1974]. Because of the deep intake of Round Butte Dam, surface currents are very slight and variable, and the combination of deep intake and temperature variation between the arms results in an unusual surface circulation pattern. During spring, surface currents used by fish as directional cues tend to be oriented downstream for the Crooked and Deschutes River arms of the reservoir, and upstream for the Metolius River arm [*Yang et al.*, 2000], because at the interface between the Metolius River and the reservoir, the plunging cold water tends to entrain the surface reservoir water [*Yang et al.*, 2000]. These countercurrents do not guide downstream-migrating salmonids to the dam where the juvenile fish collection facilities were located. Juvenile salmon attempting to emigrate from Lake Billy Chinook tended to concentrate in the upper Metolius River arm [*Korn et al.*, 1967]. Given these difficulties, passage was terminated in favor of a fish hatchery mitigation program.

In 1994, research and planning was initiated to reestablish passage of salmonids at the Pelton-Round Butte dam complex. This effort includes altering Round Butte Dam to allow withdrawal of water from the surface during most of the year [*Ratliff et al.*, 2001]. The alteration will include a facility designed to withdraw generation water from either the top or the bottom or a mix of the two. Fish will be excluded from the generation water, and those attempting to emigrate will be diverted into a capture and bypass facility. Key to the success of this facility will be the ability to mix warm surface and deep cold water to allow for management of the temperature of the water entering the lower Deschutes River. It is anticipated that only surface water will be discharged from autumn (after the reservoir surface cools) through June of the following year. During this period, waters of the warmer Crooked and Deschutes Rivers will be discharged off the surface while the reservoir fills from the bottom with cold Metolius River water. Mean reservoir temperatures approaching summer will be several degrees cooler than under present conditions [*DeGasperi et al.*, 2000]. After June, when few juvenile salmon are emigrating and the surface of Lake Billy Chinook warms, an increasing percentage of cold hypolimnetic water will be discharged, in an effort to mimic the natural pre-dam temperature cycle of the lower Deschutes River [*Huntington et al.*, 1999].

The goal of this program will be to reestablish spring chinook salmon runs in the Metolius River, and steelhead runs in the upper Deschutes River (to Big Falls) including Squaw Creek (Figure 3). Steelhead will also be reestablished in tributaries to the Crooked River system. However, it is anticipated that the species that will benefit the most with successful fish passage will be sockeye salmon. When Lake Billy Chinook was formed in 1964, kokanee (resident sockeye salmon) from Suttle Lake in the Metolius River basin naturally seeded this reservoir, and by the early 1970s were the most abundant fish present [*Thiesfeld et al.*, 1999]. With downstream passage of juvenile salmonids, it is likely that sockeye salmon, the anadromous form of kokanee, will reestablish in Suttle Lake and in the reservoirs of the Pelton Round Butte hydroelectric complex.

Reestablishing fish passage at the Pelton-Round Butte dam complex is not an easy proposition. There are questions concerning selection of fish for transport upstream, with a goal of limiting disease transmission yet allowing migration of fish in as natural a manner as if the dams were not present. There is also the question of how success of passage will be measured. Do we measure the number of juvenile fish migrating downstream, or the number of fish returning to migrate upstream past the dams? If those metrics are chosen, how do we distinguish the effects of passage from a host of other influences? These questions need to be addressed, but should not limit opportunities for restoration of migratory fishes in the Upper Deschutes, Crooked, and Metolius rivers.

