5. Anthropogenic Alterations to the Biogeography of Puget Sound Salmon

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Abstract

Geologic and geomorphic history and anthropogenic influences have altered the biogeography of Puget Sound salmon, by which we mean their morphological and genetic relationships, abundance, and distribution, from individual habitat units (e.g., pools and riffles) to the regional scale (e.g., North Sound). We focus on habitat isolation and degradation but also discuss the effects of harvest practices, hatchery practices, and the introduction of non-native aquatic species. Habitat isolation and degradation at the habitat and watershed scales have altered the biogeography of Puget Sound salmon at the regional scale because different juvenile Pacific salmon species spatially segregate into different habitats in the same watershed or biogeographic range. Harvest practices have had an impact on overall abundance at the regional scale, and at the even larger Pacific Northwest scale, while hatchery practices have altered Puget Sound salmon abundance and distribution patterns at the watershed and regional scales. Alterations due to non-native species are not as pronounced; however, these do occur at the habitat-unit scale with effects that integrate up to the watershed scale. Biogeographical information can help regional and local salmon recovery efforts by identifying and characterizing large-scale spatial and temporal variability that influence salmon abundance and distribution.

Introduction

Biogeography is the spatial and temporal distribution of organisms as explained by past and present events. In the Pacific Northwest, phylogenetic (morphological and genetic) relationships among salmonid species and the geologic, geomorphic, and anthropogenic history of an area are the two primary influences on salmon biogeography (Wiley 1983). Understanding biogeographic patterns of salmon can lead to insights about historic and current life history and can help identify differences among and variability within species occupying different areas at both large and small spatial and temporal scales. In this chapter, we examine controls on biogeographic patterns of salmon in Puget Sound at several temporal scales—millions of years, thousands of years, hundreds of years, and tens of years, and at several spatial scales—oceanic (Atlantic vs. Pacific), coastal (Pacific Northwest), regional (e.g., Puget Sound), watershed (e.g., Skagit River), reach (e.g., channel and valley segment), and specific habitat units (e.g., pools and riffles). We then use these relationships to address the question of how anthropogenic activities affect(ed) the biogeography of salmon in Puget Sound. To answer this question, we first examine how geologic and geomorphic processes help define the biogeography of salmon in the Pacific Northwest and Puget Sound. We then examine how the distribution and abundance of salmon in the Pacific Northwest and Puget Sound has been altered over the last 150 years. Lastly, we discuss how specific anthropogenic activities within Puget Sound watersheds, such as habitat isolation and degradation, harvest, hatcheries, and the introduction of non-native species, affect salmonid abundance and distribution. We focus our analysis on habitat isolation and degradation and discuss the other three human effects more generally. Our analysis leads us to hypothesize that anthropogenic effects at the habitat and watershed scales cause changes in salmon abundance and distribution at the regional scale, which in turn have altered the biogeography of salmon in Puget Sound.

Large-Scale Geological and Geomorphic Effects on Salmon

Atlantic and Pacific Salmon

Atlantic (*Salmo* spp) and Pacific (*Oncorhynchus* spp) salmon evolved from a common ancestor and are thought to have diverged 15 to 20 million years ago (Ma) during the early Miocene (Figure 1) (Stearley 1992). Pacific salmon differentiated into several species between 20 and 6 Ma (McPhail 1997), and there is strong evidence for sympatric speciation of the Pacific salmon

(Dimmick et al. 1999). Both Pleistocene glaciation and Tertiary marine cooling have been hypothesized as mechanisms for Pacific salmon speciation, but the timing of these events does not correspond well with their Miocene-Pliocene radiation (Thomas et al. 1986). Pacific salmon radiation does coincide with regional mountain building that started during the Miocene to early Pliocene (Montgomery 2000). Many of the major northwestern rivers (e.g., the Columbia, Fraser, and Skeena) that flow east to west are thought to predate this period of uplift (McPhail and Lindsey 1986), and topographic changes would have strongly influenced streams during this uplift. Hence, physiographic changes around the Pacific Rim due to tectonic activity led to topographic change and a diversity of stream types, which in turn may have triggered Pacific salmon evolution (Montgomery 2000).

Continental Glaciation and Salmonid Recolonization of Puget Sound

Continental glaciation during the Pleistocene had a major influence on potential salmon abundance and distribution in the Puget Sound region. Almost three-quarters of the landmass that currently is Puget Sound was covered with ice for approximately 1,000 years (Porter and Swanson 1998). During this

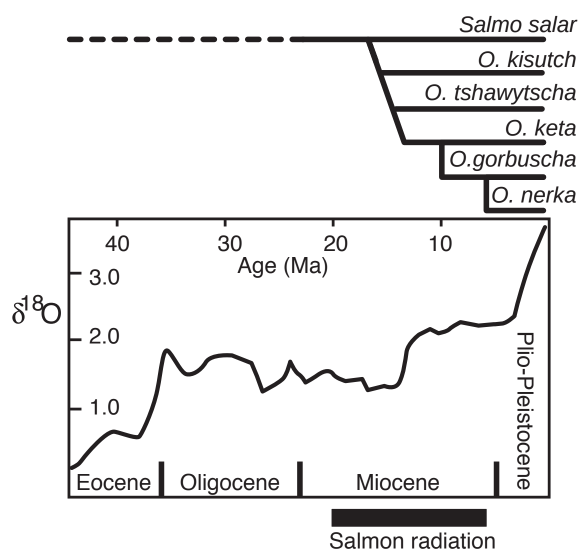

Figure 1. Phylogenetic relations of the Pacific salmon, showing the timing of their radiation 20 to 6 Ma in relation to global marine cooling as revealed from the oxygen isotope record. Based on Stearley (1992) and Montgomery (2000).

time period, pre-glacial fauna in Puget Sound were probably forced into ice-free refuges or died (McPhail and Lindsay 1986), and numerous channel networks were carved by subglacial water, creating distinct valleys or "channelways" (Booth and Hallet 1993). Much of the water from the Puget Sound lobe drained in a southerly direction through the Chehalis River basin (McPhail and Lindsey 1986). Continental ice sheet retreat also led to several processes that shaped the landscape of Puget Sound river basins, including isostatic uplift, valley erosion into glacial sediments, changes in sea level, and valley-burying mudflows (lahars) (Chapter 2). In short, salmon habitat quantity and quality during and after ice sheet retreat varied considerably.

