Return to Table of Contents
Go to Next Chapter

CHAPTER 4. DIVERSITY, STRUCTURE AND STATUS OF SALMONID POPULATIONS

> *" There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; . . . from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."*
> Charles Darwin. 1859. The Origin of Species. Penguin Books, Baltimore.
>
> *"Nothing in Biology makes sense except in the light of evolution."*
> Theodosius Dobzhansky. 1973. Nothing in biology makes sense except in the light of evolution. American Biology Teacher 35**:** 125-129.
>
> *" . . . evolution was not a change in gene frequencies, but the twin processes of adaptive change and the origin of diversity."*
> Ernst Mayr. 1991. One long argument: Charles Darwin and the genesis of modern evolutionary thought. Harvard University Press, Cambridge, Mass.

In this chapter, we briefly review the status of the native salmonids of the Columbia River, with an emphasis on the diversity observed within and among populations and species. Salmonids are well-recognized for their diversity of life history strategies, ecological adaptations, and genetic variation. These factors are thought to be linked to salmonid productivity and to long-term fitness and persistence. The chapter is organized into two major sections. In the first section, we provide background information on the stock concept, metapopulation organization, and the genetic structure of salmonid populations. In the second section, we describe the status of salmonid species in the Columbia Basin.

The Stock Concept

Diversity is an inherent attribute of salmonids in naturally functioning ecosystems (Groot and Margolis 1991; Taylor 1991; Behnke 1992; Soverel 1996). Salmonid diversity is expressed as population, life history, and genetic diversity and results in part from the ability of salmonid fishes to adapt to a wide array of habitat conditions (Taylor 1991; Healey 1994). Since habitats vary in space (i.e., from location to location) and through time at each location, diversity is likely not constant but changes as conditions in the environment change. Diversity probably contributes to the resilience and stability of regional groups of salmonid populations.

From the time of Plato until the 19th century, western scientists viewed species as fixed types, based on an idealized set of characters that described each species (i.e., the Essentialists' view). Individual variation from this fixed type or ideal was viewed as an error attributable to developmental processes. Thus, biological diversity within a species had little positive meaning.

The transition from the concept of species as a fixed type, to species being comprised of many populations, each containing individuals that vary slightly from each other, was a major advancement in biology. It was this shift that gave Charles Darwin the point of view he needed to see the struggle for existence taking place between individuals and not species. Population thinking paved the way for Darwin's work on natural selection and the revolution of biological sciences that followed (Mayr 1982).

A population, or stock, can be defined as a self-sustaining breeding group within a species that is relatively reproductively isolated from other breeding groups (Ricker 1972). In population biology, this is also called a deme. However, the term population has been used to define other kinds of aggregations of plants and animals. For example, fishery managers often define a stock as all the fishes of a species in a management area whose boundaries are set for administrative or regulatory purposes. Administrative and biological definitions of stock often come into conflict in salmon management. The implications of that conflict are discussed later in this section. The generally accepted definition of a salmon stock comes from Ricker (1972):

> *"fish spawning in a particular lake or stream (or portion of it) at a particular season, which fish to a substantial degree do not interbreed with any group spawning in a different place, or in the same place at a different season".*

Stock Concept in Fisheries

Population thinking was recognized earlier, and has undergone greater development in fisheries than in any other field of biology (Sinclair 1988). All species of fish do not have the same level of complexity in their population structure. A comparison of population richness among marine fish species from the north Atlantic (Table 4.1) placed Atlantic salmon at one end of the range (a large number of populations) and the European eel at the other end (single population) (Sinclair and Iles 1989). Pacific salmon would fall on the left-hand side of Table 4.1 at a level similar to the Atlantic salmon (Ricker 1972).

Table 4.1. The continuum of population richness in anadromous and marine species in the northern Atlantic. (Source: Sinclair and Iles, 1989).

Atlantic salmon (**Decreasing population richness → → → → → →)**
Atlantic shad
Atlantic Herring
Atlantic cod
rainbow smelt
haddock
Atlantic mackerel
Atlantic menhaden
European eel

Stock Concept in Pacific Salmon

Not long after Pacific salmon came under commercial harvest, careful observers on the West Coast recognized that salmon from different rivers varied in important life history or morphometric characteristics. R. D. Hume, who operated salmon canneries in California and Oregon and was an early proponent of the artificial propagation of salmon, observed in 1893:

> *"The fact that in rivers which enter the sea within a few miles of each other, as well as the different tributaries of the same river, the fish (salmon) will have local characteristics which enable those who are familiar with the various streams to distinguish to which river or tributary they belong.*
>
> *I firmly believe that like conditions must be had in order to bring about like results, and that to transplant salmon successfully they must be placed in rivers where the natural conditions are similar to that from which they have been taken"* (Hume 1893).

After reviewing the results of tagging experiments which supported the hypothesis that Pacific salmon homed to their natal stream, Rich (1938) concluded that the species of Pacific salmon were divided into local populations:

> *"In the conservation of any natural biological resource it may, I believe, be considered self-evident that the population must be the unit to be treated. By population I mean an effectively isolated, self perpetuating group of organisms of the same species. Given a species that is broken up into a number of such isolated groups or populations, it is obvious that the conservation of the species as a whole resolves into the conservation of every one of the component groups; that the success of efforts to conserve the species will depend, not only upon the results attained with any one population, but upon the fraction of the total number of individuals in the species contained within the populations affected by the conservation measures."*

At least some fish culturists recognized the implications of stock structure as early as 1939 and realized that the transfer of salmon between rivers was not a desirable management activity (Oregon Fish Commission 1933). Although conclusive proof was lacking, biologists working in the Columbia Basin began to recognize that the salmon species were composed of populations adapted to their local habitat (Craig 1935). Management had to take each population into consideration if it was going to be successful.

> *".... knowing further that each race is self-propagating, it becomes perfectly apparent that all parts of the salmon run in the Columbia River must be given adequate protection if the run as a whole is to be maintained. The protection of only one or two portions of the run will not be sufficient, inasmuch as certain races will be left entirely unprotected."* (Oregon Fish Commission 1931).

Elements of a conceptual foundation that recognized the importance of stocks and local adaptation emerged in the 1930s (Rich 1938). However, progress in this direction was truncated by the development of the hydroelectric potential of the basin and the plan devised to mitigate for that development, the Lower Columbia River Fishery Development Program (LCRFDP). Although the LCRFDP had six phases, the overall approach was to shift salmon and steelhead production to the lower river below the proposed McNary Dam. The desired level of production would be achieved by a combination of enhanced lower river stocks and the transfer of upper river stocks to the lower river (Laythe 1948). The belief that such a transfer could be successful seems to contradict the understanding biologists had at the time regarding the importance and management implications of the stock structure of Pacific salmon. It should be noted that the Fraser River restoration program initiated a few years before the LCRFDP did emphasize the importance of individual stocks.

> *"Management of the Fraser River sockeye population by individual genetic races was developed and perfected by the commission (International Pacific Salmon Fisheries Commission). This management philosophy was an important component of the rehabilitation of the runs in combination with the contribution of fishways and commercial fishing closures"* (Roos 1991).

The importance of stock structure in salmon management received renewed emphasis in the late 1960s and early 1970s (Calaprice 1969; Paulik 1969; Ricker 1972). The Endangered Species Act (ESA) focused attention on the stock structure of Pacific salmon in the Columbia River in the late 1980s up to the present. Recently, stocks of Pacific salmon have been inventoried and their status described (Howell et al. 1985; Nehlsen et al. 1991; Washington Department of Fisheries et al. 1993; Washington Department of Fish and Wildlife and Oregon Deptartment of Fish and Wildlife 1994; Huntington et al. 1996).

Scientists often refer to local adaptation in salmon populations, although the evidence for it is circumstantial (Taylor 1991). The term local adaptation can be misleading if adaptation is interpreted to occur only to a specific local environment, such as a spawning area in a tributary stream, rather than to all the habitats in which salmon complete their life cycle. Although salmon exist in populations that typically home to their natal stream and spawn in relative isolation from other salmon populations, they are adapted to the habitats (river, estuary, and ocean) where individuals in a population complete their life cycles, as well as to the variability that occurs in these habitats over both short- and long-term time scales. Such variation encompasses annual and decadal variations in climate, ENSO's (El Nino-Southern Oscillations), and geologic events.

Salmonid Life Histories and Habitat

Adaptation to the locally varied habitat may be expressed through variation in life history traits, although not all variation in traits among populations is adaptive. A trait exhibited by a local population is adaptive if it has a genetic basis and if it enhances survival or reproductive success (Taylor 1991). Life histories are comprised of demographic traits such as age at maturity, mortality schedules, size, and growth (Stearns 1995). Salmonid life history traits also include: a) the age and size that juveniles migrate within the river system (resident, riverine), into lakes (resident, adfluvial) or to the sea (anadromous); b) growth and maturity during riverine and laucustran migrations; c) spawning habitat preferences; d) emigration patterns; and e) age and timing of spawning migration. Many of these traits vary in response to environmental variation. For successful completion of the life history, quality habitat must exist for each life stage or mortality ultimately will exceed productivity and that life history type will be extinguished. In tributaries flowing through the shrub and shrub-steppe region of the Columbia river basin, the loss of summer migrating underyearling chinook salmon due to habitat degradation may have been a major cause of decline in spring and summer chinook salmon (Lichatowich and Mobrand 1995).

Salmon habitat simply may be thought of as seasonally important places where salmon carry out their life histories (Thompson 1959). The presence of these places is important, but so is the ability to move between them at appropriate times. Complex habitats with a high degree of spatial and temporal connectivity permit the development and expression of life history diversity, which is an essential component of salmonid productive capacity. In a life history context, salmon restoration implies re-establishment of life history diversity.

Stock Conservation

While the conservation of local populations or stocks of Pacific salmon and the preservation of their genetic resources is an important goal (Riggs 1990; Altukhov and Salmenkova 1991; Kapuscinski et al. 1991), achieving that goal is not simple or easy. Merely verifying that a local stock has different traits (size, time of spawning, time of juvenile migration, etc.) compared to other nearby stocks is not sufficient, but it is a good start. Documenting that the observed differences between populations is adaptive requires that the trait's genetic basis be documented. Variation in the trait must be related to differences in survival or reproductive success among individuals in a common environment, and the mechanism which maintains the trait in the population must be demonstrated (Taylor 1991). These are not easy criteria to meet.

One might assume, since the extinction of a stock could represent a substantial loss of genetic diversity, managers would give evidence of local adaptation, even circumstantial evidence, the benefit of the doubt when setting stock boundaries. However, the size of a stock's boundary can have critical impacts on management programs. Narrowly defined boundaries complicate or prohibit harvest management in marine and lower river areas where stocks are mixed, and they restrict the use of hatchery fish in outplanting programs.

The need to conserve biodiversity between and within locally adapted stocks of salmon and the conflict between that goal and traditional management programs has created two strongly held positions characterized by the terms "lumpers or splitters”. Lumpers tend to see a few large stocks, whereas splitters tend to see a large number of small stocks. Driving this debate is the underlying question: How much weight should we give to management strategies, as opposed to biological criteria, when setting stock boundaries? Biologists that manage salmon harvest and hatchery programs often define stocks as aggregates of populations (Thompson 1965; Wright 1965). Traditional harvest and hatchery practices based on that approach have contributed to a homogenization of the genetic differences between stocks (Calaprice 1969; Nelson and Soule 1987; Reisenbichler and Phelps 1989), reduced the productivity, and have threatened the existence of populations in smaller, less productive streams (Ricker 1958; Thompson 1965; Wright 1993).

To a large degree, the debate over the size of stock boundaries is driven by the search for the "ideal" stock designation. Managers are looking for stock boundaries that lead to the conservation of biodiversity and at the same time conveniently fit into existing harvest and hatchery management strategies.

However, there is no ideal stock designation. Even the definition used by Ricker (1972) leads to different interpretations because there is so little hard information on reproductive isolation or genotypic or phenotypic descriptions of spawning aggregations of salmon, particularly in the smaller streams. In addition, the species of Pacific salmon are organized in a hierarchical structure (this chapter, below). The biological units in the hierarchy (species, population or stock, subpopulation, individual) and their associated geographical units (region, river, tributary and redd) persist for different time intervals. The objective for most management actions should be to select the most inclusive population/geographic unit for which a management action will not cause the loss of genetic diversity contained in less inclusive groups (Mundy et al. 1995b).

The debate over the home stream theory has been settled for several decades, but the stock concept still stimulates debate. Now the debate is over the methods and criteria used to identify stocks (stock boundaries). The Council's Fish and Wildlife Program (1994) calls for a study to identify criteria for setting stock boundaries (7.1c.1). The debate between "lumpers" and "splitters" is likely to intensify with the implementation of that measure.

The biological implications of the stock concept to fisheries management are profound. Disregarding the smaller populations or managing them collectively as we often do in our mixed stock salmon fisheries, can lead to disintegration of the stock system (Altukhov 1981). It is important to consider the fate of small subunits of a stock during management of routine harvest, hatcheries, river flows, and habitat protection. It is also critical that they be considered during years of crisis (Thompson 1965; Paulik 1969). For example, during periods of sustained drought, focusing management entirely on the larger stocks or stock aggregations will quickly drive the smaller subpopulations to extinction. The small populations that inhabit the marginal habitats within the range of a metapopulation may be an important source of genetic diversity of the species (Mayr 1970; Scudder 1989). W. F. Thompson (1965) described the problem thirty years ago:

> *"We regulate our fisheries. But we concentrate them on the best races and one by one these shrink or vanish and we do not even follow their fate because we have not learned to recognize their independent component groups or to separate them one from the other. We continue our unequal demands, knowing only that our total catches diminish, as one by one small populations disappear unnoticed from the greater mixtures which we fish".*

Salmonid Metapopulations

The metapopulation concept is a relatively new approach to various issues in population biology (Hanski and Gilpin 1997) and has important management and conservation implications for Columbia River and Pacific Northwest salmonids. Two key assumptions drive the metapopulation approach. The first is that populations are spatially structured into assemblages of local breeding populations (i.e., the metapopulation), while the second is that migration among the local populations has some effect on local dynamics, including the possibility of population reestablishment following extinction (Hanski 1991; Hanski and Gilpin 1991; Hanski and Gilpin 1997).