CONCLUSIONS

Although the geomorphology of a watershed is often invoked as a primary template for understanding the organization of biological systems [*Swanson*, 1980; *Montgomery*, 1999], the interaction among geology, geomorphology and ecosystems has many different facets. As illustrated by the Deschutes River, geology exerts a first-order control on fish populations through two broad mechanisms. First, geology determines the hydrologic, sediment transport, and temperature regimes of the watershed that define the environmental niches and gradients to which organisms are adapted. Second, the history of geological disturbances and events in the basin generates landforms that define critical habitat, and also constrain or define the extent to which species and populations of aquatic organisms can interact with each other. The history of geological blockages and their impacts on ecosystems is still poorly understood, but genetic composition of fish populations in the Deschutes River and elsewhere suggests that ecosystems may retain a long "memory" of geological events in the past. In some cases, the genetics of organisms may even provide clues as to the direction of geomorphic evolution, as in cases where similarities between currently separated populations may show where past drainage network changes have isolated formerly connected river systems. Modern dams affect ecosystems in a similar manner to geological blockages, and the Deschutes River dams have made their greatest impact on fish by isolating lower river from upper river populations. Dams may also influence water, sediment, and temperature regimes, although this impact is modest on the Deschutes River. Because of their sheer size and engineering characteristics, dams may introduce new processes into the landscape to which fish are poorly adapted, often requiring heroic and expensive human efforts and interventions to restore fish runs. The jury is still out on the success of these restoration ventures in the Deschutes River basin and elsewhere.

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REFERENCES

Barrett, J. C., G. D. Grossman, and J. Rosenfeld, Turbidity-induced changes in reactive distance of rainbow trout, *Trans. Amer. Fish. Soc.*, *121*, 437-443, 1992.

Berman, C. H., and T. P. Quinn, Behavioral thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River, *J. Fish Biol.*, *39*, 301-312, 1991.

Bishop, E. M., and G. A. Smith, A field guide to the geology of Cove Palisades State Park and the Deschutes Basin in central Oregon, *Oregon Geology*, *52*, 3-16, 1990.

Bjornn, T. C., and D. W. Reiser, Habitat requirements of salmonids in streams, *Amer. Fish. Soc. Spec. Pub. 19*, 83-138, 1991.

Chapman, D. W., Critical review of variables used to define effects of fines in redds of large salmonids, *Trans. Amer. Fish. Soc.*, *117*, 1-21, 1988.

Currens, K. P., C. B. Schreck, and H. W. Li, Allozyme and morphological divergence of rainbow trout (*Oncorhynchus mykiss*) above and below waterfalls in the Deschutes River, Oregon, *Copeia*, 730-746, 1990.

DeGasperi, C. T., T. Khangaonkar, S. Breithaupt, and K. Marshall, Design of optimum selective withdrawal operation for temperature management at Round Butte Dam, Lake Billy Chinook, Oregon, *Proceedings of the Water Environment Federation (WEF) 73rd Annual Conference and Exposition on Water Quality and Wastewater Treatment (CD-ROM)*, October 18, 2000, Anaheim, California, 2000.

Ebersole, J. L., W. J. Liss, and C. A. Frissell, Relationship between stream temperature, thermal refugia and rainbow trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States, *Ecology of Freshwater Fish, 10*, 1-10, 2001.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley, Restricted movement in resident stream salmonids: a paradigm lost?, *Can. J. Fish. Aquat. Sci., 51*, 2626-2637, 1994.

Hagen, R. M., and E. B. Roberts, Ecological impacts of water storage and diversion projects, in *Environmental Quality and Water Development*, edited by C. R. Goldman, J. McEvoy, and P. J. Richardson, W. H. Freeman, San Francisco, California, 1973.

Healey, M. C., Life history of chinook salmon (*Oncorhynchus tshawytscha*), in *Pacific Salmon Life Histories,* edited by C. Groot and L. Margolis, UBC Press, Vancouver, British Columbia, pp. 313 – 393, 1991.

Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn, Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon, *Science, 290*, 516-518, 2000.

Huntington, C., T. Hardin, and R. Raymond, Water temperatures in the Lower Deschutes River, Oregon, Portland General Electric Company, Portland, Oregon, 1999.

Jonasson, B. C., and R. B. Lindsay, Fall chinook salmon in the Deschutes River, Oregon, Oregon Department of Fish and Wildlife, *Inf. Rep. 88-6*, Portland, Oregon, 1988.