Several hypotheses have been offered regarding the recolonization of Pacific Salmon in Puget Sound. The most well known describes dispersal of salmon from ice-free refuges such as the Columbia River, Chehalis River, and Coastal areas (Figure 2) (McPhail and Lindsey 1986). McPhail and Lindsey (1986) believe the majority of fish fauna dispersing into the Puget Sound region came from the marine environment because most of the fish fauna presently found in Puget Sound are high salinity tolerant species, while only one-third are low salinity tolerant species. Most salmonids are hypothesized to have recolonized Puget Sound rivers through the Chehalis River due to the large drainage connection through the glacial outflow (McPhail and Lindsey 1986).

Many of the Puget Sound salmonid populations, such as chinook (*Oncorhynchus tshawytscha*), steelhead (*O. mykiss*), coho (*O. kisutch*), and chum (*O. keta*) appear to constitute a genetically distinct group (Utter et al. 1989; Marshall et al. 1995; Weitkamp et al. 1995; Busby et al. 1996; Johnson et al. 1997; Myers et al. 1998). Specifically, Puget Sound chinook are genetically distinct from the coastal populations of chinook from California, Oregon, Washington (including the Chehalis), coastal British Columbia, and inland populations including the lower Fraser and Columbia rivers (Marshall et al. 1995; Meyers et al. 1998). One exception is Elwha River chinook, which is more transitional and lies between Puget Sound chinook and coastal populations (Marshall personal communication 2001). Puget Sound steelhead show a similar genetic distinction as chinook (Busby et al. 1996). Puget Sound coho show less genetic distinction than chinook and steelhead with some northern populations such as that from the Strait of Georgia (Weitkamp et al. 1995). However, the data are insufficient to conclude any relationship to Puget Sound coho (Weitkamp et al. 1995). Puget Sound chum also are genetically similar to populations in the Strait of Georgia (Johnson et al. 1997). Hood Canal and Strait of Juan de Fuca summer-run chum salmon are considered distinct from Puget Sound chum due to both genetic and life history traits (Johnson et al. 1997).

Several scientists have hypothesized that Puget Sound salmonids are genetically distinct because they were reproductively isolated from coastal and inland populations, and they subsequently remained within Puget Sound and did not migrate to the Pacific Ocean (Healey 1980; Marshall personal communication 2001). However, the time period for this isolation is unknown. It appears that some of the presently observed genetic diversity for several species already existed during the Pleistocene (Utter et al. 1989), meaning that the most recent glaciation was not the main cause for the genetic distinction.

Other factors predating the most recent glaciation may have had a large effect on genetic diversity. For example, Puget Sound populations of river-type sockeye salmon (*O. nerka*) are genetically more similar to river-type sockeye salmon in rivers more than 2,000 km away (e.g., Chilkat River in northern Southeast Alaska) than to lake-type sockeye salmon within Puget Sound (Gustafson and Winans 1999). This suggests that the common ancestry of river-type sockeye salmon is a greater influence on present-day genotypes than geographic proximity (Gustafson and Winans 1999).

Historic and Current Abundance and Distribution of Salmon

Gresh et al. (2000) estimated that salmon abundance (defined as the number of salmon returning to spawn) in the Pacific Northwest (from Alaska to northern California) has declined 20% to 40% since European settlement. The distribution of salmon during this time period has also changed (Figure 3).

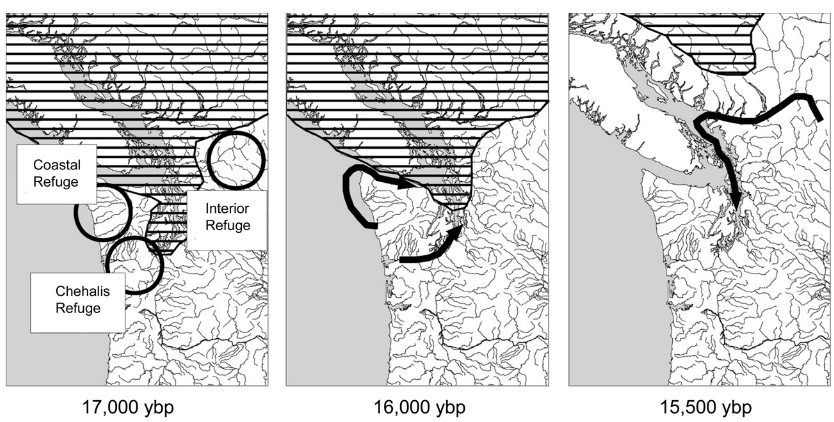

Figure 2. Potential pathways for post-glacial recolonization of salmonids in Puget Sound. Adapted from McPhail and Lindsey (1986). The lined patterns denotes the extent of continental glaciation at different points in time.

Historically, 84% of wild salmon returned to rivers in Alaska and British Columbia, and 16% returned to rivers in Washington, Oregon, Idaho, and California. Currently, 99% of wild salmon return to Alaska and British Columbia, while 1% return to Washington, Oregon, Idaho, and California. In Puget Sound, returns have declined an estimated 92% since the 1850s (Gresh et al. 2000).

This dramatic shift in the distribution and abundance of salmon in the Pacific Northwest, including Puget Sound, has ecological implications that may be proportionally greater than the species decline when the contribution of salmon to the nutrient cycle and stream productivity is considered. Salmon returning to spawn and die are an important source of nutrients, such as nitrogen and phosphorus, which enhance the growth and survival of young salmon and overall stream productivity (Bilby et al. 1998; Wipfli et al. 1998; Gresh et al. 2000). The historic decrease in salmon abundance may represent a larger ecological loss than originally suspected because many of the streams in the Pacific Northwest, including Puget Sound, are naturally nutrient-poor systems (Li et al. 1987).

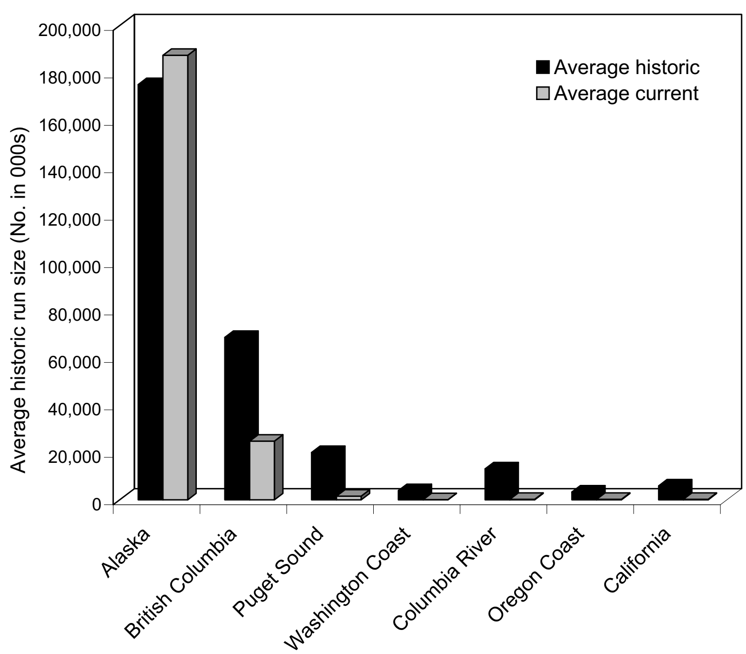

Figure 3. Estimated historic (~1800s) and current (~2000) Pacific salmon run sizes in the Pacific Northwest. Adapted from Gresh et al. (2000).