Metapopulation structure is likely in salmonids (Rieman and McIntyre 1993; Mundy et al. 1995b; Schlosser and Angermeier 1995; National Research Council (NRC) 1996) because adult salmonids display high fidelity of homing to their natal streams (Helle 1981), while at the same time exhibiting relatively low, but variable levels of straying. Metapopulation structure is thought to be hierarchical in nature, and in Columbia River salmonids, may exist at various scales ranging from linkages among populations within a tributary of a watershed, to aggregations at the subbasin or even ecological province level (NPPC 1997; NPPC 1998). Linkages among populations are likely to be the strongest at the smallest geographic scale, because dispersal among local populations is more likely than dispersal between geographically distant populations. The persistence of a metapopulation is determined by the balance of local population extinction and re-establishment of extinct populations through recolonization. Dispersal from neighboring local populations functions in recolonization of habitats where local extinction has occurred.

Recent studies suggest that salmonid metapopulations may maintain core-satellite (mainland-island) structures (Rieman and McIntyre 1993; Li et al. 1995a; Schlosser and Angermeier 1995). Core populations are generally persistent, large, productive populations occupying high quality habitat. In contrast, satellite populations generally are less abundant, occupy lower quality habitats, and are more vulnerable to extinction (Diamond 1984; Hanski 1991; Harrison 1991; Schoener 1991; Harrison 1994).

Core populations can buffer metapopulations against environmental change and contribute to the resiliency of regional salmonid production. Core populations also serve as important sources of colonists (Harrison 1991; Schoener 1991; Rieman and McIntyre 1993; Harrison 1994; Schlosser and Angermeier 1995) that reestablish satellite populations in habitats where extinction had occurred and sustain populations whose abundance had been severely depleted, i.e., the "rescue effect" (Brown and Kodric-Brown 1977; Gotelli 1991). Rescue effects may be particularly important for the persistence of smaller populations where environmental variation is high causing high variability in demographic parameters (Stacey and Taper 1992).

Spatial and temporal variation in habitat shapes metapopulation structure (Frissell et al. 1986; Reeves et al. 1995; Schlosser and Angermeier 1995). The mosaic of alluvial and constrained reaches within watersheds, as described earlier in this chapter, influences the spatial distribution and proximity of local spawning populations (Schlosser and Angermeier 1995; Rieman and McIntyre 1996; Stanford et al. 1996). Moreover, favorability of connecting habitats influences the ability of dispersing individuals to move successfully among habitats (Rieman and McIntyre 1993; Li et al. 1995a; Rieman and McIntyre 1995; Schlosser and Angermeier 1995).

Spawning populations with the highest abundances likely occurred historically in alluvial segments with well-developed floodplains and gravel bars (Stanford et al. 1996). These areas provide a complex habitat mosaic highly suitable for spawning, egg incubation, and juvenile rearing and may have functioned as centers of habitat stability. Channel morphology and hydraulics suggest that habitat in the lower reaches of streams is more stable than in smaller streams in the upper parts of watersheds (Naiman 1992). Productive populations spawning in large alluvial mainstem reaches may have functioned as critical core populations (Stanford et al.

1996). At a larger spatial scale, an entire watershed may function as a core area for neighboring watersheds within a region (Lindsey and McPhail 1986; McPhail and Lindsey 1986; Rieman and McIntyre 1993; Schlosser and Angermeier 1995).

Geographic Organization of Chinook Salmon

The complex of spatially distributed local spawning populations associated with major subbasins and contiguous areas of the mainstem Columbia or Snake rivers probably formed metapopulations. Fall chinook spawning in mainstem reaches of the Columbia and Snake and the lower reaches of major subbasins could have formed one type of metapopulation, while summer and spring chinook spawning in the upper mainstems of major subbasins and spring chinook spawning in headwater areas could have comprised another type.

Both genetic and life history evidence distinguish spring chinook from fall chinook in the Columbia and Snake basins. Additionally, genetic and tagging data show that Columbia River chinook are well differentiated from Snake River chinook, suggesting significant long-term reproductive isolation between the two groups (Utter et al. 1989; Matthews and Waples 1991; Waples et al. 1991b; Utter et al. 1995). In the Snake River, fall chinook are differentiated from the spring and summer races with respect to life history characteristics such as annual timing of adult migration, geographic distribution of spawning habitat, and genetic attributes (Matthews and Waples 1991; Waples et al. 1991b). French and Wahle (1959) observed summer and spring chinook on the spawning grounds of the Wenatchee and Methow rivers, whereas Mullan et al. (1992b) reported mixing of summer and fall fish on the spawning areas of mid-Columbia river tributaries. In contrast to the Snake River, there has been a tendency to group Columbia River summer chinook and fall chinook because they both migrate downstream as subyearlings.

Historically, chinook population sizes and probabilities of extinction probably varied along a continuum determined in part by habitat size and quality. At one end of the continuum were the large core-type populations spawning in high quality mainstem habitats. Other local populations likely had characteristics similar to satellite populations. Local chinook populations most prone to extinction and probably most variable in abundance may have been those inhabiting smaller streams in arid terrain. In periods of drought, salmon populations inhabiting these streams may have had difficulty in persisting. Chinook populations intermediate in size and sensitivity to extinction may have occupied streams in regions with higher precipitation and streams draining mountainous terrain whose headwaters are in high elevation areas. In these streams, both flows and temperatures may be more suitable for juvenile rearing.

Human Impacts

Extinctions of chinook salmon populations have increased over the last 100 years (Nehlsen et al. 1991; Williams et al. 1992; Frissell 1993b; National Research Council (NRC) 1996) and altered the organization of regional systems of populations in the Columbia basin (Figures 3.4, 3.5, and 3.8 and associated discussion). Fragmentation and degradation of habitat can disrupt regional production and linkages among populations through extirpation of vital core populations and isolation of remaining populations (Rieman and McIntyre 1993; Harrison 1994; Schlosser and Angermeier 1995). As a result, regional production declines and the vulnerability of individual populations to extinction increases (Rieman and McIntyre 1993; Harrison 1994; Li et al. 1995a; Schlosser and Angermeier 1995).

While most fall chinook populations spawning in the mainstem reaches of the Columbia and Snake Rivers have been driven extinct, one remaining viable mainstem population is the fall chinook population spawning in the Hanford Reach (Becker 1985; Geist 1995). This population, averaging 40-50 thousand returning adult fish since the mid-1960's, is the largest naturally spawning population of chinook salmon above Bonneville Dam (see Figure 3.6). It has been stable over the years when populations in other parts of the basin have undergone severe decline (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995). Adult chinook salmon returning to the Hanford Reach area in late September appear to spend up to eight weeks moving throughout the mainstem Snake and Columbia rivers and the lower reaches of adjacent tributary systems (see Figure 3.7). These observations suggest that chinook salmon from the Hanford Reach could function as a core population in the Columbia-Snake river confluence area by providing colonists into adjacent reclaimed habitats if ecological conditions were restored or improved in them.

Regional Stochasticity

The probability of metapopulation extinction is enhanced if the dynamics of local populations and their individual probabilities of extinction become temporally correlated or synchronized (Harrison and Quinn 1989; Hanski 1991). Regional stochasticity refers to the correlated or synchronized dynamics of local populations resulting from the operation of common environmental factors (Hanski 1991). An important consequence of human development in watersheds likely is increased synchrony in the dynamics of naturally and artificially produced salmon.

Regional stochasticity can reduce metapopulation persistence time (Gilpin 1987; Quinn and Hastings 1987; Gilpin 1988; Harrison and Quinn 1989; Hanski 1991; Rieman and McIntyre 1993). Regional stochasticity tends to have less impact on metapopulation persistence when metapopulation size is large (the metapopulation is composed of many local populations), local extinction rates are low, and dispersal is high (Hanski 1989; Harrison and Quinn 1989; Hanski 1991).

Adjacent local populations are more likely to respond synchronously to environmental factors, whereas local populations that are more geographically distant are more likely to experience asynchronous dynamics (Harrison and Quinn 1989; Hanski 1991; Rieman and McIntyre 1993). However, the dynamics of geographically diverse populations can become correlated if, at some stage in their life history, individuals from diverse populations share a common environment, such as the ocean or a common migratory pathway (Rieman and McIntyre 1993).

Salmon likely experience some degree of synchrony in dynamics due to the effects of natural environmental factors acting on regional scales in the ocean and in freshwater. Historically, if natural extinction rates in most local populations of salmon were relatively low, as they appear to be for many vertebrates (Schoener 1983; Harrison and Quinn 1989; Schoener 1991) and metapopulation size was large, theoretically salmon could withstand the impacts of regional stochasticity (Harrison and Quinn 1989). Synchrony also could be reduced if diverse populations or life history types migrated through mainstem areas at somewhat different times. For example, downstream migration of juveniles through the mainstem Columbia River historically appears to have occurred throughout the year, but is now restricted to specific periods during the late spring and summer (Lichatowich and Mobrand 1995). Deleterious effects of environmental correlation among habitats also could be moderated if individuals within each local population responded differentially to the same set of environmental conditions, inducing a kind of within-population asynchrony.

Human activities have not only increased extinction rates of local salmonid populations (Nehlsen et al. 1991; Williams et al. 1992; Frissell 1993b; National Research Council (NRC) 1996), but they probably also synchronized the dynamics of remaining populations and thus, rendered regional metapopulations more susceptible to extinction (Rieman and McIntyre 1993). For example, land use activities can have pervasive, region-wide effects on geographically diverse local populations (see Chapter 5). Synchrony can also be induced in common migratory pathways and the ocean as a result of mortality due to excessive harvest, construction of dams, and degradation of mainstem habitats. Synchrony may be more likely if migration timing of diverse populations is seasonally restricted. Moreover, over the last century, extinction rates have been elevated by human development of the basin, and local population and metapopulation sizes and dispersal rates have been reduced, possibly making salmon more susceptible to the effects of correlated natural environmental changes (Harrison and Quinn 1989).

Redd counts in index areas of the Imnaha and Grande Ronde rivers and their tributaries suggest that some local spring chinook populations have been experiencing synchronous decline since the late 1960's - mid 1970's (see Figure 3.9). Since the habitat where these stocks spawn is of relatively high quality, and considering that the Wenaha River (a tributary of the Grande Ronde River) is nearly entirely within a wilderness area, the synchronizing influence is likely downstream from the spawning areas, either in lower mainstems of the Grande Ronde and Imnaha, in the mainstem Snake or Columbia River, or in the ocean.

Human impacts may have shifted metapopulation structure from core-satellite to non-equilibrium metapopulations. In non-equilibrium metapopulations, extinction rates are consistently greater than recolonization rates and the metapopulations are undergoing regional decline (Harrison 1991). Once stabilizing core populations have been driven extinct, recolonization and re-establishment of extinct local populations is limited or does not occur, and only isolated satellite populations remain. Isolated populations have little chance of being refounded after a local extinction compared to a population that is close to other populations. As populations become isolated, local extinctions become permanent and the entire metapopulation moves incrementally toward extinction (Rieman and McIntyre 1993).

Conclusions for Metapopulations

1. The metapopulation concept, a spatially-structured system of local populations connected to some degree by dispersal, offers a different paradigm for understanding salmon life histories, population dynamics, and population persistence. Although largely untested and still developing theoretically, metapopulation structure, is a logical construct derived from the natural life history attributes of salmon, which include high homing fidelity to natal streams and low dispersal between populations, which results in local adaptation and genetic divergence among populations in a watershed.

2. We hypothesize that the large chinook populations that existed historically in the mainstem Columbia and upper Snake Rivers may have formed core populations for regional metapopulations. Core populations are large productive populations with low probabilities of extinction, that may have served to stabilize regional salmon production and probably functioned as source populations for recolonization of less favorable habitats where satellite populations occurred.

3. Human development has altered the organization of salmon populations, and consequently has probably altered metapopulation organization. This has very likely caused losses in resilience, life history diversity, and adaptive capacity, and has resulted in a reduction in regional stability of production.

4. Present restoration efforts have focused primarily on remaining satellite populations, which are smaller and less productive and may have higher probabilities of extinction than core populations.

5. Human development and management actions have increased the potential for synchrony among geographically diverse local populations and may have rendered present metapopulation organization more sensitive to the effects of regional stochasticity by reducing metapopulation size, increasing local population extinction rates, and reducing dispersal between populations.

Genetic Structure of Anadromous Salmonid Populations

> *"Sustainable increases in salmon and steelhead productivity in the Columbia River Basin can only be achieved if the genetic resources required for all forms of production, present and future, are maintained in perpetuity."*
>
> Riggs, Larry A. 1990. Principles for Genetic Conservation and Production Quality. Northwest Power Planning Council, Portland.

Anadromous salmonids occur widely throughout the Northern Hemisphere in river systems north of approximately 40^{o}N latitude. Native species in the genus *Salmo* occur across the northern arc of the Atlantic basin, while species in *Oncorhynchus* occur throughout the northern arc of the Pacific Basin. Species in *Salvelinus* occur in both Atlantic and Pacific Basin river systems. As a group, the salmonid species exhibit a remarkable range of diversity in life history characteristics, ecological attributes, and molecular genetic variability (Groot and Margolis 1991; Taylor 1991; Quinn and Unwin 1993). Although the exact mechanisms and relationships are poorly understood, genetic diversity is recognized as a major contributor to productivity, fitness, and adaptability (Allendorf and Leary 1986; Quattro and Vrijenhoek 1989; Liskauskas and Ferguson 1991; Beatty 1992). Therefore, it is important to understand how genetic variation in salmonids is structured within each species and among its populations, in order to preserve existing genetic diversity and to insure the persistence of evolutionarily derived aggregates of populations (Allendorf and Phelps 1981b; Allendorf and Phelps 1981a; Allendorf and Leary 1988; Allendorf and Waples 1996). The importance of local adaptation, and the microgeographic scale under which it may occur (Philipp and Clausen 1995), is only now receiving increasing attention, in spite of its recognition by early fisheries managers (Rich 1939; Schuck 1943). Increasing recognition is also occurring that a biologically and economically feasible way to increase salmonid production is to utilize the natural productive capacity of existing native stocks that are adapted to their local environments, rather than attempting to rely on hatchery-reared fish that may not be adapted to specific local environments for production boosts.