Kinoshita, A., T. Mizuyama, M. Fujita, T. Sawada, and M. Yoshikiyo. An impact of sediment flushing from a sabo dam on char in Hiru-Dani River. *River Technical Papers, 7*, 363-368, 2001.

Korn, L., L. H. Hreha, R. G. Montagne, W. G. Mullarkey, and E. J. Wagner, The effect of small impoundments on the behavior of juvenile anadromous salmonids, Fish Commission of Oregon Research Division (now Oregon Department of Fish and Wildlife), Clackamas, Oregon, 1967.

Kurenkov, S. I., Two reproductively isolated groups of kokanee salmon, *Oncorhynchus nerka kennerlyi*, from Lake Kronotskiy, *J. Ichthyology, 17*, 526-534, 1978.

Li, H. W., C. B. Schreck, C. E. Bond, and E. Rexstad, Factors influencing changes in fish assemblages of Pacific Northwest streams, in *Community and Evolutionary Ecology of North American Stream Fishes*, edited by W. J. Mathews and D. C. Heins, pp. 193-202, University of Oklahoma Press, Norman, Oklahoma, 1987.

Lichatowich, J., A conceptual foundation for the management of native salmonids in the Deschutes River, Portland General Electric Company, Portland, Oregon, 1998.

Ligon, F. K., W. E. Dietrich, and W. J. Trush, Downstream ecological effects of dams: a geomorphic perspective, *Bioscience, 45*, 183-192, 1995.

Lindsay, R. B., B. C. Jonasson and R. K. Schroeder, Spring chinook salmon in the Deschutes River, Oregon, *Inf. Rep. 89-4*, April 1989, Fish Division, Oregon Dept of Fish and Wildlife, Portland, Oregon, 1989.

Mathews, W. J., Patterns in Freshwater Fish Ecology, Chapman and Hall, New York, 1998.

McPhail, J. D., and C. C. Lindsey, Zoogeography of the freshwater fishes of Cascadia (the Columbia System and rivers north to the Stikine), in *The Zoogeography of North American Freshwater Fishes*, edited by C. H. Hocutt and E. O. Wiley, pp. 615-637, John Wiley and Sons, New York, 1986.

McPhail, J. D., and C. B. Murray, The early life-history and ecology of Dolly Varden (*Salvelinus malma*) in the Upper Arrow Lakes, Vancouver, B. C., University of British Columbia, Department of Zoology and Institute of Animal Resources, 1979.

Morita, K., S. Yamamoto, and N. Hoshino, Extreme life history change of white-spotted char (*Salvelinus leucomaenis*) after damming, *Can. J. Fish. Aquat. Sci., 57*, 1300-1306, 2000.

Montgomery, D. R., Process domains and the river continuum, *J. Amer. Water Resour. Assoc., 35*, 397-410, 1999.

Nehlsen, W., Historical salmon and steelhead runs of the upper Deschutes River and their environments, Portland General Electric Company, Portland, Oregon, 1995.

Oregon Department of Fish and Wildlife (ODFW), Biennial report on the status of wild fish in Oregon Portland, Oregon, 1995.

Pratt, K. L., A review of bull trout life history, in *Proceedings of the Gearheart Mountain Bull Trout Workshop*, edited by P. J. Howell and D. V. Buchanan, pp. 5-9, Oregon Chapter American Fisheries Society, Corvallis, Oregon, 1992.

Ratliff, D. E., Bull trout investigations in the Metolius River–Lake Billy Chinook system, in *Proceedings of the Gearheart Mountain Bull Trout Workshop*, edited by P. J. Howell and D. V. Buchanan, pp. 37 – 44, Oregon Chapter of the American Fisheries Society, Corvallis, Oregon, 1992.

Ratliff, D. E., and E. E. Schulz, Fisheries program at the Pelton-Round Butte Hydroelectric Project (Oregon) 1956-1995, Portland General Electric Company, Portland, Oregon, 1999.