Anthropogenic Affects on the Biogeography of Salmonids

Habitat isolation and degradation, the harvest of salmonids, hatchery practices, and the introduction of non-native species over the last 150 years have affected the fish assemblages throughout Pacific Northwest streams (Li et al. 1987). Habitat isolation and degradation in Puget Sound has resulted in the virtual eradication of certain habitat types, such as large freshwater wetland and forest floodplain habitats in the lower portion of river basins (Chapter 4). Other habitats in both the freshwater and estuarine environment, including blind-tidal channels, side-channel sloughs, and beaver ponds, have been reduced to less than 20% of their historic occurrence (Beechie et al. 1994, 2001; Chapter 4). In addition, mainstem and tributary habitats have been lost due to hydropower or fish passage blockages such as culverts, or degraded due to forest practices, land conversion, and stream-cleaning practices that have led to the loss of instream wood and preferred stream-channel types (Beechie et al. 1994; Montgomery et al. 1995, 1999).

Harvest of salmonids and hatchery practices have also altered the abundance, distribution, and phylogenetics of salmonids in Puget Sound (Weitkamp et al. 1995; Busby et al. 1996; Meyers et al. 1998; Gresh et al. 2000). Late nineteenth and early twentieth century harvest practices that focused on the selective removal of older and larger salmonids in gillnet fisheries resulted in an increase in the proportion of small precocious males, or jacks, among the fish that were not caught and returned to spawn (Rutter 1904; Hamley 1975). More recently, trolling gear that captures more fish early in the season when they grow rapidly could also lead to the loss of larger salmonids and could be one reason why the average size of salmonids, such as chinook, has decreased over the last several decades (Ricker 1980, 1981). A decrease in the size of adult salmonids could lead to a shift in the size and age structure of spawning salmonids, which could lead to a greater proportion of smaller, younger spawners (Rutter 1904). Smaller parental size has been shown to result in a significant decrease in offspring survivorship (Helle 1989).

Hatchery practices have altered salmonid populations to the point where the majority of coho and chinook returning to Puget Sound streams are of hatchery origin (Weitkamp et al. 1995; Meyers et al. 1998). This has an effect on the distribution and abundance of these salmonids at the reach, watershed, and regional scale. Hatchery populations have also altered the life history of specific salmonids such as coho (Weitkamp et al. 1995). The spawn timing of several coho hatchery populations has contracted from 10 weeks to 3 weeks, a decrease by more than 50% over a 25-year period of record (Flagg et al. 1995). These population-level changes in hatchery coho may affect the distribution and abundance of naturally spawning populations by hatching earlier, growing faster, and displacing the fry of later, naturally spawning coho (Nickelson et al. 1986). Large outplantings from hatcheries can also force naturally spawned coho fry into less desirable habitats, resulting in lower survival potential (Solazzi et al. 1990).

Introduced non-native species comprise 25% to 50% of the fish species currently found in Washington State (Rahel 2000). Many of these species that have been introduced to the Pacific Northwest and Puget Sound are warmwater species from the eastern United States (Li et al. 1987; Rahel 2000). In particular, the increase in piscivorous (fish-eating) fishes greatly increases the risk of predation to the native fauna and primarily affects the young-of-the-year salmonids and other species, such as sculpins, cyprinds, and catostomids (Li et al. 1987). Non-native species also compete with indigenous species for food and habitat, and they hybridize with existing species such as bull trout (*Salvelinus confluentus*) (Li et al. 1987; Markle 1992).

The degree to which non-native species have affected the biogeography of salmonids varies throughout the Pacific Northwest. For example, Li et al. (1987) found that dams in the Columbia River have created conditions that favor warmwater fishes and have considerably altered fish assemblages and the food web to the point where the fish community now resembles that found in Midwest rivers. In Puget Sound there is less documentation of such a large-scale effect, although there are some smaller scale changes. Fayram and Sibley (2000) found that introduced non-native smallmouth bass (*Micropterus dolomieu*) prey on out-migrating juvenile sockeye salmon from Lake Washington, where 28% to 38% of the bass diet consists of juvenile sockeye. However, they concluded that smallmouth bass predation had little impact on the observed decline in sockeye salmon survival in recent years, because of the relatively small amount of time these two species overlap in areas where smallmouth bass can prey upon out-migrating sockeye.

Habitat Loss and Degradation

How have habitat loss and degradation affected salmonid distribution and abundance? The spatial scales that we focus on include regional (e.g., Puget Sound), watershed (e.g., Skagit River), reach (e.g., channel and valley segment), and habitat unit (e.g., pool, riffle, glide). We believe that anthropogenic effects at the habitat unit scale have caused changes in salmonid abundance and distribution that have effects up to the regional scale.

Biogeographic patterns of salmonids in Puget Sound have been substantially altered by changes in land use since 1850. The most obvious changes are due to removal or isolation of habitats, but changes in physical characteristics of accessible habitats have also changed local abundance of some salmonids. We illustrate these changes with examples documenting habitat change in three Puget Sound river basins (the Skagit River, the Stillaguamish River, and the Snohomish River). By linking these changes to habitat preferences for different species, we show how shifts in availability of habitat types affect distribution and abundance of chinook salmon, coho salmon, and steelhead trout.

There is significant overlap in the ranges of the three species, and life history patterns vary considerably (Groot and Margolis 1991). Coho salmon and steelhead trout generally spawn in smaller and steeper streams, although steelhead trout also spawn in smaller mainstem rivers of the three basins. Juveniles of both species spend their first year or two in freshwater. Juvenile coho salmon show strong preferences for pools and woody debris cover in summer and for off-channel slough or pond habitats in the winter. Juvenile steelhead are more generalized in their selection of rearing habitats, but they are less reliant on woody debris cover and generally avoid ponds or sloughs as winter habitat (Williams et al. 1975). Chinook salmon typically spawn in the larger rivers, and most juveniles migrate to sea soon after they emerge from the gravel (Williams et al. 1975). Estuaries provide an important rearing area during smoltification for all species. Figure 4 illustrates habitat preferences for juveniles of each species.