Significant population genetic research, most of it relying on allelic variation at protein coding loci (i.e., allozymes), has occurred on salmonids in the last twenty years. These studies have described general patterns of genetic variation that are common to both anadromous and resident forms of salmonids. More recent direct analyses of mitochondrial and nuclear DNA, while frequently providing additional resolution beyond that provided by allozyme analysis, have largely revealed the same general principles of genetic structure within and among populations.

General Patterns

Due to the commercial value and problems related to harvest, culture, and conservation (Utter 1991), considerable effort has been directed into large-scale genetic studies of Pacific salmonids. The initial purpose of these studies was to identify genetic differences among geographic populations within different species, such that samples from a mixed stock fishery as typically occurs in ocean catches could be examined for contributions by each of the geographic populations (Fournier et al. 1984; Milner et al. 1985; Utter et al. 1987; Shaklee et al. 1990; Utter and Ryman 1993). An extensive multi-agency program has resulted in the creation of very large datasets that can be used to assess genetic structure within some species over much or all of their natural distributions. For example, geneticists from a number of federal, state, and provincial agencies, as well as universities, have compiled a dataset for chum salmon (*O. keta*) that examines 50-75 gene loci from over 150 populations throughout the Pacific Rim (Washington, British Columbia, Alaska, Russia, and Japan) (Beacham et al. 1985; Kondzela et al. 1994; Phelps et al. 1994; Wilmot et al. 1994; Winans et al. 1994; Phelps et al. 1995).

Such studies of genetic variation commonly indicate strong patterns of geographic structuring in salmonid species (Allendorf and Utter 1974; Allendorf and Utter 1979; Loudenslager and Gall 1980; Stoneking et al. 1981; Utter et al. 1989; Bartley and Gall 1990; Gall et al. 1992; Bernatchez and Dodson 1994; Kondzela et al. 1994; Phelps et al. 1994; Shaklee and Varnavskaya 1994; Varnavskaya et al. 1994a; Wood et al. 1994). Geographically adjacent populations are typically less distinct from one another than from geographically distant populations based on suites of molecular genetic characters. Thus, genetic structuring among most salmonid species is hierarchical in nature, with the first level of differentiation occurring as geographical aggregates of populations (Figure 4.1).

Phylogenetic or evolutionary analysis of such data often reveals that the primary geographic groupings correspond to major evolutionary or ancestral lineages within each species (Utter et al. 1989; Busack and Shaklee 1995; Utter et al. 1995; Williams et al. 1997). These lineages reflect clear evolutionary divergence from other lineages within the species as a result of genetic differences that have accumulated over evolutionary time between the lineages. For example, pink salmon (*O. gorbuscha*) can be separated into two major evolutionary lineages, based on even-year and odd-year occurrence (see species summaries below). The two lineages exhibit large genetic differences that are an expected consequence of the rigid two-year life history of pink salmon leading to the nearly complete reproductive isolation of the even- and odd-year broodlines.

Below the level of the major evolutionary lines, salmonid species exhibit further genetic structuring that is also typically geographic in nature (Figure 4.1). The major evolutionary lines shown in Figure 4.1 are equivalent to the major ancestral units of Utter et al. (1995) and the major ancestral lineages (MALs) of Busack and Shaklee (1995).

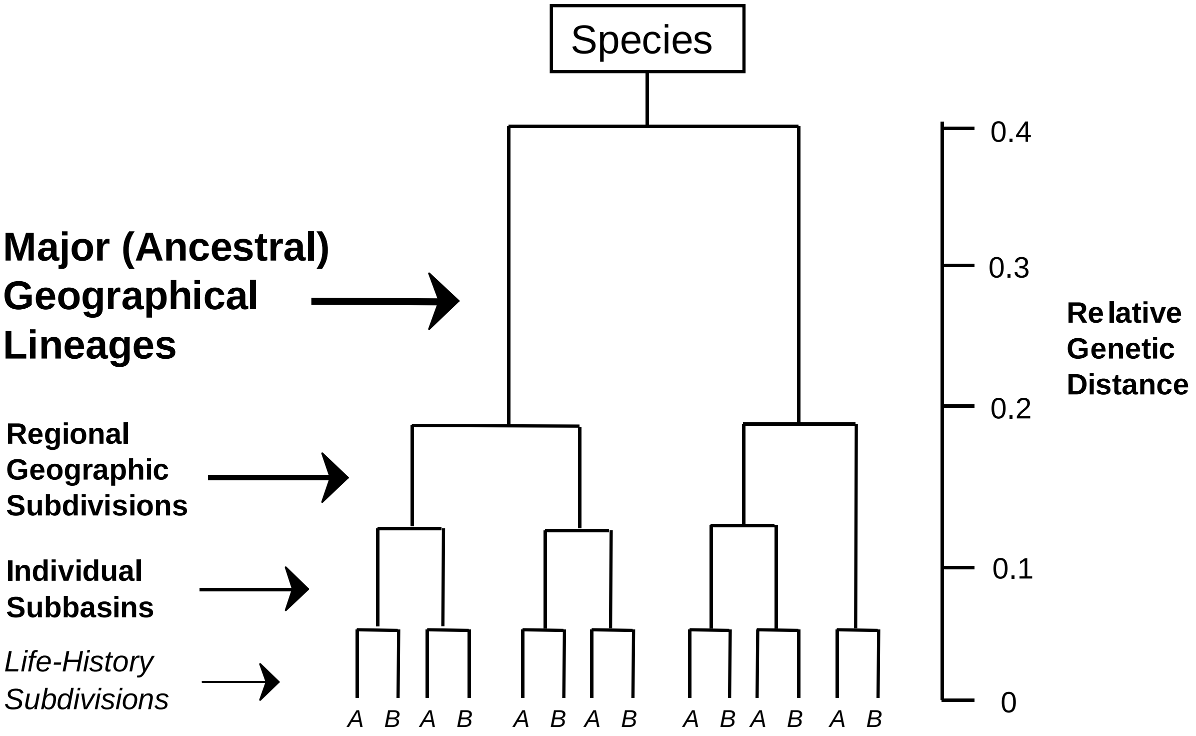


Figure 4.1. Conceptual diagram of the hierarchical genetic structuring in salmonids from species down to the local population level (Utter et al. 1989).

Such regional differentiation has been observed in chum salmon in Washington (Kondzela et al., 1994), British Columbia (Beacham et al. 1985), Alaska (Phelps et al. 1994; Wilmot et al. 1994), and the western Pacific Basin (Russia and Japan) (Winans et al. 1994), where populations clustered on the basis of major islands, major river systems, and along major contiguous coastlines.

Typically, the next level of genetic structuring observed in salmonids is that of the individual watershed or subbasin, within which populations are usually closely related to one another (Figure 4.1; Utter et al., 1989). Nevertheless, populations within an individual subbasin may exhibit diverse life history strategies that include differences in run-timing, age and size at maturity, etc. Presently, we do not know the lower limit of genetic structuring within salmon populations (Utter et al. 1993); however, recent work by Gharrett and colleagues (Gharrett and Smoker 1991; Gharrett and Smoker 1993) on pink salmon in a small creek near Juneau, Alaska, has revealed heretofore unexpected levels of genetic substructuring within a single salmon population.

Although salmonids are known for their ecological and behavioral plasticity, results such as these suggest a very strong role for local adaptation (with fitness implications) for many populations.

Genetic Structure of Columbia Basin Chinook Salmon

Genetic structure of individual Columbia Basin salmonid species are presented later in this chapter; however, it is instructive to briefly review the genetic structure of chinook salmon in the Columbia Basin for two reasons. In general, they demonstrate the hierarchical patterns discussed above, however, they also reveal a second specific pattern that that is an exception to the general discussion above that seems to occur only in large river systems.

Across their geographic distributions, chinook salmon form a genetically complex network of populations that are structured primarily on the basis of geography into large regional groups (see Figure 4.2; Wilmot et al. 1994), that correspond to the large regional groups identified for many other Pacific salmon species (Utter et al. 1989).

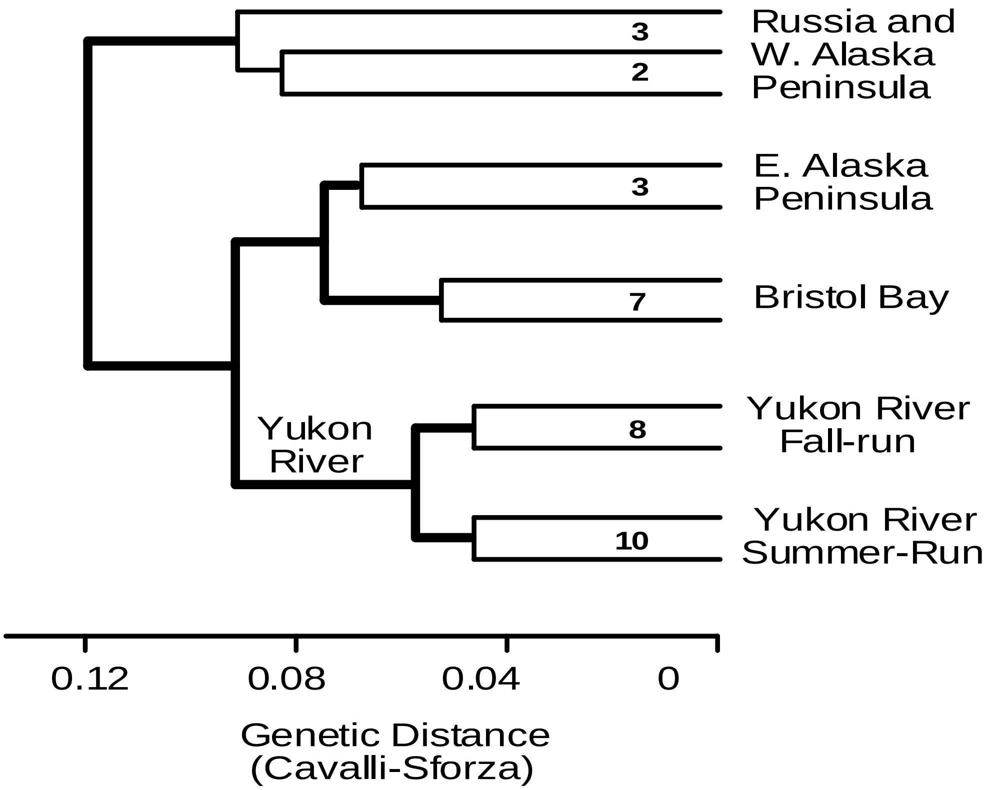


Figure 4.2. An example of geographic structure in the genetic architecture of chinook salmon from North America and Asia surveyed by protein electrophoresis (Wilmot et al. 1994). Numbers on the minor branches equal the number of populations surveyed.

Within the large regional groups, chinook also show substantial geographic substructuring, largely on the basis of subbasins or individual watersheds. Time of adult return to the river was not a major factor in establishing relationships of stocks among areas. Instead, populations with different run timings from the same stream were more similar genetically to one another than to populations with similar run-timing from different areas (Utter et al., 1989). Thus, one major conclusion from these observations is that run-timing differences between stocks within subbasins have evolved via life-history diversification from a single founding stock, regardless of the run timing of the founder stock. Therefore, the seasonal races of chinook salmon that occur in many subbasins have evolved many times as independent events. Evidence from introductions of Pacific salmon into exotic locations further supports this idea. For example, Kwain and Thomas (1984) observed the development of spring-spawning chinook salmon in the Great Lakes from introductions of fall-spawning chinook, while Quinn and Unwin (1993) described five different life history strategies in chinook salmon introduced to New Zealand from a single founding source.

In contrast to the general pattern described above, chinook populations in the upper Columbia and Snake Rivers (Matthews and Waples 1991; Waples et al. 1991b; Utter et al. 1995) exhibit substructuring on the basis of run timing first, then geography (Figure 4.3).

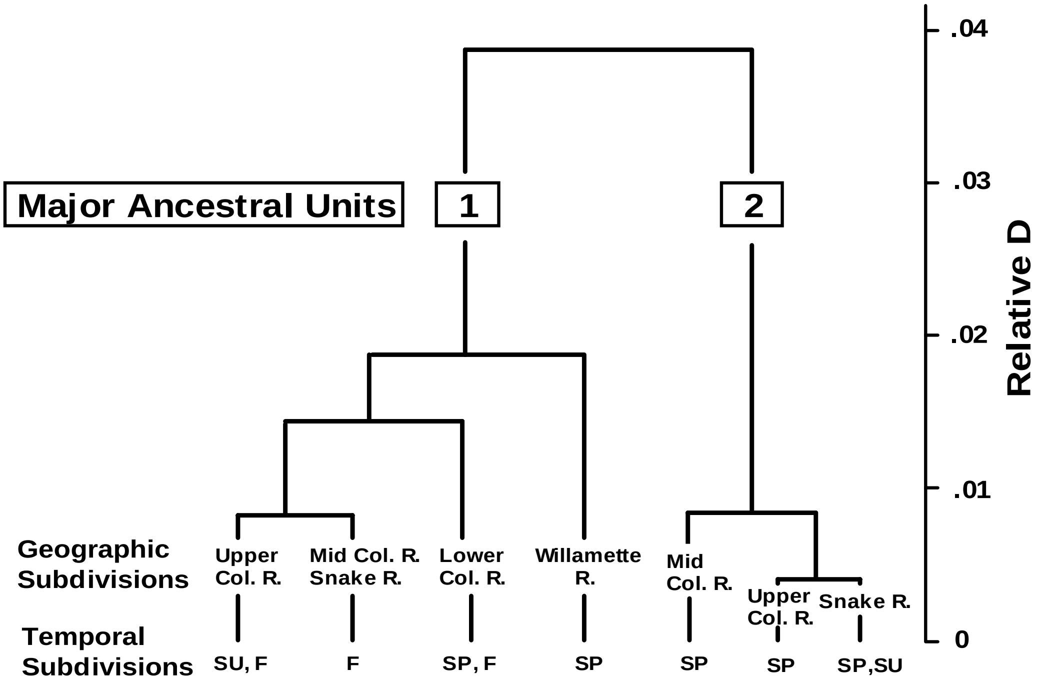


Figure 4.3. Geographic and temporal associations in the genetic structure of chinook salmon populations from the upper Columbia and Snake rivers (Matthews and Waples 1991; Utter et al. 1991; Waples et al. 1991b).