Ratliff, D. E., E. E. Schulz, and S. D. Padula, Pelton-Round Butte Project, Fish Passage Plan, Second Edition, Portland General Electric, Portland, Oregon, The Confederated Tribes of the Warm Springs Reservation of Oregon, Warm Springs, Oregon, 2001.

Reeves, G. H., F. H. Everest, and J. D. Hall, Interactions between redside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature, *Can. J. Fish. Aquat. Sci., 44*, 1603-1613, 1987.

Reeves, G. H., P. A. Bisson, and J. M. Dambacher, Fish communities, in *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*, edited by R. J. Naiman and R. E. Bilby, pp. 200-234, Springer-Verlag, New York, 1998.

Rosenfeld, J., M. Porter, M. Pearson, et al. The influence of temperature and habitat on the distribution of chiselmouth, *Acrocheilus alutaceus*, in British Columbia, *Environmental Biology of Fishes, 62*, 401-413, 2001.

Sherrod, D. R., M. W. Gannett, and K. E. Lite Jr., Hydrogeology of the upper Deschutes Basin, Central Oregon: A young basin adjacent to the Cascade Volcanic Arc, in *Field Guide to Geologic Processes in Cascadia*, edited by G. W. Moore, *Oregon Dept. Geol. Min. Ind. Spec. Pap. 36*, pp. 109-144, 2002.

Sherrod, D. R., E. M. Taylor, M. L. Ferns et al., Geologic map of the Bend 30′ X 60′ Quadrangle, central Oregon, *U. S. Geol. Surv. Geol. Inv. Map I-2683*, scale 1:100,000, in press.

Smith, J. R., Distribution of seaward-migrating chinook salmon and steelhead trout in the Snake River above Lower Monumental Dam, *Marine Fish. Rev., 36*, 42-45, 1974.

Spruell, P., and F. W. Allendorf, Nuclear DNA analysis of Oregon bull trout, Final Report to the Oregon Department of Fish and Wildlife, University of Montana, Wild Trout and Salmon Genetics Laboratory Report 97/5, 1997.

Stanford, J. A., and J. V. Ward. Stream regulation in North America, in *The Ecology of Regulated Streams*, edited by J. V. Ward and J. A. Stanford, pp. 215-236, Plenum Press, New York, 1979.

Swanson, F. J., Geomorphology and ecosystems, in *Forests: Fresh Perspectives from Ecosystem Analysis: Proceedings of the 40th Annual Biology Colloquium*, edited by R. W. Waring, pp. 159-170, Oregon State University, Corvallis, Oregon, 1980.

Thiesfeld, S. L., J. C. Kern, A. R. Dale, M. W. Chilcote, and M. A. Buckman. Lake Billy Chinook sockeye salmon and kokanee research study, 1996-1998, Contract Completion Report. Oregon Department of Fish and Wildlife, Portland, Portland General Electric Company, Portland, Oregon, 1999.

Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh, Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon, *Ecol. Appl.*, *9*, 301-319, 1999.

Tyus, H. M., and J. F. Saunders III, Nonnative fish control and endangered fish recovery: lessons from the Colorado River, *Fisheries*, *25*(9), 17-24, 2000.

Yang, Z., T. Khangaonkar, C. DeGasperi, and K. Marshall, Three-dimensional modeling of temperature stratification and density-driven circulation in Lake Billy Chinook, Oregon, in *Proceedings of the 6^{th} International Conference on Estuarine and Coastal Modeling*, edited by M. L. Spaulding and H. L. Butler, pp. 411-425, American Society of Civil Engineers, New Orleans, 2000.

Zimmerman, C. E., Ecological relation of sympatric steelhead and resident rainbow trout in the Deschutes River, Oregon, PhD Dissertation, Oregon State University, Corvallis, Oregon, 2000.

Zimmerman, C. E. and G. H. Reeves, Population structure of sympatric anadromous and nonanadromous *Oncorhynchus mykiss*: evidence from spawning surveys and otolith microchemistry, *Can. J. Fish. Aquat. Sci.*, *57*, 2152-2162, 2000.

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