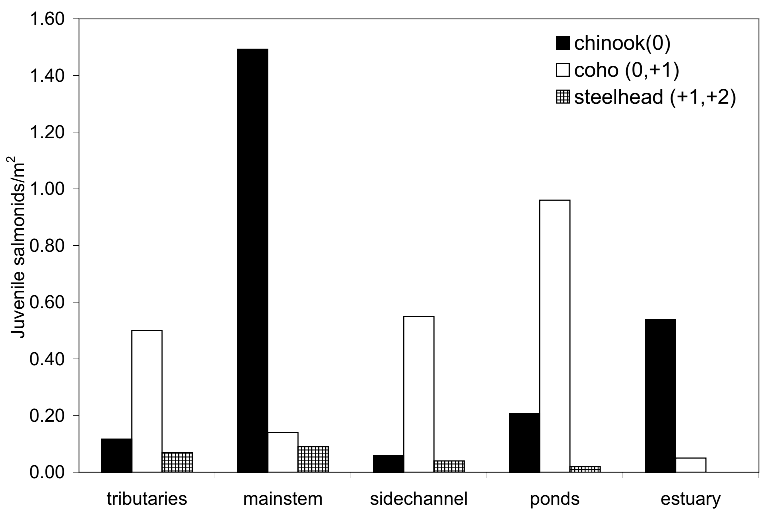

Figure 4. General juvenile salmonid use at the habitat scale. Compilation of over 60 references. Age class 0 denotes juvenile salmonids that have recently emerged or are less than one year of age. Age +1 denotes juvenile salmonids that are greater than one year of age.

Skagit and Stillaguamish Rivers

Historically, the freshwater range of coho salmon and steelhead trout in the Skagit and Stillaguamish Rivers was limited mainly by natural barriers to upstream migration such as bedrock falls. Chinook salmon have shorter migrations and were limited in range by availability of preferred habitats. Upstream migration to the Baker River system (tributary to the Skagit River) has been blocked by the installation of two hydroelectric dams, but access is presently maintained through trapping and hauling operations (Figure 5). Migration into the upper South Fork of the Stillaguamish River was naturally blocked at Granite Falls until 1954, when a fish ladder was constructed to allow anadromous fish into the upper basin.

Most of the salmonid habitat in the Skagit and Stillaguamish River watersheds were historically located in the floodplains and deltas (Beechie et al. 2001). However, intensive land uses such as agriculture and urbanization have also concentrated in these landforms, leading to large losses in off-channel habitats (Figure 6). The majority of distributary slough habitat in the Skagit delta has been removed or made inaccessible by levees, resulting in the loss of more than 75% of the delta habitat area (Beechie et al. 1994). Side-channel slough areas on the floodplain have been reduced by nearly half, and roughly 90% of beaver ponds have been isolated (Beechie et al. 1994, 2001). By contrast, in the Stillaguamish River basin the loss of beaver ponds is by far the greatest habitat loss. These two examples illustrate variation in the types of habitat losses from basin to basin within Puget Sound and also suggest variation in causes of habitat loss.

Habitat changes do not affect all species equally because different species prefer different habitat types. For example, detailed analyses of losses in coho salmon smolt production potential, based on the model of Reeves et al. (1989) show that declines in potential production of juvenile coho smolts are greater than 50% in both basins (Beechie et al. 1994, 2001); however, contractions in coho salmon distribution are focused mainly in the delta and floodplain of the Skagit basin and in floodplain and tributaries (the location of most ponds) in the Stillaguamish basin. These same habitat losses would have different effects on chinook salmon and steelhead trout distributions. The range of chinook salmon in the Skagit river basin may be most compressed in the delta because losses there are large compared to those in mainstem rivers. Compression of the chinook range in the Stillaguamish basin may also be focused in the delta, although the magnitude of effect is likely much lower than in the Skagit due to the smaller amount of historic habitat there (Chapter 4). Steelhead trout appear to depend less on delta habitats than either chinook or coho, so alterations of estuary habitats are less likely to impact their distribu-

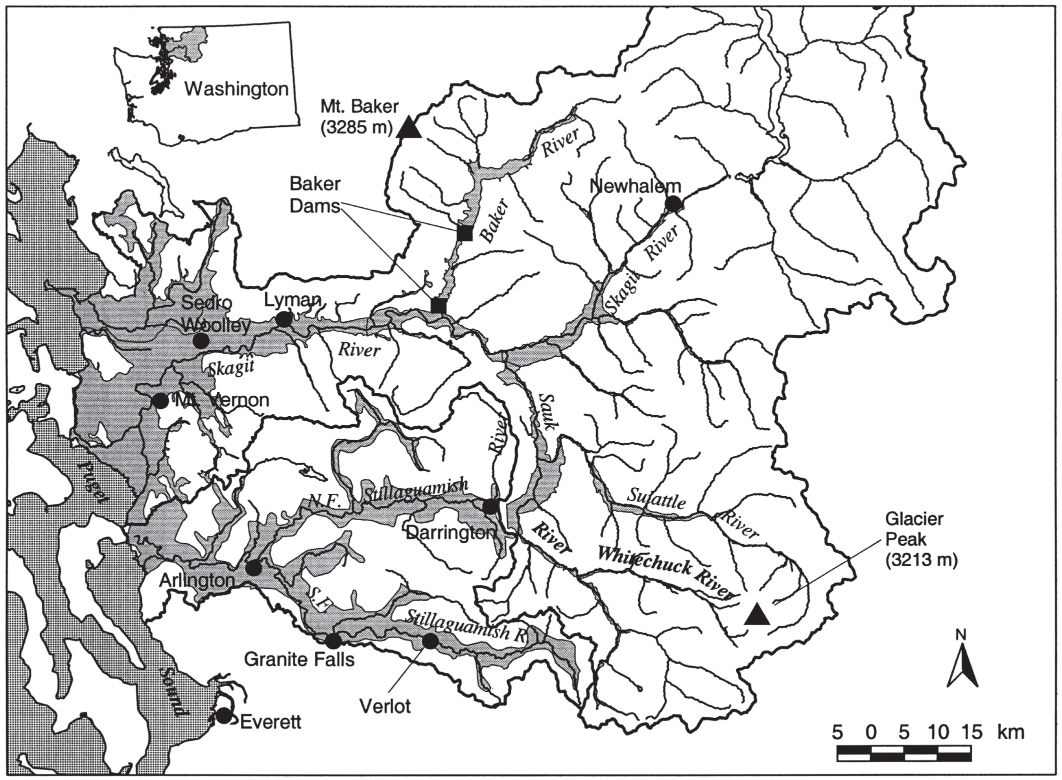

Figure 5. Location map of Skagit and Stillaguamish Rivers.