In these instances, populations with similar run-timing were more similar to each other than they were to geographically proximate populations with different run-timing. In the Columbia Basin, these differences result in four distinct evolutionary groupings: (1) Snake River spring and summer chinook; (2) Snake River fall chinook; (3) Columbia River spring chinook; and (4) Columbia River summer and fall chinook.

Run-timing associations among populations, which are not apparent throughout most of the chinook salmon's range, occur in the Columbia and Yukon rivers. These are among the largest of the rivers systems draining into the North Pacific, and their large size and nature may have provided chinook salmon core habitats that were stable over long periods of time, allowing local adaptation and divergence of populations based on run-timing. Because strong heritability is associated with run-timing (Helle 1981), divergence between run types seems likely over evolutionary time. However, the lack of association in run-timing among populations through out most of the chinook salmon's range suggests that the turnover time for populations may be short enough to counteract the processes of local adaptation, isolation, and divergence. This process can be looked at much like ecological succession, where there is an endpoint towards which things move if the system is left undisturbed long enough. However, frequent disturbance events continually reset the system back to or back towards its starting point, which for salmonids is the initial colonization of a watershed. Very large river systems like the Columbia and Yukon, although highly variable temporally, may have allowed long persistence of populations and the emergence of run-timing associations among populations.

Pacific Salmon Species

Pacific salmon, as well as resident salmonids, have disappeared from much of their historic range, and in many locations once abundant populations have been extirpated or are severely depressed. For overviews of the decline and current status of Columbia River basin stocks see Nehlsen et al. (1991), Huntington et al. (1996), and the NRC report (1996).. Detailed status reviews also are available for mid-Columbia and Snake River salmon and steelhead stocks (Craig and Hacker 1940; Chapman et al. 1994a; Chapman et al. 1994b; Chapman et al. 1995). At the present time, only Lewis River (WA) and Hanford Reach (WA) fall chinook, Wenatchee River (WA) sockeye, and five summer steelhead stocks in the John Day River (OR) can be classified as healthy (Huntington et al. 1996). Indigenous resident salmonids are now restricted to 10-30% of their original range (Trotter 1987; Behnke 1992; Quigley et al. 1996). We also review the status of white and green sturgeon and Pacific lamprey in this chapter. These species are important food web corollaries of anadromous salmonids in freshwaters and recovery actions for the endangered Kootenay river sturgeon seem to be at odds with actions for endangered salmon (Marotz et al. 1996).

Chinook Salmon
(***Oncorhynchus tshawytscha***)

Background

Chinook salmon are distributed in Asia from Hokkaido, Japan, north to the Anadyr River, Russia, and on the Pacific Coast of North America from central California to Kotzebue Sound in Alaska (Healey 1991). North of the Columbia River, the post glacial radiation of chinook salmon came from two principal refugia: The two thirds of the Columbia River that remained ice free and Beringia, an ice free area in the lower Yukon River and adjacent coastal areas of the Bering Sea (Lindsay et al. 1986; McPhail and Lindsey 1986). Chinook salmon radiated south from Beringia to about 56^{o}N and chinook salmon from the Columbia River recolonized deglaciated streams north to 56^{o}N.

Chinook salmon may enter rivers of the northwest in any month of the year (Healey 1991). In the Columbia River, the spawning migration is divided into three distinct races: spring, summer and fall. At the present time, the largest run enters the river in the fall. Historically, the spring and summer runs were much larger than they are today, but they were depleted by over harvest and habitat degradation (Chapman et al. 1991; Chapman et al. 1994a; Chapman et al. 1994b; Lichatowich and Mobrand 1995; National Research Council 1995; Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995).

Gilbert (1912) divided the juvenile life histories of chinook salmon into ocean and stream types. The ocean type migrates to sea in the first year, often within three months after emergence. The stream type migrates to sea in the spring after a year or more in freshwater (Healey 1991). The ocean type is the dominant life history in streams south of the Columbia River. Both ocean and stream types occur from the Columbia River north to 56^{o}N with the ocean type predominantly in the coastal areas and the stream type in inland areas. North of 56^{o}N the stream type life history is dominant (Taylor 1990). After an analysis of the distribution of stream and ocean type life histories, Taylor (1990) concluded that variability in life history is in part a response to growth opportunity (environmental conditions) and selection for size at migration.

Evolutionary History and Genetic Structure of Chinook Salmon.

Neave (1958) argued that the Pacific salmon diverged into seven species entirely within the Pleistocene 500,000 to 1,000,000 years ago. However analysis of mitochondrial DNA suggests the ancestral line that produced chinook salmon is two to three million years old (Thomas and Beckenbach 1989).

Genetic data exist for chinook salmon populations ranging from California (Utter et al. 1989; Gall et al. 1992), Oregon, Washington, British Columbia (Utter et al. 1989; Matthews and Waples 1991; Waples et al. 1991b; Utter et al. 1995), to Alaska (Gharrett et al. 1987). Chinook salmon form a genetically complex network of populations that are structured primarily on the basis of geography into large regional groups (Utter et al. 1995), that correspond to the large regional groups identified for many other Pacific salmon species. Within the large regional groups, chinook also show substantial geographic substructuring, largely on the basis of subbasins or individual watersheds. Although chinook salmon show hierarchical levels of geographically-based genetic structuring throughout most of their range, chinook populations in the upper Columbia and Snake Rivers (Matthews and Waples 1991; Waples et al. 1991b; Utter et al. 1995), exhibit substructuring first on the basis of run-timing, then geographically (Figure 4.3). In these instances, populations with similar run-timing were more similar to each other than they were to geographically proximate populations with different run-timing.

Research on the genetic structure of chinook salmon in the Columbia Basin has focused on the higher levels in the hierarchy of genetic organization, which have been defined variously as major ancestral lineages (Utter et al. 1995), genetic diversity units (Busack and Shaklee 1995), Evolutionarily Significant Units (ESU); (Waples 1991a), and stocks. These efforts, largely driven by questions of genetic stock identity, have provided information critical to our understanding of genetic structure within species and for the identification of genetic conservation units, such as ESUs. However, little effort has been expended on the genetic infrastructure within populations or stocks.

The genetic infrastructure of a stock allows the population to adapt to fluctuating environments and to survive long-term environmental change (Gharrett and Smoker 1993). One visible indication of variation within a population and an indication of infrastructure is the existence of life history diversity. Studies of chinook salmon have shown considerable variation in life history patterns (Reimers 1973; Schluchter and Lichatowich 1977; Carl and Healey 1984). However, only one of these studies examined both life history and genetic diversity in the same population and that study did demonstrate a relationship between juvenile migration patterns and genetic diversity (Carl and Healey 1984). In the Columbia Basin, Lichatowich (1995) hypothesized that the observed loss of life history diversity in spring and summer chinook salmon was due to depletion of the runs.

Historic and Present Distribution of Chinook Salmon

The predevelopment abundance of chinook salmon in the Columbia Basin was estimated at 4.7 to 9.2 million fish (NPPC 1986). In 1994, 400,000 chinook salmon of both hatchery and wild origin entered the river (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995).

Chinook salmon generally spawn in the mainstem and larger tributaries in the Columbia Basin (see Figures 3.5, 3.6, and 3.8). Therefore, the construction of mainstem dams has had a major impact on their spawning distribution and production. The spring/summer runs of chinook salmon migrated to and spawned throughout the Columbia and Snake rivers. Summer chinook spawned in the mainstem below the outlet of Windermere Lake in British Columbia, 1,200 miles from the sea (Fulton 1968). In the Snake River, spring chinook migrated to Rock Creek, a tributary below Shoshone andAuger Falls, 900 miles from the sea (Fulton 1968). Historically, the Salmon River (a Snake Basin tributary) alone produced 39 to 45 percent of the spring/summer chinook salmon in the Columbia Basin (National Marine Fisheries Service 1995a). Spring and summer chinook salmon are totally blocked in their upstream migration in the Columbia River at Chief Joseph Dam and in the Snake River by Hells Canyon Dam. Fulton (1968) described the historical spring/summer chinook salmon spawning areas which were eliminated by development in the basin:

> *"Major areas of the John Day and Umatilla rivers, parts of the Clearwater and Powder rivers, all of the Payette, Owyhee, Boise, and Bruneau, major portions of the Walla Walla, Yakima and Okanogan rivers, important tributaries above Chief Joseph Dam including the San Poil, Spokane, Kettle, Pend Oreille, and Kootenay rivers."*

The fall run of chinook salmon spawned in the lower tributaries and in the lower and middle mainstem of the Columbia River and in the Snake River up to Augur Falls (Fulton 1968). Some of the most valuable spawning areas were in the mainstems of the Columbia River, nearly all of which were inundated by construction of dams. The Hanford Reach and the Snake River below the Hells Canyon complex of dams are the only remaining free flowing reaches in the Columbia Basin, however, the only significant remaining mainstem spawning area for fall chinook salmon is the Hanford Reach. Irrigation and habitat degradation eliminated spawning areas in many of the lower reaches of tributaries such as the John Day, Umatilla, and Walla Walla rivers. In 1957-1960, the largest group of fall chinook (41,000 fish) spawned in the Snake River and the second largest (34,000 fish) spawned in the mainstem Columbia River in the area now inundated by the John Day Dam.

Life History Diversity in Chinook Salmon

The geographic organization of chinook salmon in the Columbia basin prior to extensive human development likely consisted of a complex mosaic of spring, summer, and fall races of salmon distributed among mainstem and headwater spawning areas (see Figures 3.5 and 3.9). Local populations of fall chinook salmon whose juveniles migrated as subyearlings spawned in mainstem areas of the Columbia and Snake rivers and lower mainstem segments of Columbia River tributaries (Fulton 1968; Howell et al. 1985; Mullan et al. 1992a). Spring and summer chinook that migrated as subyearlings reproduced in upper mainstem segments of major subbasins and lower reaches of tributaries to subbasin mainstems (Lichatowich and Mobrand 1995). Summer chinook probably spawned lower in the subbasin mainstems than spring chinook (French and Wahle 1959; Fulton 1968; Lichatowich and Mobrand 1995). Populations of spring chinook with yearling life histories reproduced in headwater streams of subbasin tributaries.

The complex of spatially distributed local spawning populations associated with major subbasins and contiguous areas of the mainstem Columbia or Snake rivers may have formed metapopulations composed of local populations connected at least to some degree by dispersal. One type of metapopulation was composed of fall chinook spawning in mainstem reaches of the Columbia and Snake rivers and the lower reaches of major subbasins, while summer and spring chinook spawning in the upper mainstems of major subbasins and spring chinook spawning in headwater areas comprised another type of metapopulation.

Present metapopulations organization, which is fragmented as compared to probable historic organization, may result in reduced resilience; but, in theory at least, metapopulations have the ability to recover from catastrophic decline. Habitat fragmentation has increased isolation of populations and probably reduced dispersal rates due both to increased distances between populations and the degraded quality of connecting habitats. Most mainstem spawning populations, which may have served as stable sources of colonists, are virtually extinct and viable naturally spawning populations are confined to relatively isolated headwater areas. Thus, dispersal among populations may be restricted making “rescue” of severely depleted populations and recolonization of habitats where extinction has occurred much less likely. Moreover, confining populations to headwater areas may increase their susceptibility to habitat alterations from land use such as grazing and logging (see Chapter 5) unless the populations inhabit areas protected from adverse land use.

Both genetic and life history evidence suggests that spring chinook are distinguished from fall chinook in the Columbia River Basin. Fall chinook are differentiated from the spring races with respect to life history characteristics such as annual timing of adult migration, geographic distribution of spawning habitat, and genetic attributes (Waples et al. 1991b). Summer chinook in the Upper Columbia River appear to be more closely related to fall chinook, than to spring chinook; whereas, in the Snake River, summer chinook are more closely related to spring chinook (Utter et al. 1995). French and Wahle (1959) observed summer and spring chinook on the spawning grounds of the Wenatchee and Methow rivers, whereas Mullan et al. (1992a) reported mixing of summer and fall fish on the spawning areas of mid-Columbia river tributaries. There may be tendency to group summer chinook and fall chinook because they both migrate downstream as subyearlings. Conventional wisdom suggests that all spring chinook exhibit yearling juvenile migration even though there is evidence to the contrary.

Redd (salmon nests) counts in index areas of the Imnaha and Grande Ronde rivers and their tributaries suggest that spring chinook populations have been experiencing synchronous decline since the late 1960's - mid 1970's (Figure 3.9). In 1994 and 1995, no redds were located in the index areas in Bear, Hurricane, Indian, and the North and South Forks of Catherine Creeks. No redds were recorded in Sheep Creek from 1993-1995. Since the habitat where these stocks spawn is of relatively high quality, and considering that the Wenaha River is nearly entirely within a wilderness area, the synchronizing influence may be downstream from the spawning areas, either in lower mainstems of the Grande Ronde and Imnaha, in the mainstem Snake or Columbia River, or in the ocean.

Harvest Summary of Chinook Salmon

Intensive fisheries did not begin until cannery technology reached the Columbia River in 1866 (Craig and Hacker 1940). Chinook salmon, and especially the spring or summer run fish, brought the highest price and made the highest quality canned product so the early fishery targeted those runs (Craig and Hacker 1940). After 1866, the catch of chinook salmon increased rapidly and peaked in 1883 at 19,413 metric tons (Beiningen 1976). The harvest of chinook salmon can be divided into four phases (Figure 4.4.):

A. Initial development of the fishery (1866—1888);
B. A period of sustained harvest with an average annual catch of about 25 million pounds (1889—1922);
C. Resource decline with an average annual harvest of 15 million pounds (1923—1958);
D. Maintenance at a depressed level of production of about 5 million pounds (1958 to the present).

Recent declines may indicate the system is slipping to a new, lower level of productivity.