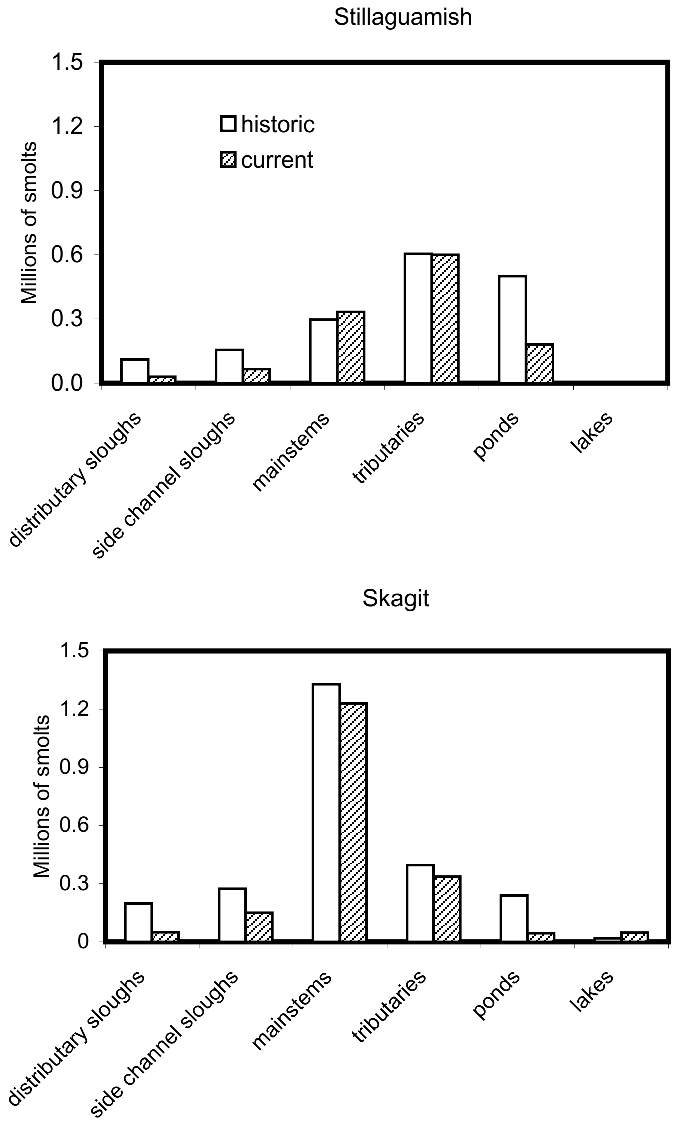

Figure 6. Changes in the range of coho salmon in the Stillaguamish and Skagit River basins as illustrated by losses of potential juvenile production in different types of summer rearing habitat. Note that most of the range compression, and subsequent juvenile production, in the Stillaguamish results in the loss of ponds, which are located in the tirbutaries. The range of Skagit coho rearing has been compressed by both loss of ponds and losses in the river delta and floodplains (adapted from Beechie et al. 2001).

tion. Rather, they are most likely affected by the loss or degradation of tributary and mainstem habitats. Because historic availability of different habitat types and the relative losses of each type vary by river basin, we anticipate that each basin in Puget Sound will exhibit different changes in the distribution and potential production of each species.

Snohomish River

Similar to the Skagit and Stillaguamish Rivers, the majority of salmonid habitat in the Snohomish River basin was historically located in the floodplains and deltas. In the Snohomish River basin, the spread of agriculture has coincided with the destruction and isolation of off-channel and wetland areas over the last 70 to 120 years (Chapter 4). Removal of riparian and floodplain vegetation began in the 1860s, and agriculture was well established in the basin by 1900 (Chapter 4).

Today, the Snohomish River floodplain and neighboring foothills along the channel are located predominantly in rural residential, agricultural, and urbanized areas. Throughout much of the lower portion of the Snohomish River basin, forested and agricultural areas are zoned to allow future development to rural residential, suburban, and urban land use. Even with this extensive change and loss of lowland habitat, more than 75% of the Snohomish River basin is still forested, with the vast majority in upland areas. The combination of extensive habitat loss in the lowlands and relatively intact-forested areas in the uplands provides an interesting and typical description of land-use patterns and habitat conditions in Puget Sound. These land-use patterns may have also led to changes in fish distribution and abundance due to changes in habitat- and reach-scale characteristics, such as the loss of off-channel over-wintering habitat due to floodplain isolation, or the loss of in-channel wood and subsequent reduction in pool habitat quantity and quality (Beechie et al. 1994; Montgomery et al. 1995). Both impacts reduce either the production potential or survival of salmonids (Beechie et al. 1994; Kruzic et al. 2001).

For example, adult Snohomish River coho show a definite trend in salmon abundance by land-use category (Figure 7). Stream reaches in forests support more than 2.5 times more coho than rural, urban, or agricultural streams. Streams in agricultural areas support the fewest salmon, where average weighted fish-days were 4 times lower than the other land-use categories. Differences in relative salmon abundance are observed between hydrologically altered and unaltered wetlands (Figure 8). Hydrologically altered wetlands included those ditched or separated from the stream channel by bank

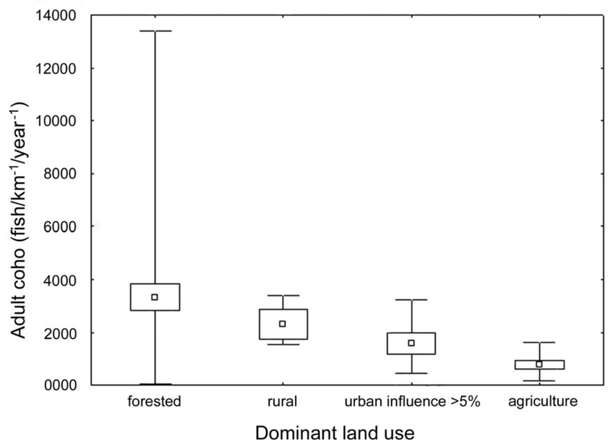

Figure 7. Plot of annual adult coho salmon returns per kilometer of stream length in fish-days by dominant land-use type within 100 m of the stream channel in the Snohomish River basin in northern Washington from 1984 to 1998. Clear squares are mean values, top and bottom of the clear rectangles are the mean value plus one standard error, and horizontal lines at the top and bottom are minima and maxima. Data from Pess et al. (1999). Fish-days were calculated by multiplying the number of live fish observed on each survey date by the number of days between surveys.

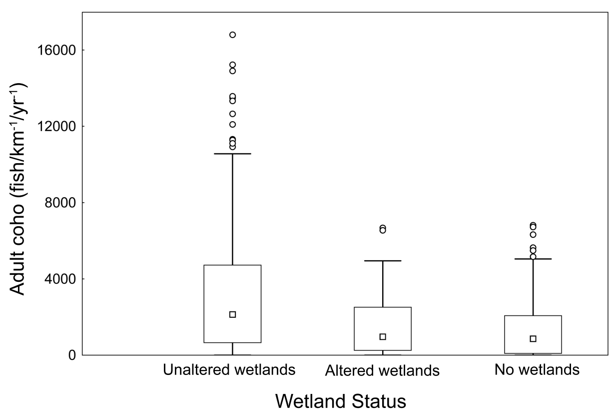

Figure 8. Relationship between wetland status and adult coho salmon per kilometer of stream length per year in fish-days in the Snohomish River basin from 1984 to 1998. Clear squares are median values, top and bottom of the clear rectangles are the 25th and 75th percentile, horizontal lines at the top and bottom are 5th and 95th percentile, and clear circles are outliers. Data from Pess et al. (1999).

armoring or diking. Stream reaches with unaltered wetlands associated with the stream channel (i.e., wetlands present at the reach scale) had adult coho salmon densities 2 to 3 times greater than spawner survey reaches with altered wetlands. Stream reaches with altered wetlands exhibited salmon densities comparable to stream reaches without wetlands. Changing habitat characteristics at the habitat-unit and reach-scale due to land-use effects, such as channel modification, can alter abundance patterns and redistribute salmonids, such as coho, to preferred habitats on a watershed-scale. If the relationships identified above are correct, then an increase in specific land-uses, such as urban or agricultural areas, or a decrease in specific reach-scale habitat characteristics, such as wetlands, can further alter coho abundance and future distribution.

Harvest, Hatcheries, and Non-Native Species

Harvest

Direct mortality from harvest (fishing) has reduced the overall abundance of salmonids at the entire Puget Sound scale. Total harvest rates for Puget Sound chinook, coho, and steelhead, including ocean and terminal fisheries from the 1970s to the 1990s, ranged between 60% and 90% (Weitkamp et al. 1995; Busby et al. 1996; Meyers et al. 1998). During the 1990s, decreased harvest rates for chinook ranged between 15% and 50% and averaged approximately 30% (PSSSRG 1997; Grayum personal communication 2001). Some stocks are targeted for a greater proportion of the total harvest, particularly if they have a large hatchery component, and such targeting practices could result in a change in the distribution and abundance patterns over time, although we did not find evidence for this in the most recent records at the regional scale (Figure 9).

Hatcheries

Hatchery practices have an effect at the Puget Sound, regional, and watershed-scale. Hatchery practices have altered salmonid populations to the point where the majority of chinook and coho returning to Puget Sound streams are of hatchery origin (Figure 10) (Weitkamp et al. 1995; Busby et al. 1996; Meyers et al. 1998). Chinook returning to hatcheries account for 57% of the adult fish returning to spawn (spawning escapement) (Meyers et al. 1998), while the average hatchery contribution rate for monitored coho stocks with

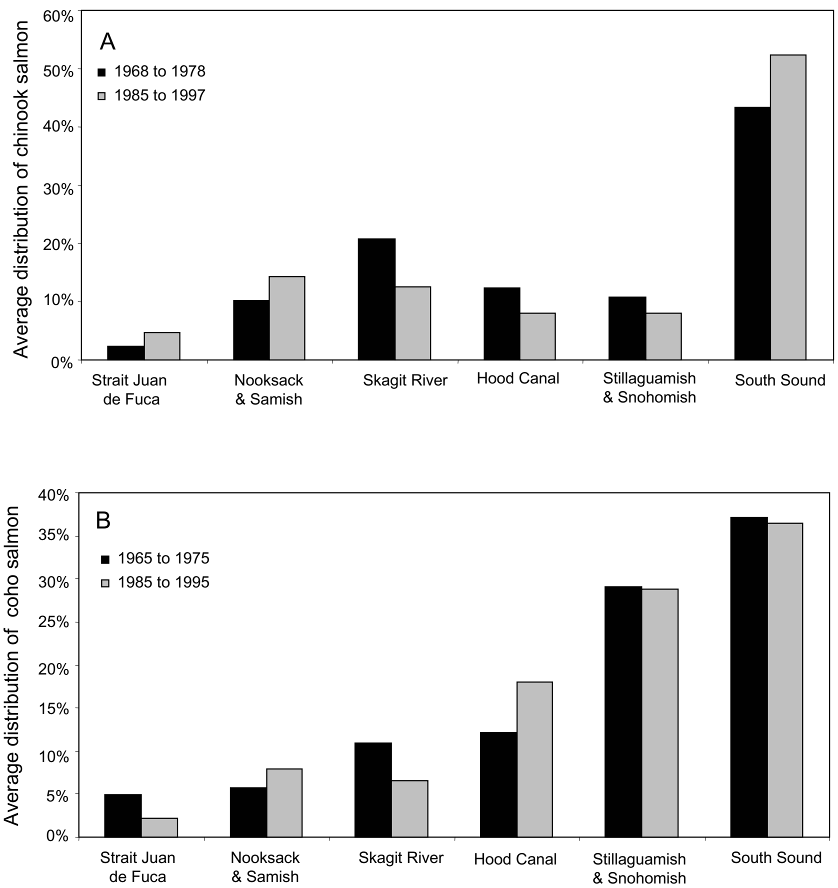

Figure 9. Distribution of harvested chinook (A) and coho (B) by region within Puget Sound from 1965 and 1975 and 1985 and 1997. Run-reconstruction data are for salmon landings and were developed by the Northwest Indian Fisheries Commission. Data is from http://www.nwifc.wa.gov/fisheriesdata/runreconstruction.asp. Regions include the following main rivers: Strait of Juan de Fuca—Dungeness and Elwha Rivers; Nooksack and Samish—Nooksack and Samish Rivers; Skagit River— Skagit River; Hood Canal—Dosewallips, Duckabush, Hamma-Hamma, Quilcene and Skokomish Rivers; Stillaguamish and Snohomish basins—Stillaguamish and Snohomish Rivers; South Sound—Lake Washington, Green-Duwamish, Puyallup, Nisqually, Deschutes Rivers, and Minters and Chambers Creeks.