Between 1889 and 1920, the harvest of chinook salmon was relatively stable, however, catch data alone mask a major qualitative shift in the fishery (Figure 4.4). During that period, the spring and summer races of chinook salmon were declining and harvest was maintained by a shift from the spring/summer fish to fall chinook salmon. In 1892, fall chinook made up 5 percent of the harvest and by 1912, it had risen to 25 percent. In 1920, fall chinook salmon made up 50 percent of the catch. The harvest of all chinook salmon underwent a rapid decline after 1923, however, the decline in the spring and summer races started as early as 1911 (Craig and Hacker 1940). One of the factors contributing to this decline was the development of the offshore troll fishery which started in 1910 and expanded in the 1920s. Decline in abundance reached the point that two in-river fisheries were closed: 1965 was the last summer chinook season and 1977 was the last spring chinook season (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1993). In 1994, the Young's Bay fishery accounted for 81 percent of the commercial landings below Bonneville Dam (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995).

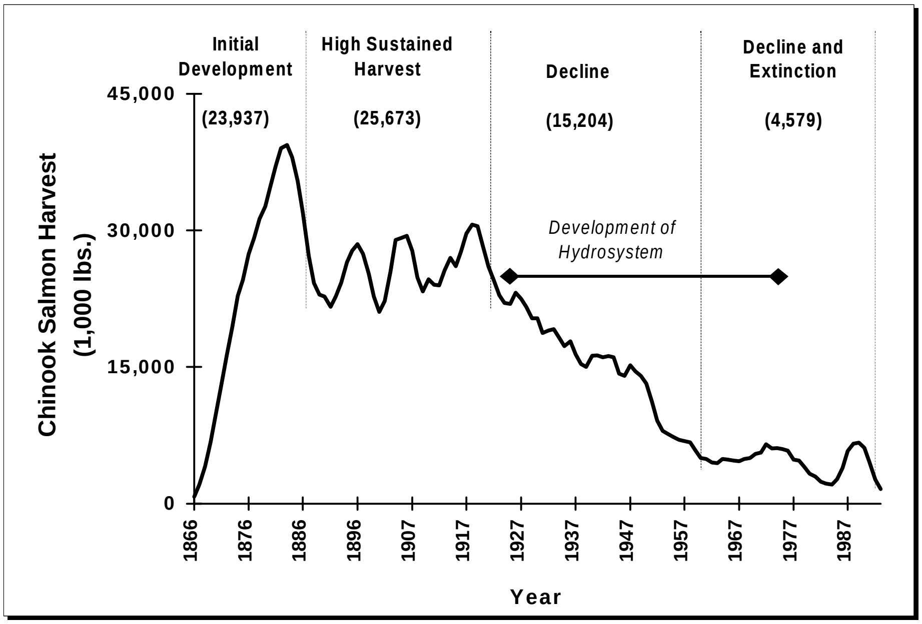


Figure 4.4. Five year running average of chinook salmon harvest in thousands of pounds in the Columbia River, 1866 to 1992, with the average harvest for four periods of development.

Propagation Efforts for Chinook Salmon

Chinook salmon were the first fish to be artificially propagated in the Columbia Basin. In 1877, a private company, the Oregon and Washington Propagation Company, constructed the first hatchery on the Clackamas River. The hatchery program grew rapidly and remained an important management activity even though there was little evidence that artificial propagation was in fact enhancing chinook salmon in the basin. After 1960, with the introduction of better feeds and hatchery practices artificially propagated chinook salmon began making significant contributions to the fisheries. The hatchery program for chinook salmon has grown from releasing 61 million juveniles in 1960 to 160 million in 1988. For more detailed discussion of artificial propagation see Chapter 8.

Status under the Endangered Species Act

Throughout the range of chinook salmon south of the Canadian border, NMFS recognizes 17 ESUs, 8 of which lie in the Columbia River drainage. Within the Columbia Basin, ESA status of chinook salmon is shown in Table 4.2 below.

Table 4.2. ESA status for chinook salmon in the Columbia and Snake rivers.

River system	***Run-timing***	***ESA status***
Upper Columbia River	spring	Endangered
	summer-fall	Not Warranted
Mid-Columbia	spring	Not Warranted
	summer-fall	Not Warranted
Lower Columbia	all	Endangered
Upper Willamette	spring	Threatened
Snake River (SR)	summer-spring	Threatened
	fall	Threatened

Coho Salmon
(***Oncorhynchus kisutch***)

Background

The spawning distribution of coho salmon in the western Pacific extends from as far south as Chongjin on the east coast of North Korea north to the Anadyr River. In the Eastern Pacific, coho salmon are distributed from the San Lorenzo River on Monterey Bay to Point Hope in Alaska (Sandercock 1991). Coho salmon generally enter the rivers to spawn in late summer or fall although spawning migrations in other seasons have been noted. More than one seasonal spawning migration into a single river is rare (Sandercock 1991).

Evolutionary History and Genetic Structure of Coho Salmon

Coho salmon spawn in small tributary and headwater streams more frequently than other salmon species (Aro and Shepard 1967). Coho exhibit low levels of genetic variation as compared to the other Pacific salmon species (Utter et al. 1973; Olin 1984; Wehrhahn and Powell 1987), but still show large regional geographic differentiation. Analysis of mitochondrial DNA suggest that three phyletic lines of salmonids diverged more than two million years ago and in one of those lines a subsequent divergence one to one and a half million years ago led to rainbow, coho and chinook salmon (Thomas and Beckenbach 1989). Weitkamp et al. (1995) identified six potential coho salmon ESUs in California, Oregon and Washington: Central California coast, southern Oregon/northern California coasts, Oregon coast, lower Columbia/southwest Washington coast, Olympic Peninsula, Puget Sound/Strait of Georgia. The lower Columbia/southwestern Washington coast contains the stocks of coho salmon remaining in the Columbia Basin. Unfortunately, most of the native coho stocks in the Columbia River were extinct before an analysis of their genetic structure could be completed.

Historic and Present Distribution of Coho Salmon

The predevelopment run size of coho salmon was estimated at 903,000 to 1,780,000 fish (NPPC 1986). In 1994, the minimum number of coho salmon entering the Columbia River was 178,900 fish (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995) nearly all of which were of hatchery origin.

The principal spawning areas for coho salmon were in the tributaries to the lower river, however, Fulton (1970) also identified coho spawning in tributaries above Bonneville Dam including Hood, John Day, Grande Ronde, Spokane, Entiat, Wenatchee, and Methow rivers. All coho stocks above Bonneville Dam with the exception of the Hood River stock were classified extinct by Nehlsen et al. (1991).

At present, production of coho salmon is almost entirely from artificial propagation. The NMFS could not identify any remaining natural populations of coho salmon in the lower Columbia River that warranted protection under the Endangered Species Act (Johnson 1991). The possible exception is the late run of coho salmon into the Clackamas River. Whether the Clackamas stock is the last remaining wild stock in the Columbia River or a stock similar to the other hatchery stocks in the lower river is uncertain (Weitkamp et al. 1995). Remnant wild populations may also exist in the Hood River and Klickitat River. Habitat degradation and overharvest contributed to the depletion and extinction of the wild coho salmon stocks in the Columbia River. The massive hatchery program, which included interstock transfers, was an additional factor in the decline of coho salmon (Flagg et al. 1995b).

Harvest Summary of Coho Salmon

Coho salmon were not as abundant as chinook salmon in the Columbia River. Coho salmon were considered inferior by the cannery operators so they were not harvested in the early years of the intensive fishery in the Columbia River (DeLoach 1939; Craig and Hacker 1940). The first coho salmon were commercially harvested in 1892 (Figure 4.5) in conjunction with a shift in harvest to fall running fish when the prime spring run of chinook salmon became depleted (Lichatowich and Mobrand 1995). The fishery for coho salmon intensified after 1920 when chinook salmon went into rapid decline, however, by the mid 1930s coho salmon were also in a steep decline that persisted for 30 years (Figure 4.5). The decline was real, but part of the apparent decline was due to a shift to offshore fishing by the growing troll fleet. After 1930, harvest in the Oregon Production Index (OPI) is a better indication of the pattern of abundance of Columbia River coho salmon. The OPI includes in-river and ocean catch of coho salmon from southwestern Washington to northern California (Figure 4.6).

In the mid 1960s, improved hatchery practices and favorable ocean conditions combined to produce an apparent recovery of coho salmon production which persisted until 1976 (Figures 4.5 and 4.6). The recovery was primarily due to increased survival of hatchery reared fish. The wild component of the OPI harvest remained depressed throughout the 1960s and 1970s. By 1991, habitat degradation and fisheries on mixed stocks of wild and hatchery coho salmon led to the conclusion that no viable wild stocks of coho salmon existed in the Lower Columbia River (Johnson 1991).

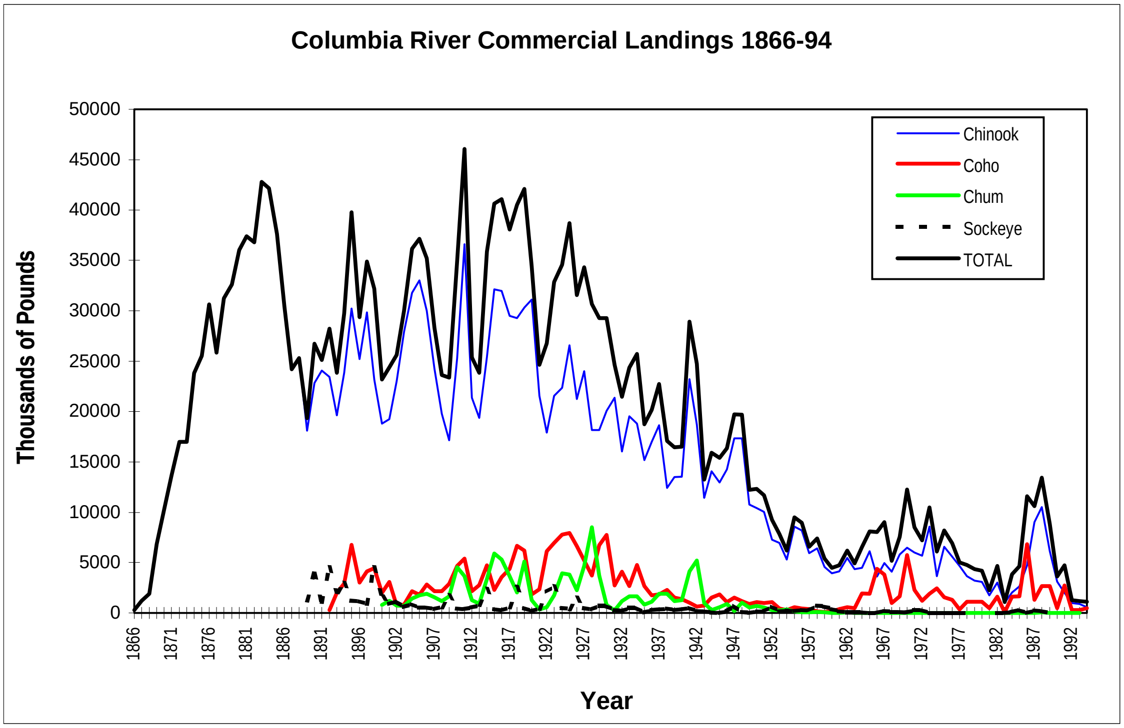
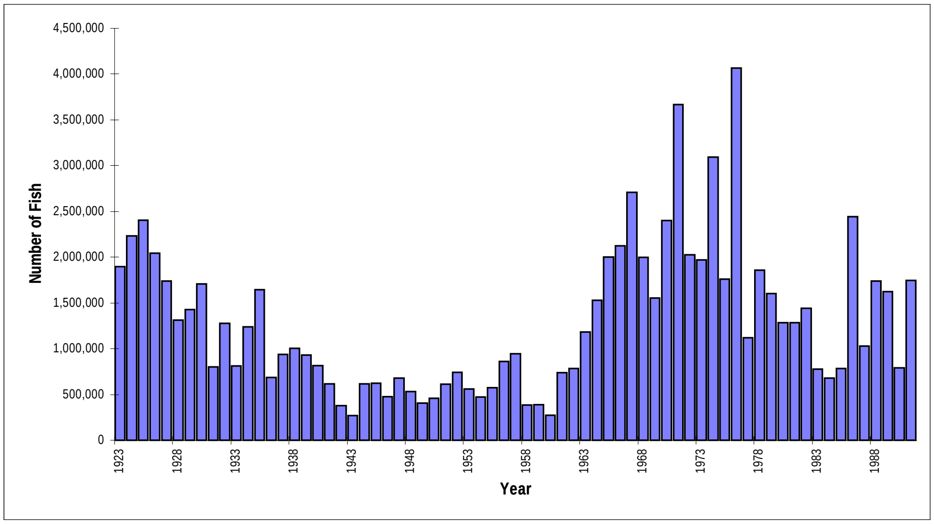


Figure 4.5. Columbia River commercial salmon fishery landings, 1866-1994 (Beiningen 1976; ODFW and WDF 1993).

A)



B)

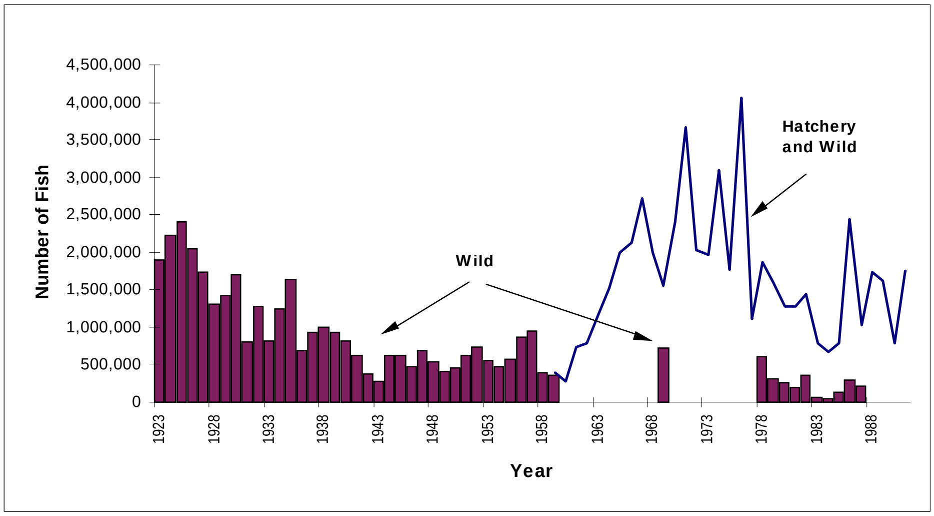


Figure 4.6. Annual ocean harvest of coho salmon in numbers of fish for the Oregon Production Index area, 1923 - 1991. Plot A is for total catch, while Plot B shows wild and hatchery produced components of total catch (Oregon Department of Fish and Wildlife 1982; Borgerson 1992; Pacific Fishery Management Council 1992).