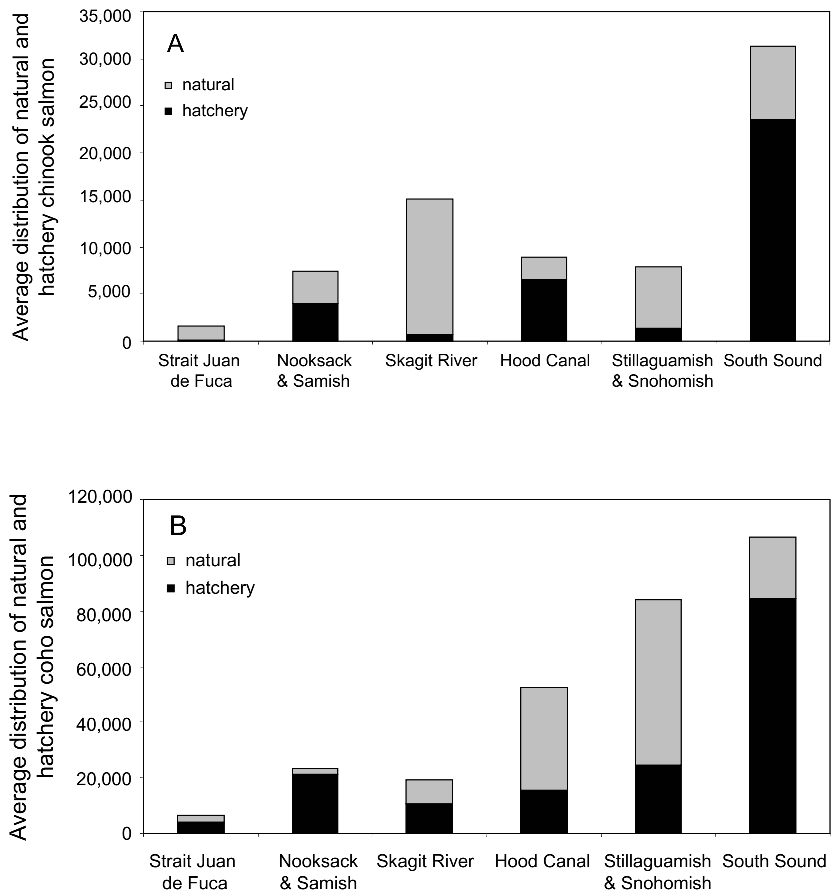

Figure 10. Distribution of natural and hatchery chinook (A) and coho (B) by region within Puget Sound from 1985 to 1995. Run-reconstruction data is for salmon landings and was developed by the Northwest Indian Fisheries Commission. Data can be accessed at http://www.nwifc.wa.gov/fisheriesdata/runreconstruction.asp. Regions include the following main rivers: Strait Juan de Fuca—Dungeness and Elwha Rivers; Nooksack and Samish—Nooksack and Samish Rivers; Skagit River—Skagit River; Hood Canal—Dosewallips, Duckabush, Hamma-Hamma, Quilcene and Skokomish Rivers; Stillaguamish and Snohomish basins—Stillaguamish and Snohomish Rivers; South Sound—Lake Washington, Green-Duwamish, Puyallup, Nisqually, Deschutes Rivers, and Minters and Chambers Creeks.

Puget Sound was 62% from 1981 to 1992 (Weitkamp et al. 1995). The proportion of steelhead spawning escapement derived from hatchery fish ranges between 1% and 51%, with higher proportions of hatchery steelhead occurring in Hood Canal and the Strait of Juan de Fuca (Busby et al. 1996).

Distribution of natural versus hatchery origin salmonids varies by region within Puget Sound. Hatchery influence is greatest for coho and chinook in the most northernly (e.g., Nooksack and Samish) and southerly (e.g., Green-Duwamish, Puyallup, and Nisqually) regions of Puget Sound, while north-central Puget Sound (e.g., Skagit, Stillaguamish, and Snohomish) has less of a hatchery influence. The Strait of Juan de Fuca has more hatchery influence with respect to coho than chinook, while Hood Canal is the opposite. Chinook salmon abundance appears to be closely correlated with hatchery effort, with greater abundance for stocks that have a large hatchery component than for those which have little influence from hatchery programs (Compare Figures 9 and 10) (Meyers et al. 1998).

The overall influence of hatchery salmonids on genetic diversity to Puget Sound has been similar for chinook, coho, and steelhead, because most of the hatchery-introduced species have been a within-Puget Sound transfer of stocks between river basins. Many of the chinook hatchery fish within Puget Sound are inter-watershed stock transfers from the Green River Hatchery, which has been ongoing since the early 1900s (Meyers et al. 1998). As late as 1995, 20 hatcheries and 10 net-pen programs were regularly releasing Green River Hatchery chinook in locations throughout Puget Sound (Marshall et al. 1995). The extensive use of Green River fall chinook has had an impact on among-stock diversity with the South Puget Sound, Hood Canal, and Snohomish stocks, and may have also impacted genetic diversity elsewhere in Puget Sound and the Strait of Juan de Fuca (Marshall et al. 1995) by reducing the genetic diversity and fitness of the naturally spawning chinook populations (Meyers et al. 1998). Only recently have stock integrity and genetic diversity become part of chinook management objectives (Meyers et al. 1998).

Similar to chinook, most coho salmon stock transfers have been derived from within the Puget Sound, although some stocks have been imported from the Columbia River and Olympic Peninsula (Weitkamp et al. 1995). Artificial propagation of coho salmon appears to have had a substantial impact on native, natural coho salmon populations, to the point that the NMFS Biological Review Team had difficulty identifying self-sustaining, native stocks in the Puget Sound (Weitkamp et al. 1995). Most steelhead hatchery transfers to Puget Sound Rivers come from two stocks—one within Puget Sound and the other from the Columbia River (Crawford 1979). Hatchery fish are considered a major threat to the genetic integrity of Puget Sound steelhead (Busby et al. 1996).

Hatcheries have also been identified as a potential factor in the change of the size of Puget Sound salmonids. Between 1972 and 1993, the average size of coho caught in the final fishery before entering their natal streams (terminal landings) has decreased from 4 kg to almost 2 kg, which could result from several causes including hatchery influence (Weitkamp et al. 1995). This size reduction can seriously reduce fecundity and fitness of naturally spawning fish (Weitkamp et al. 1995).

Non-native Species

Non-native species interaction first occurs at the habitat-unit scale and can alter the habitat and trophic interactions of different ecological communities. For example, *Spartina* spp., a cordgrass indigenous to the Eastern United States and the Gulf Coast, can alter mudflats in the Pacific Northwest into salt marshes and subsequently alter primary productivity, food-web dynamics, and overall community composition by out-competing native flora (Feist and Simenstad 2000). Another example of non-native species interaction at the habitat-scale is that between brook trout (*Salvelinus fontinalis*) and juvenile chinook salmon in the Salmon River basin, Idaho. The survival of juvenile chinook salmon was two times greater when non-native brook trout were absent and was positively associated with habitat quality; conversely, when brook trout were present, there was no relationship between habitat quality and juvenile chinook survival (Levin et al. in press). Thus the effects of non-native species interaction with native salmonids masked any effect of habitat quality on juvenile chinook survival. Little is known with respect to the impact of non-native species on salmonids in Puget Sound, but completed studies suggest that the habitat scale is where most of the interaction occurs (Fayram and Sibley 2000).

An example of habitat-scale interactions between non-native and native species that can scale up to the reach or watershed level in Puget Sound is cutthroat trout (*O. clarki*) and coho salmon competition in Huckleberry Creek, a tributary to the Deschutes River in south Puget Sound. Coho salmon are non-native to the Deschutes River, but they now occupy areas throughout the entire watershed (Haring and Konovsky 1999). Cutthroat trout occur in high densities only in those portions of Huckleberry Creek where coho salmon densities are low, which may be due to several reasons, including competition for food or space resources (Figure 11A) (Fransen et al. 1993). Time series data from Huckleberry Creek show that after adult coho salmon passage was blocked by a landslide in February of 1990, the age-0 cutthroat trout population in-

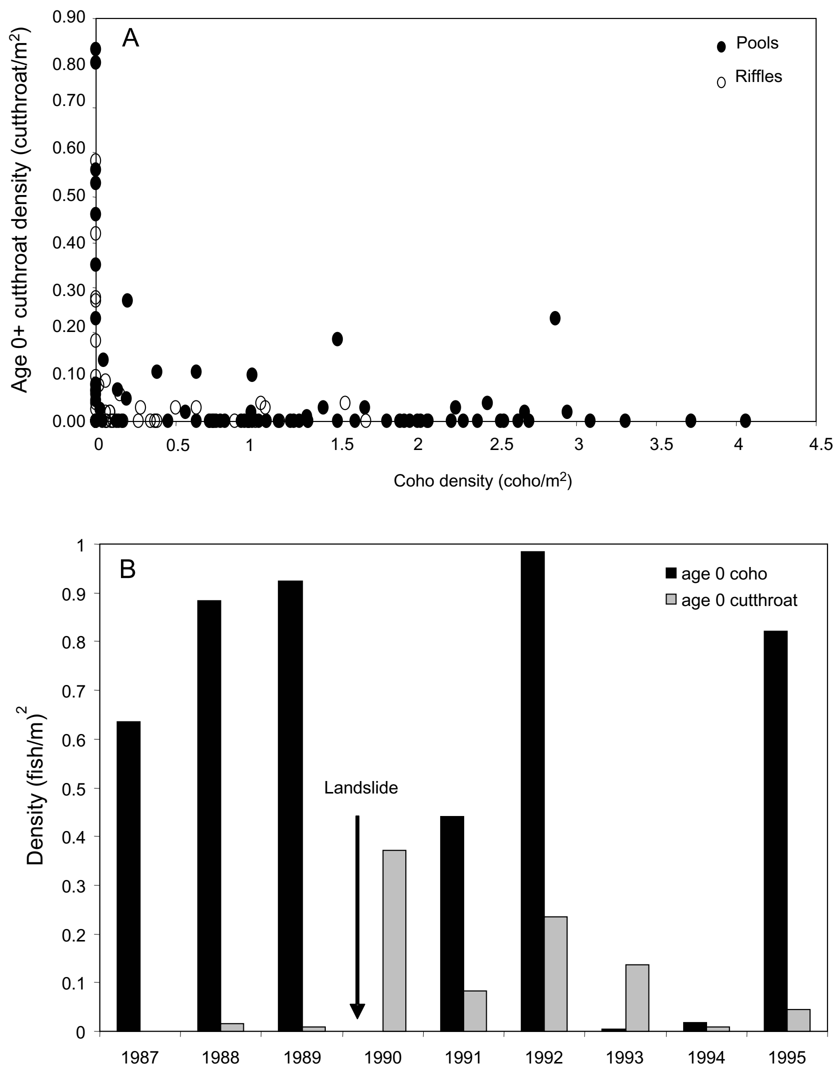

Figure 11. (A) Density of age 0+ cutthroat and juvenile coho salmon for 100 habitat units in Huckleberry Creek, Deschutes River, South Puget Sound. (B) Average density of age 0+ cutthroat and juvenile coho salmon from 1987 to 1995 in Huckleberry Creek, Dechutes River, South Puget Sound. Data from Fransen et al. (1993).

creased dramatically the following spring and remained a more conspicuous component of the fish community for several years afterwards, even though adult coho were moved around the landslide deposit by fall of 1990 (Figure 11B) (Fransen et al. 1993).

Conclusions

Habitat isolation and degradation, the harvest of salmonids, hatchery practices, and the introduction of non-native species over the last 150 years have affected the distribution and abundance patterns of Puget Sound salmonids. Many of these alterations, particularly habitat changes, begin at the habitat scale but are eventually seen at the reach, watershed, and regional scales. Historic availability of different habitat types such as forested floodplain, freshwater wetlands and off-channel habitats, and estuarine habitats, and the relative losses of each type, varies by river basin in Puget Sound. Species-specific preferences on a habitat and reach scale will also mean differences in salmonid distribution and production potential. Together, the effect of habitat-scale loss will depend upon which habitats were available historically and how salmonids evolved to utilize them. Changes in physical characteristics, such as the quality of current instream and off-channel conditions, or the hydrologic alteration of wetlands due to land-use practices, have also changed the abundance of some salmonids.

Large-scale shifts in the biogeography of salmon in the Pacific Northwest seem to correlate with salmon harvest practices. Today a larger percentage of salmonids are found farther north in their range than 150 years ago. Harvest has had more of an effect on abundance in the Puget Sound, while hatcheries seems to have had an effect on abundance, distribution, and phylogenetics. Hatchery fish now comprise the majority of chinook, coho, and steelhead produced in Puget Sound, and they have altered the distribution of salmonids towards the south Sound. Less is known about the effects of non-native species on salmon biogeography, although the documented interactions also seem to occur at the habitat scale.

In combination, the wide variety of natural and anthropogenic influences on salmonid biogeography indicate that a broad level of understanding should underlie salmon recovery efforts. In particular, we need to understand the historic types, abundance, and distribution of both salmon and their habitats, how such distributions have changed to the present, and the nature of the natural processes or human actions that have triggered such changes. Most importantly, the wide range of influences on salmonid biogeography mean that development of restoration (or rehabilitation) goals requires such understanding for the paticular river system of interest and for the species of interest.

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