Propagation Efforts for Coho Salmon

The first plant of artificially propagated coho salmon in the Columbia Basin took place in 1896. Coho salmon have been propagated continuously since 1900 (Cobb 1930). There are now

16 hatcheries operating in the lower Columbia River (Johnson 1991) which have released 29 to 54 million juvenile coho salmon in recent years (1984 to 1992). The origin of the coho salmon brood stocks in Oregon's lower Columbia River hatcheries is uncertain. Johnson et al. (1991) described the brood stocks as mixtures of fish from a variety of sources, including coastal populations, Washington stocks, and native stocks. These mixed stocks have been extensively outplanted throughout the basin (Flagg et al. 1995b). For additional information on the hatchery program see Chapter 8.

Status under the Endangered Species Act

Throughout the range of coho salmon south of the Canadian border, NMFS recognizes six ESUs, only one of which lies in the Columbia River drainage. Coho in the Lower Columbia Southwest Washington ESU are considered candidates for listing, while Oregon coastal coho populations form a threatened ESU.

Chum Salmon
(*Oncorhynchus keta*)

Evolutionary History and Genetic Structure of Chum Salmon

Chum salmon populations exhibited the kind of geographic and regional differentiation described in Figure 4.1 (Beacham et al. 1985; Kondzela et al. 1994; Phelps et al. 1994; Wilmot et al. 1994; Winans et al. 1994; Phelps et al. 1995), where populations clustered on the basis of major islands, major river systems, and along major contiguous coastlines (see Figure 4.2 showing the genetic distances among chinook salmon populations from northern Alaska and Russia). In some instances, however, chum salmon populations in regional aggregates sorted by run-timing, rather than by subbasin. In other words, as is the case for chinook salmon outside the Columbia River basin, chum salmon populations in several regions including the Yukon River (see Figure 4.2; summarized from Wilmot et al., 1994), Hood Canal, and Puget Sound (Phelps et al. 1995) were more similar to distant populations with similar run-timing than they were to adjacent populations (within the same subbasin) with different run-timing.

Historic and Present Distributions of Chum Salmon

The three remaining spawning areas for chum salmon are in Washington State in tributaries to the lower river below Bonneville Dam (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1993) in Hamilton Creek, Hardy Creek and the Grays River.

Harvest Summary of Chum Salmon

Chum salmon were not as abundant as chinook salmon in the Columbia River and were considered inferior by the cannery operators, so they were not harvested in the early years of the intensive fishery in the Columbia River (DeLoach 1939; Craig and Hacker 1940). Chum salmon entered the fishery in 1894 (Figure 4.5) in conjunction with a shift in harvest to fall running fish as the prime spring run chinook became depleted (Lichatowich and Mobrand 1995). From the early 1900s through the 1950s, the harvest of chum salmon was more variable but generally followed the trend in harvest of coho salmon (Figures 4.5 and 4.6). Since chum salmon were the lowest grade of canned salmon in the Columbia River, some of the variability in harvest was due to a fluctuating demand for cheap fish (Craig and Hacker 1940).

Propagation Efforts for Chum Salmon

Chum salmon were not propagated extensively in hatcheries and their abundance did not increase in the 1960s as observed for coho and chinook salmon, which were propagated (Figures 4.5 and 4.6). The collapse of Columbia River chum salmon in the 1940s and 1950s paralleled the decline of coastal chum salmon populations in Oregon, Washington, and British Columbia suggesting that an overall decline was occurring due to a regional climatological or oceanic factor (Oakley 1996).

Status under the Endangered Species Act

Throughout the range of chum salmon south of the Canadian border, NMFS recognizes four ESUs, with the Columbia River ESU listed as threatened.

Sockeye Salmon
(*Oncorhynchus nerka*)

Background

Sockeye salmon are distinguished from other Pacific salmon species by their use of lakes for the freshwater rearing of juveniles. Sockeye are widely distributed in western North America and eastern Asia (Burgner 1991), however sockeye have been extirpated from most of the localities formerly occupied in the contiguous United States (California, Oregon, Washington, and Idaho).

Substantial information exists on reproductive biology, age structure, growth, and productivity of Columbia River sockeye. Columbia River sockeye salmon spawn in tributaries and outlets of Lakes Wenatchee and Osoyoos in August and September (Mullan 1986; Hatch et al. 1995) and hatch and swim into rearing lakes in the late winter and spring of the following year. Depending on growth, sockeye juveniles will spend one to three winters in the rearing lake and one to three winters in the ocean. Slower growing sockeye take longer to pass through each life history stanza than faster growing sockeye. The typical Columbia River sockeye spends one winter in freshwater and two winters in the ocean to return as an adult in its fourth year of life.

Lake Osoyoos (Okanogan River) sockeye are unique among sockeye populations in occasionally having three-year-old adults as the dominant age class (one winter in freshwater and one in the ocean). Size at age, growth, productivity, and historical zoogeography are reviewed by Fryer (1995). Columbia River sockeye from Lake Osoyoos tend to be large as smolts, greater than 10 cm, and small as adults, less than 45 cm, and less than 2 kg, whereas Wenatchee sockeye tend to be smaller than Osoyoos sockeye as smolts, and larger and older as adults. Differences between the attributes of Wenatchee and Osoyoos sockeye are ascribed to the physical and biological differences in the characteristics of the rearing lakes (Fryer 1995).

Evolutionary History and Genetic Structure of Sockeye Salmon

Sockeye salmon occur in rivers associated with nursery lakes or in groundwater dominated streams widely along the Pacific coast north of the Columbia River and within a limited distribution in Russia along the Kamchatka Peninsula and the northern coast of the Bering Sea (Varnavskaya et al. 1994a). Like coho salmon, sockeye exhibit a low level of genetic variation as compared to pink, chum, or chinook salmon (Varnavskaya et al. 1994a; Varnavskaya et al. 1994b; Wood et al. 1994). This may be the result of inbreeding related to the greater extent of reproductive isolation between spawning populations, a consequence of well-developed homing behavior in sockeye as demonstrated by tagging experiments and gene flow calculations (Quinn et al. 1987; Altukhov and Salmenkova 1991).

Nevertheless, the genetic architecture of sockeye salmon shows large scale geographic differentiation, with groups from Kamchatka, western Alaska, southeastern Alaska, northern British Columbia, southern British Columbia, and Washington being well differentiated (Varnavskaya et al. 1994b; Wood et al. 1994). Large genetic differences occur between sockeye from some of the different regions, reflecting major ancestral or evolutionary lineages, which appear to have been influenced by recent historical glaciation events. Present distributions and genetic relationships among sockeye populations appear to be related to historical expansion and recolonization from a few ice-free refugia (Wood et al. 1994). Within each of these larger regions, sockeye salmon populations showed additional geographical substructuring; however, populations within regions were well-differentiated from one another, reflecting the relative reproductive isolation of individual sockeye populations from one another.

Historic and Present Distribution of Sockeye Salmon

At least twenty-seven lakes originally supported populations of Columbia River sockeye in Oregon, Washington, and Idaho (Fryer 1995). Loss of access to spawning areas due to construction of small agricultural storage and diversion dams has reduced the number of lakes open to sockeye, a reduction of 96% in juvenile rearing habitat between settlement during the 1840s and the present (Rich 1941; Mullan 1986; NPPC 1986; Fryer 1995). Sockeye occur in the Columbia River basin in three localities: Lake Wenatchee, Washington; Lake Osoyoos, Washington and British Columbia; and Redfish Lake, Idaho. However the Idaho population is a federally listed endangered species as of December, 1991.

Age, growth and stock identification studies and spawning ground surveys are conducted by the Columbia River Inter-Tribal Fish Commission under the auspices of the Pacific Salmon Treaty.

Harvest Summary of Sockeye Salmon

Historical annual abundances in the area of two to three million adults (Chapman 1986; NPPC 1994a) supported annual commercial landings which twice exceeded 4.5 million pounds during the 1890's. As measured by commercial catches, adult returns of Columbia River sockeye declined sharply after 1900. Present levels of returns are in the tens of thousands, with spawning escapements to both Osoyoos and Wenatchee being less than ten thousand adults each, in 1995. The number of adults deemed by the management entities to be sufficient for fully seeding sockeye spawning grounds, i.e., the escapement goal, for the Columbia River basin is presently 75,000 (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995). No commercial fishing has occurred since 1988, and the annual commercial season has often been canceled during the past twenty-five years. A sport fishery occurs on Lake Wenatchee when abundances permit, yielding a catch of 7,000 sockeye as recently as, 1993 (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995). Subsistence and ceremonial harvests by treaty Indian tribes occur above Bonneville Dam, with harvests being in the area of 5,000 adults per year, prior to the limiting of sockeye salmon as a federally endangered species in Idaho.

Propagation Efforts for Sockeye Salmon

Current propagation efforts for sockeye occur on the Lake Wenatchee, Redfish Lake, and a small population in the Lake Osoyoos sockeye populations. Sockeye have proven difficult to culture with standard hatchery methods due to their susceptibility to disease. The alternative that has been developed is to move the fry soon after hatching into net pens in the lake where they are reared for a time and then released into the lake to overwinter before spring outmigration.

Propagation efforts at Lake Wenatchee, funded by the Chelan County P.U.D. as part of a FERC agreement, have added about 15% to the sockeye outmigration from Lake Wenatchee.

The program for the recovery of the endangered Redfish Lake, Idaho sockeye is administered by the National Marine Fisheries Service in cooperation with the Bonneville Power Administration, the State of Idaho and other concerned fisheries agencies, including Indian tribes. The program involves and relies heavily on artificial production using all returning Redfish Lake sockeye, along with genetic input from the resident beach spawning kokanee, which are part of the same ESU.

Considerable propagation efforts have been directed at kokanee, the resident form of sockeye salmon. Stocks have been widely transferred throughout the basin, and kokanee populations in most large lakes or reservoirs are genetic mixtures of multiple stocks (R. Williams and M. Powell, unpublished data). There is interest in the basin in attempting to reestablish anadromous sockeye runs from residualized kokanee populations; however, the probability of that occurring may be decreased as a consequence of the mixed genetic heritage of most kokanee populations.

Status under the Endangered Species Act

Throughout the range of sockeye salmon south of the Canadian border, NMFS recognizes seven ESUs, three of which lie in the Columbia River drainage. Only the Snake River sockeye ESU is listed (endangered), while the Okanogan River and Lake Wenatchee ESUs were not deemed warranted for listing.

Pink Salmon
(*Oncorhynchus gorbuscha*)

Evolutionary History and Genetic Structure

Pink salmon can be separated into two major evolutionary lineages, based on even-year and odd-year occurrence that exhibit large genetic differences (Gharrett et al. 1988). This is an expected consequence of their rigid two-year life history and results in the nearly complete reproductive isolation of the even- and odd-year broodlines. Within the even- and odd-year broodlines, pink salmon populations show typical hierarchical geographic differentiation as described above (Beacham et al. 1988; Gharrett et al. 1988; Varnavskaya and Beacham 1992; Shaklee and Varnavskaya 1994; Shaklee et al. 1995).

In spite of the near reproductive isolation of the two broodlines throughout their native distribution, Kwain and Chappel (1978) reported the development of even-year pink salmon runs from a single release of odd-year breeding pink salmon into the Great Lakes.

Historic and Present Distributions of Pink Salmon

Pink salmon occur irregularly along the Oregon and Washington coasts, including the Columbia River, but spawning distributions occur from Puget Sound and the Olympic Peninsula north to Norton Sound in Alaska (Groot and Margolis 1991; Hard et al. 1996).

Status under the Endangered Species Act

Throughout the range of pink salmon south of the Canadian border, NMFS recognizes only two ESUs, one for even-year and another for odd-year broodlines. Neither are deemed as warranted for listing.

Trout and Char:

Overview

Background

Rainbow and cutthroat trout exist in both anadromous and resident forms. Anadromous rainbow trout, known as steelhead, have historically been managed more in concert with the five anadromous salmon species described above, than with resident rainbow and cutthroat trout. This distinction continues today, with the National Marine Fisheries Service supervising ESA concerns for steelhead and anadromous coastal cutthroat trout, while the US Fish and Wildlife Service provides ESA oversight for all other rainbow and cutthroat trout taxa as they are not anadromous. Because of the importance of steelhead trout within the Columbia River basin fisheries resource, they will be discussed further separately from resident (non-anadromous) rainbow trout.

Distributions and abundance of the many species and forms of rainbow and cutthroat trout have declined in the last 150 years to fractions of their historic ranges (10-30% depending upon species) (Trotter 1989; Behnke 1992; Quigley et al. 1996). Reasons for declines are similar for all taxa. The declines are reasonably well-documented and concerns over the status of various species, subspecies, or distinct local populations have prompted a series of petitions for review or listing under the Endangered Species Act. These include reviews of the status of steelhead populations coast-wide and sea-run coastal cutthroat trout from the Umpqua River for anadromous forms, as well as reviews of the status of interior rainbow trout (i.e., redband trout) and bull trout (species wide). At present, bull trout, Umpqua River coastal cutthroat trout, five ESUs of steelhead trout, and the Kootenai River sturgeon are listed as threatened or endangered under the ESA.

Rainbow trout and cutthroat trout have suffered primarily from habitat degradation and competition with introduced non-native salmonids, usually hatchery rainbow trout (Behnke 1992). In addition to habitat degradation, steelhead distributions and abundance have been impacted by hydroelectric construction, which eliminated access to large spawning areas above Grand Coulee Dam and the Hells Canyon complex of dams, as well as inducing passage mortalities on both adult and juvenile migrants. Bull charr or bull trout have suffered primarily from habitat degradation, but also from past fisheries management practices and from the introduction of non-native brook trout (actually a charr also) (Leary et al. 1993; Rieman and McIntyre 1993)

Introduction of non-native salmonids impacts native salmonids in two major ways. First, introduced salmonids may serve as ecological competitors with native salmonids and reduce their abundance through competition for food or specific microhabitats (Fausch 1988). Second, non-native salmonids are frequently able to hybridize with native salmonids. This results in the introduction of non-native genes into the native population, which can reduce the reproductive fitness of the progeny. The degree to which the native population is affected depends, among other things, on the degree of outbreeding depression (i.e., reduction in fitness) that occurs after hybridization. For brook trout and bull trout hybrids, genetic and abundance data from Leary et al. (1993) suggests that brook X bull hybrids are strongly selected against. Brook trout appear to be replacing bull trout in several index streams in Montana and Idaho, probably due to earlier sexual maturation by brook trout and aggressive breeding behavior by brook trout males.

Hybridization and genetic introgression have also been documented many times for native rainbow and cutthroat trout populations (Campton and Johnston 1985; Campton and Utter 1985b; Currens et al. 1990; Williams et al. 1996); however, this work has rarely been extended into an examination of fitness consequences of introgression. Nevertheless, introductions of non-native salmonids are generally recognized as one of the major factors in the decline of native salmonids in the Interior West (see indigenous species lists in Tables 4.3 and 5.1). Most states have taken steps to inventory native trout populations and protect those that are identified as remnant native stocks free of introgression from non-native salmonids.

All of these taxa exhibit a range of life history strategies, which include both migratory and resident (i.e., non-migratory) forms. All of the coastal salmonids as well as interior rainbow trout exhibit anadromy. Other interior salmonids exhibit resident and migratory life history strategies, the latter, which may include adfluvial and fluvial forms.

Table 4.3. Indigenous species-level taxa of trout and char with coastal or interior distributions.

Coastal species (anadromous and resident forms)
Coastal Cutthroat Trout (*O. clarki clarki*)
Coastal Rainbow Trout (*O. mykiss irideus*)
Dolly Varden Char (*Salvelinus malma*)

Interior species (non-anadromous forms only)
Yellowstone Cutthroat Trout (*O. c. bouvieri*)
Westslope Cutthroat Trout (*O. c. lewisi*)
Interior Rainbow Trout (“redband” trout) (*O. mykiss gairdneri*)
Bull Trout or Bull Char (*S. confluentus*)

Interior species (also exhibiting anadromy)
Interior Rainbow Trout (“redband” steelhead trout) (*O. mykiss gairdneri*)

Evolutionary History and Genetic Structure

Genetic structure has been examined in some detail in cutthroat trout (Loudenslager and Gall 1980; Campton and Johnston 1985; Martin et al. 1985; Leary et al. 1987; Allendorf and Leary 1988; Behnke 1992) and bull trout (Leary et al. 1993; Kanda et al. 1997; Williams et al. 1997), but less so in rainbow trout (Wishard et al. 1984; Campton and Johnston 1985; Currens et al. 1990; Williams et al. 1996). Nevertheless, all three species show geographic patterns of genetic variation and divergence into major evolutionary lines. Cutthroat trout and bull trout show additional geographic substructuring within major evolutionary lines, however, such patterns are less clear in rainbow trout, probably due to the more recent evolutionary derivation of many of the inland rainbow forms.

Rainbow and Steelhead Trout
(*Oncorhynchus mykiss*)

Background.

The rainbow trout group, which includes the rainbow trout and allied forms, such as the Mexican golden (*O. chrysogaster*), Gila (*O. gilae gilae*), Apache (*O. g. apache*), California golden (*O. m. aquabonita*), and the redband trout, occurs throughout coastal rivers from northern Mexico to the Kuskokwim River in Alaska. In the Pacific Northwest, rainbow trout can be divided (by the Cascade Crest) into coastal and inland forms. Behnke (1992) has suggested subspecies level distinction for the two groups and refers to the coastal form as *O. mykiss irideus* and the interior form as *O. m. gairdneri*. Inland rainbow trout (e.g., redbands) occur throughout the Columbia River Basin to barrier falls on the Snake, Spokane, Kootenay, and Clark Fork rivers. Both coastal and interior rainbow trout exhibit anadromous and resident forms. Anadromous rainbow trout, regardless or coastal or interior origin, are referred to as steelhead.

Evolutionary History and Genetic Structure of Rainbow Trout

Rainbow (and steelhead), rainbow-like, and cutthroat trout evolved from a common ancestor that diverged from Pacific salmon approximately 5 million years ago (Behnke 1988; Behnke 1992). The rainbow and cutthroat lines diverged from one another about 2 million years ago. Substantial evolutionary divergence has occurred in each species; however, considerable controversy exists among systematists concerning delineation of species and subspecies forms in rainbow trout. Taxa relationships in the rainbow group are less clear than within the cutthroat species, probably due to the more recent evolutionary derivation of many of the inland rainbow forms.

Historical and Present Distributions of Rainbow Trout

Native populations of rainbow trout, including coastal rainbow trout, have been reduced from their historic distributions (Behnke 1992; Quigley et al. 1996). Coastal and interior forms of rainbow trout have been dramatically affected by habitat degradation and by widespread introductions of hatchery reared rainbow trout. In many larger river systems in the Interior West, such as the Kootenay and its tributary creeks, hatchery rainbow trout have survived in many instances and interbred with native interior rainbow trout populations (Sage and Leary 1995; Williams and Jaworski 1995). In contrast, hatchery rainbow trout stocked into small desert streams in southern Idaho and northern Nevada have had almost no genetic effect on native rainbow trout populations (Williams et al. 1996). Survival of hatchery rainbow trout is probably extremely low in the harsh environmental conditions of these cold desert stream systems.

Propagation Efforts of Rainbow Trout

Rainbow trout have been extensively propagated (Behnke 1992). The majority of hatchery rainbow trout strains appear to have been developed from coastal rainbow trout, including both resident and anadromous forms, from the northern California area (Needham and Behnke 1962; Busack et al. 1979; Crawford 1979; Busack and Gall 1980). Hatchery reared rainbow trout have been widely planted throughout the western U. S. and are thought to be one of the major factors, along with habitat degradation, in the decline of interior rainbow (i.e. redband) and cutthroat trout populations.

Status under the Endangered Species Act

Throughout the range of steelhead trout south of the Canadian border, NMFS recognizes 15 ESUs, five of which occur in the Columbia River Basin. The ESUs and their status are listed in Table 4.4 below.

Table 4.4. ESA status for steelhead trout in the Columbia and Snake rivers.

ESU	***ESA status***
Upper Columbia River	Endangered
Middle Columbia River	Threatened
Lower Columbia River	Threatened
Upper Willamette River	Threatened
Snake River Basin	Threatened

Redband trout were petitioned for listing under the Endangered Species Act in 1995, however the listing was judged as not warranted at that time, in part due to lack of information. Future petitions for listing are expected to occur.

Cutthroat Trout
(***Oncorhynchus clarki***)

Background

The cutthroat trout is a polytypic species that occurs over a wide geographic range of coastal and interior waters in the western United States and Canada. Sixteen subspecies have been recognized in the recent literature (Loudenslager and Gall 1980; Leary et al. 1987; Behnke 1992). Eight of these have large geographic distributions; while another eight are either undescribed subspecies, native to a very small geographic area, or both. Four subspecies occur within the Columbia River drainage. Three of these (coastal cutthroat, *O. c. clarki*; westslope cutthroat, *O. c. lewisi*; and Yellowstone cutthroat, *O. c. bouvieri*) have large geographic distributions, while the Snake River Finespot, *O. c. spp.*, has a restricted distribution in the upper Snake River and its tributaries in eastern Idaho and western Wyoming. Yellowstone and Snake River Finespot cutthroat trout occur only above Shoshone Falls, near Twin Falls, Idaho, and therefore rarely figure into resident fish concerns in the Columbia River drainage. However, water abstractions from reservoirs upstream of Shoshone Falls (e.g., Pallisades Reservoir) can affect populations of these subspecies (Thurow et al. 1988).

Evolutionary History and Genetic Structure of Cutthroat Trout

Cutthroat and rainbow trout diverged from one another about 2 million years ago (Behnke 1992). Substantial evolutionary divergence has occurred in cutthroat trout, resulting in great diversity in morphology, phenotypic traits, behavior, genetic attributes, and ecological adaptations (Leary et al. 1987; Trotter 1987; Allendorf and Leary 1988; Behnke 1992). Cutthroat trout invaded the Columbia River before rainbow trout and diverged into four major evolutionary lines between 0.5 - 1 million years ago. The evolutionary lines are represented by the present subspecies of coastal, westslope, Yellowstone, and Lahontan (*O. c. henshawi*) cutthroat trout. The Columbia River drainage, including the Snake River above Shoshone Falls, includes populations of the first three of these subspecies, and therefore contains a substantial portion of the genetic diversity and evolutionary heritage of the cutthroat trout species. No other major river system in the western United States or Canada contained such taxonomic diversity with regards to western trout. Our discussion is restricted to coastal and westslope cutthroat only.

Subsequent evolution of the four major lines of cutthroat trout into the approximately 16 subspecies recognized today occurred quite recently; that is, within the last 100,000 years or less. Genetic divergence among the more recently evolved subspecies is low to non-existent (Leary et al. 1987; Shiozawa and Evans 1995), reflecting their recent evolutionary separation. Patterns of genetic structure within subspecies are not uniform. Some subspecies appear to have little divergence among populations (e.g., Yellowstone, Snake River Finespot, Lahontan, Humboldt), while others appear to have local adaptation and greater divergence among populations (e.g., westslope and coastal) (Loudenslager and Gall 1980; Leary et al. 1987; Shiozawa and Evans 1995). Obviously, strategies to conserve genetic diversity would differ for these two groups of subspecies. Where little divergence occurs among populations, preservation of a small number of populations is likely to conserve a large portion of the genetic diversity that exists within that subspecies. In contrast, where substantial divergence occurs among populations within a subspecies, conservation efforts are going to have to be directed at the local population level in order to conserve genetic diversity.

Coastal and westslope cutthroat trout appear to contain substantial amounts of genetic variation that is highly structured as compared to most other inland subspecies of cutthroat trout. Genetic studies of coastal cutthroat trout (Campton and Utter 1985a) revealed genetic differences among groups of populations from different geographic locations, suggesting a lack of gene flow among populations over geographic scales and the likelihood of substantial local adaptation for populations. Genetic variation among westslope cutthroat populations (Leary et al. 1987; Allendorf and Leary 1988) showed significant differences among populations, but did not reveal any particular geographic structuring to the variation. Nevertheless, for both subspecies, genetic structuring is apparent among local populations. Thus conservation efforts for both subspecies must be directed at least at the local watershed scale, if not at the population level.

Propagation Efforts for Cutthroat Trout

Most of the interior subspecies of cutthroat trout were propagated at one time or another (Behnke 1992); however, little recognition was given to the uniqueness of each subspecies, so that stocks from different subspecies were frequently mixed or transplanted. For example, because of the ease of collection of spawning adults from tributary streams of Yellowstone Lake, the Yellowstone cutthroat trout has had more propagation effort and been more widely distributed via stocking than other cutthroat trout subspecies (Gresswell 1979; Gresswell 1988). In spite of these early, large-scale hatchery and stock transfer programs, genetic assays of present day cutthroat trout populations reveal little incidence of genetic introgression (Shiozawa and Evans 1995, R. Williams unpublished data). Thus, it appears that most stock transfers of cutthroat trout outside their native distribution, did not result in hybridization with the indigenous trout (Williams 1991; Williams and Jaworski 1995).

Coastal Cutthroat Trout
(*Oncorhynchus clarki clarki*)

Background.

Coastal cutthroat trout occur from Prince William Sound in Alaska south to the Eel River in California. Their distribution corresponds closely with the Pacific coastal rainforest belt (Trotter et al. 1993). Typically, coastal cutthroat do not occur east of the Cascade Range in Washington and Oregon. Throughout its range, both anadromous and non-migratory resident forms exist. Anadromous forms show little differentiation across the range, whereas, isolated resident forms exhibit considerable divergence in morphological characters. Like many of the other cutthroat trout subspecies, coastal cutthroat exhibit a diversity of life history strategies, even among resident forms (Trotter 1989; Behnke 1992; Johnson et al. 1994). Trotter et al. (1993) identify at minimum three life history strategies among resident populations (resident, fluvial, and adfluvial), in addition to the anadromous form.

Historic and Present Distribution of Coastal Cutthroat Trout

Like all subspecies of cutthroat trout, coastal cutthroat trout distributions and abundance have declined dramatically since historic times. The subspecies probably suffers more from decreases in abundance than decreases in distribution. Nehlsen et al. (1991) considered almost all native populations of sea-run cutthroat in the western U.S. to be at some risk of extinction due largely to pervasive continuing declines in stock size.

Causes of decline are typical for cutthroat trout in general; habitat degradation due to logging, urban development, or mainstem passage, competition or hybridization from non-native and hatchery trout, and overharvest by anglers (Trotter 1987; Trotter 1989; Nehlsen et al. 1991). Coastal cutthroat throughout its range and westslope cutthroat in the Columbia drainage, co-evolved with rainbow trout. Although low levels of gene flow probably occur between the two species (Leary et al. 1987), hybridization with non-native rainbow trout has probably had little effect on coastal cutthroat. In contrast, hybridization with non-native rainbow trout is one of the major factors in the decline of other interior cutthroat trout subspecies, which historically had allopatric distributions from rainbow trout.

Status under the Endangered Species Act

Throughout the range of coastal cutthroat trout south of the Canadian border, NMFS recognizes seven ESUs, two of which occur in the Columbia River Basin. The southwestern Washington/Columbia River ESU is proposed for threatened status, while the Upper Willamette ESU is deemed not warranted for listing. The Umpqua River coastal cutthroat ESU is presently listed as endangered.

Westslope Cutthroat Trout
(*Oncorhynchus clarki lewisi*)

Background.

Westslope cutthroat trout are native to the upper Missouri and Columbia drainages. West of the Continental Divide, the natural distribution includes the following rivers: upper Kootenay, Clark Fork, Spokane, Coeur d'Alene, St. Joe, Clearwater, and Salmon. Isolated disjunct populations of westslope are also thought to occur in the John Day River and various tributaries of the middle Columbia, including the Lake Chelan drainage, and numerous tributaries of the Methow River. These disjunct populations may be remnants from the late-Pleistocene flooding of Lake Missoula.

Historical and Present Distribution of Westslope Cutthroat Trout

Westslope cutthroat trout have undergone dramatic range reductions. Liknes and Graham (1988) estimated that genetically pure westslope cutthroat trout in Montana currently occur in 2.5% of their historical range. The Salmon, Clearwater, St. Joe, and upper Flathead River all appear to be strongholds for westslope cutthroat trout. In Idaho, their occurrence is strongly correlated with federal land status; i.e., most strong populations of westslope cutthroat occur in designated or proposed wilderness areas.

Causes of decline are typical for inland cutthroat trout in general; habitat degradation, competition or hybridization from non-native and hatchery trout, and overharvest by anglers (Nehlsen et al. 1991; Trotter et al. 1993). Fisheries agencies have realized the greater vulnerability of cutthroat trout to angling harvest than rainbow or brown (*Salmo trutta*) trout, and frequently, westslope cutthroat populations are now protected by special regulations, specifically catch-and-release. These special regulations have helped maintain westslope cutthroat trout populations in the St. Joe River, Kelly Creek in the Clearwater River, and the Middle Fork of the Salmon. All three locations are well-known in the angling world and function as fishing destinations because of the cutthroat trout and the special regulations.

Bull Charr
(*Salvelinus confluentus*)

Background.

Bull trout, more correctly know as bull charr, are one of five currently recognized species in the genus *Salvelinus* in North America. It has been recognized as a “species of special concern” by the American Fisheries Society (Williams et al. 1989) and by many State agencies. Concern for the bull charr’s status prompted petitions for review or listing under the Endangered Species Act in October 1992 and January 1993. Review by the U.S. Fish and Wildlife Service (USFWS) resulted in a decision that listing was warranted, but precluded. A mnore recent review by the USFWS resulted in the listing of bull charr populations in the Columbia and Klamath rivers as threatened.

Evolutionary History and Genetic Structure of Bull Charr

The genus *Salvelinus* includes a number of species complexes that have confounded systematists for some time. As many as 45 different scientific names have been applied to North American char (Bond 1992); however, most current systematists recognize only five species. The bull charr was formally described by Cavender (1978) after he examined them and Dolly Varden (*S. malma*) specimens from throughout their respective ranges and identified species level diagnostic morphological characters. Cavender (1978) suggested that bull charr originated in the Columbia River and has extended and constricted its range according to climate changes. Its recent historic distribution extends from the McCloud River in northern California through inland western North America to the upper Yukon and MacKenzie drainages in Canada (Bond 1992).

Genetic studies of bull charr populations throughout the Columbia and Klamath River drainages (Leary et al. 1993; Williams et al. 1997) show evidence of macrogeographic genetic structure. Both allozyme and mitochondrial DNA analyses differentiated bull charr in the

Klamath drainage from bull charr in the Columbia drainage at a level typical of the major subspecies in cutthroat trout. Within the Columbia River drainage, bull charr from the lower Columbia (Deschutes and Lewis rivers) formed an evolutionarily distinct group from bull charr populations in the remainder of the Columbia River above the John Day River (Williams et al. 1997). Bull charr populations in the Columbia River system above the Deschutes River shared a common mitochondrial DNA pattern that is suggestive of a single founding populations (Williams et al. 1997). Allozyme data for the same populations (Leary et al. 1993), in spite of showing little overall genetic variation, revealed significant differences among upper Columbia River bull charr populations. Taken together, the mtDNA and allozyme data show that populations were once linked genetically, but have been separated long enough to accrue population specific allozyme profiles. Thus, historic linkages among bull charr populations in the upper Columbia River have been broken. The genetic data do not provide insight into whether fragmentation of the historic metapopulation structure is a result of natural processes (gradual warming and drying of climate in the Intermountain West) or human induced changes in habitat quality.

Riemen and McIntyre (1993) advocate a conservation approach for bull charr protection and restoration that focuses on identifying core areas that contain linked bull charr populations in high quality habitat. The Flathead River system in northwestern Montana above Flathead Lake may represent one such potential core area. Genetic studies of bull charr within the Flathead subbasin (Kanda et al. 1997) suggest intact metapopulation structure within most of the major drainages, but little gene flow among populations from different drainages.

Historical and Present Distribution of Bull Charr

The current distribution of bull charr in the Pacific Northwest and Intermountain West is fragmented. Populations occur primarily in pristine or nearly pristine headwater regions of the Columbia and Klamath drainages (Rieman and McIntyre 1993). Many populations have undergone significant declines in recent years (Howell and Buchanan 1992; Thomas 1992). Because bull charr populations are now restricted to headwater regions and much of the historic metapopulation structure is now fragmented, vulnerability to extinction has increased for individual populations (Rieman and McIntyre 1993).

Propagation Efforts for Bull Charr

Bull charr have been little used in propagation efforts; however, recently the U.S. Fish and Wildlife Service has initiated some propagation efforts at the Creston National Fish Hatchery in Montana.

Status under the Endangered Species Act

Throughout the range of bull charr south of the Canadian border, the USFWS recognizes three ESUs, two of which occur in the Columbia River Basin. All three ESUs (Klamath River, Columbia River and Jarbidge River) are listed as threatened.

Indigenous Species other than Salmonids

Sturgeon

White Sturgeon (*Acipenser transmontanus*)

Green Sturgeon (*Acipenser medirostris)*

Background

Sturgeon are an ancient anadromous fish, which were formerly widely distributed on all continents in the northern hemisphere. Two species of sturgeon occur in the Columbia River basin. During the twentieth century, extensive disruption of freshwater and estuarine habitats coupled with heavy exploitation severely reduced populations of sturgeon throughout their range.

Historic and Present Distribution of Sturgeon

Green sturgeon are found in the lower 40 miles of the Columbia River, in its estuary, and in the adjacent marine waters. The green sturgeon has not been reported in the Columbia River above Bonneville Dam, River Mile 145, and it is thought to be concentrated in the lower 40 miles of the main river (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995). Green sturgeon reach lengths of up to seven feet, and females are sexually mature at five to six feet. Information on the spawning period, spawning behavior, and other details of the reproductive biology of green sturgeon in the Columbia River is lacking (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 1995).

White sturgeon were once widely distributed among the watersheds of the Columbia River basin, and they still enjoy a higher abundance and wider geographic distribution than the green sturgeon. White sturgeon below Bonneville Dam exhibit the anadromy characteristic of the species; however, sturgeon in the reservoirs above Bonneville Dam may be capable of completing their reproductive cycle within a single reservoir (Parsley et al. 1993; Parsley and Beckman 1994). Sexual maturity is found in males of four feet and longer and in females six feet and longer. Females have fecundity proportional to length, with one to three hundred thousand eggs per female. However spawning does not occur annually, but at two to four year intervals. Fecundity may be proportional to the length of time between spawnings. Spawning requires fast flowing waters over rocky substrate at temperatures of 48 - 62°F in May and June.

White sturgeon in the lower Columbia River three feet long or less grow at the rate of about 3 inches per year. Sturgeon beyond three feet in length grow at 3 inches per year until sexual maturation, when annual growth slows substantially. Sturgeon are about eight inches long at one year of life and attain the length of six feet at 23 years of age. The time span between the lengths of 3.5 to 5.5 feet in length is about ten years.

Dams constrain the movements of white sturgeon, creating isolated populations in the reservoirs of the Columbia River power system (Beamesderfer and Nigro 1993; Parsley et al. 1993; Parsley and Beckman 1994). Productivity of the isolated populations is lower than in the unimpounded river system due to impacts of hydroelectric system operation on the reproductive activities. Low flows in May and June inhibit spawning and subsequent recruitment. Appropriate rearing habitats for juvenile and adult sturgeon are provided within the reservoirs. However, severe population reductions occurred during the early 1980s in the John Day and The Dalles reservoirs as a result of fishing.

Harvest of Sturgeon

Commercial white sturgeon fisheries began in the 1880s reaching a peak of six million pounds in 1892, with catches declining sharply by 1899. During this time the average individual in the harvest were seven feet and 150 pounds. With protection of the broodstock afforded by maximum size limits on harvests imposed in 1950, recovery of the populations became possible. Sturgeon stocks appeared to rebound in the 1970s approximately 20 years after the maximum size limit on harvests was imposed. Contemporary fisheries harvest the same number of sturgeon harvested during the 1890s; however, the average size is much lower, so the annual harvest is about one million pounds. Population levels in the John Day and The Dalles pools have declined sharply, probably in response to levels of exploitation. In the upper Columbia River and in the Snake River, sturgeon populations vary from one impounded section to another, with some sections perhaps approximating historic numbers.

Research and Propagation of Sturgeon

Ongoing research programs are conducted by the Columbia River Inter-Tribal Fish Commission, and the states of Washington, Oregon, Idaho, and the Nez Perce Tribe of Idaho. Research is focused on understanding the harvest, population dynamics, and reproductive biology of white sturgeon, following recommendations made by Beamesderfer and Nigro (1993). Some hatchery production of sturgeon has occurred in Oregon and Idaho.

Status under the Endangered Species Act

The Kootenai River sturgeon are listed by the USFWS as an endangered ESU.

Pacific Lamprey

(*Lampetra tridentata*)

Background, Distribution, and Status

The Pacific lamprey is a jawless anadromous fish, which is widely distributed in western North America and eastern Asia. It is one of three species of lamprey in the Columbia River basin along with the anadromous river lamprey (*L. ayresii*) and the resident brook lamprey (*L. richardsoni*). Numerous factors, including loss of freshwater habitat and construction of hydroelectric dams have contributed to its near extirpation in the Snake River portion of the Columbia River basin, and to the reduction in numbers of adults seen at the counting windows on the hydroelectric dams (Close et al. 1995)

During its marine residency, adult lamprey are obligate parasites on adult bony fishes, including salmon (Scott and Crossman 1973). Because of this, management agencies have either ignored it, or attempted to eradicate it. In any event, specific data on the age, growth, and productivity of Pacific lamprey in the Columbia river basin is limited (Kan 1975). In general, adults spawn in small tributaries at an age of about seven years. The young rear in tributaries in the form of early juveniles called ammocoetes, and in the main river as late juveniles, neither of which are parasitic life history stages. As adults in the marine environment, lamprey attach themselves to hosts where they subsist on bodily fluids extracted through a hole bored in the host's side. Lamprey may return to spawn at around age seven.

Lamprey have had difficulty adapting to the hydroelectric dams. Because lamprey utilize much the same freshwater spawning habitat as do spring chinook salmon, it may be inferred that lamprey have been reproductively disadvantaged to the same extent as have the chinook due to logging, grazing, agriculture, mining, and other natural resource extraction activities.

The role of lamprey in the ecosystem as a prey item, and as a force in the biogeochemical cycle, merits consideration. Their role in bringing nutrients into the predominantly oligotrophic Snake River basin may have contributed directly to salmon production in that region.

Research and Propagation of Pacific Lamprey

Native Americans prize the lamprey as a ceremonial food item, and annual subsistence and ceremonial harvests on the order of several thousand "eels" are taken by the tribes. The Council has called for a lamprey research program, and several institutions have developed background information and recommended an approach to monitoring and management (Close et al. 1995).

Conclusions and Implications

Different species and populations of salmonids in the Columbia River and elsewhere exhibit remarkable phenotypic, life history, ecological, behavioral, and genetic diversity. The diversity described in this chapter, which is a hallmark of salmonids in general, arose from differential or local adaptation to the varied and variable environments within the complex landscapes of the Columbia Basin. The diversity has resulted from the plasticity, adaptability, productivity, and long-term persistence of salmonids in the fluctuating geological and environmental landscapes of the Pacific Northwest. Such diversity, which buffers salmonid populations against both short- and long-term scales of environmental variation, has become even more important today as human activities have increased the rate and amplitude of environmental fluctuations over those salmon experienced historically. We believe diversity (phenotypic, life history, genetic, ecological, etc.) within and among salmon populations is critical to the long-term persistence of salmon in the Columbia River ecosystem. We also believe salmon populations in the Columbia River today can form the base for rebuilding salmon abundance and diversity.

Conclusions (and Levels of Proof)

1. Diversity within and among salmon populations has been substantially reduced in the Columbia River Basin due to the extinction of many local populations, as well as a reduction in population size of most extant populations. (1)

2. Many fisheries management practices (e.g., harvest, dam operation, hatchery operations, transportation, etc.) have the potential to reduce variation in salmonid stocks. (1) Data exist that document losses of diversity associated with harvest and hatchery practices (see detailed discussion in Chapter 8). (1)

3. The use of hatchery stocks, in many instances, has reduced the between-population component of genetic variation in some species (e.g., Lower Columbia River coho, Upper Columbia River chinook). <u>Note</u>: see detailed discussion in Hatchery section, Chapter 8. (1)

4. The importance of local adaptation to salmonid populations and their long-term persistence has been underestimated. This is supported by the general lack of success of salmonid introductions and re-establishments, within the basin, most of which have failed. (2-3)

5. Losses of genetic diversity may have decreased the reproductive and ecological fitness, and therefore, decreased the probability of long-term persistence for many stocks. Habitat fragmentation and degradation have disrupted historic metapopulation structure. Under unconstrained conditions, metapopulation structure would act to stabilize losses of diversity and reproductive fitness, as well as persistence, within individual populations. (3)

6. Re-establishment of metapopulation structure among Columbia River salmon populations, where possible, would function to slow or even stabilize the loss of diversity in presently isolated local populations. As metapopulation linkages become well-developed, phenotypic, genetic, and life history diversity should stabilize and increase. (2-3)

Management Implications

1. We recommend that management include explicit recognition of the importance of stock diversity in all aspects of the restoration effort. The success of the Hanford Reach fall chinook, which exist in the only free flowing stretch of the mainstem Columbia River that is accessible to anadromous stocks, supports our conceptual foundation described in Chapter 3.

2. Wherever possible, management actions should not be stock or life history selective. For example, all life history types should benefit equally from the action. Monitoring and evaluation should be used to verify that certain life history types are not favored by the action and other life history types selected against.

Return to Table of Contents
Go to Next Chapter