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Population Structure of Columbia River Basin Chinook Salmon and Steelhead Trout

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The population structure of chinook salmon and steelhead trout is presented as an assimilation of the life history forms that have evolved in synchrony with diverse and complex environments over their Pacific range. As poikilotherms, temperature is described as the overwhelming environmental influence that determines what life history options occur. The different populations represent ecological types referred to as spring-, summer-, fall, and winter-run segments, as well as stream- and ocean-type, or stream- and ocean-maturing life history forms. However, they are more correctly described as a continuum of forms that fall along a temporal cline related to incubation and rearing temperatures that determine spawn timing and juvenile residence patterns. Population structure of chinook salmon and steelhead in the Columbia Basin, therefore, is the reflection of the genetic composition of the founding source or sources within the respective region, shaped by the environment, principally temperature, that defines life history evolutionary strategy to maximize fitness under the conditions delineated. The key in developing an effective recovery program for chinook salmon and steelhead is to recognize that measures taken must address the genetic and biological requirements of the population unit within the environmental template identified.

Keywords salmonid life history, salmonid genetics, temperature

Introduction

The Pacific salmonids evolved with the Pacific ecosystem under very dynamic and harsh conditions that are believed to have had overwhelming influences on the evolution of the salmonid species, life history strategies, and the population structure that each ultimately

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developed. The dynamics of plate tectonics and geological formations peculiar to the Northeastern Pacific Rim created opportunities for speciation among salmonids that have resulted in seven anadromous oncorhynchids distributed over a range from the Arctic to lower California, with four oncorhynchids becoming stream dwellers during their freshwater resident phase. Two of these were chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*), unique in that they are similarly distributed throughout freshwater stream systems from the lower mainstem all the way to the upper headwaters of their respective rivers. The Columbia River system is considered the general center of chinook (Healey, 1991) and steelhead (Busby et al., 1996) abundance and geographical distribution along the eastern Pacific. However, with development of the Columbia Basin to assist economic growth of the Pacific Northwest, the river system and its supporting habitats for chinook and steelhead have been altered substantially (Figure 1).

Of the 673,400 square kilometers of basin (Mullan et al., 1992), 191,660 square kilometers were made inaccessible to anadromous species with the construction of Grand Coulee Dam on the mainstem (Fish and Hanavan, 1948), and 189,070 square kilometers were blocked by Hells Canyon Dam on the Snake River, reducing access to about 40% of the original area available (Netboy, 1980). Furthermore, 64% of the remaining mainstem habitat on the Columbia and Snake rivers has been changed from flowing stream to reservoir environments [Oregon Department of Fish and Wildlife (ODFW) and Washington Department of Fish and Wildlife (WDFW), 2000]. Consequently, the potential for natural production of these species has been significantly reduced, and the prospects for any level of

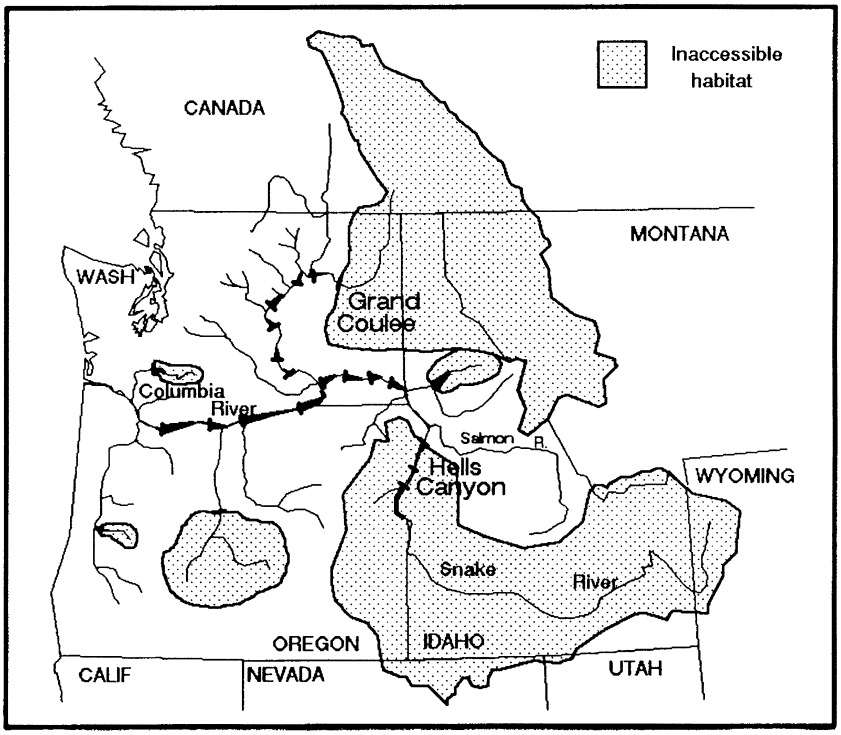


Figure 1. Columbia River Basin showing dams on the mainstem and inaccessible habitat.

recovery in the system must consider what is possible under present river conditions, given the biological and physical restraints in which chinook and steelhead are now confronted.

Our objectives, therefore, are to describe the population structure of chinook salmon and steelhead in the Columbia River Basin,[1] and to suggest how knowledge of the factors affecting their life history should influence management and recovery plans for these species. After a brief review of chinook salmon and steelhead biology, the assessment continues with a commentary on chinook salmon life history and the model that was developed to explain the origin of life history types (Healey, 1991), which we refer to as the "racial model." We challenge the application of that model in explaining chinook life history options because of the implications that the model has on defining population structure, and propose an alternative mechanism where temperature is the primary influence responsible for life history differences in both chinook and steelhead.

Our premise is that genetic differentiation occurs through continuing selection, synchronizing life history temporal patterns with environmental temperatures, and that life histories taken collectively with their genetic signatures define population structure. In support of this alternative theory, which is referred to as the "temperature model," we review the predominant influence of the environment on the biological and ecological identities of these species and the options that segregate life history forms across their entire range. Finally, given the importance of spatial and temporal environmental variation on species life history, the implications of management and recovery measures in the altered river system are discussed. For clarification, population structure of Columbia River chinook and steelhead refers to the sum of their component population elements in the various sub-basins, which are presented as a system of metapopulations (Williams et al., 2000) within the Columbia Basin.

Biological and Ecological Diversity

Chinook salmon and steelhead evolved as separate species sometime prior to the Pleistocene (Neave, 1958; Thorpe, 1982). Segregation into their present forms followed a series of events early in the phylogeny of the genus that were believed precursors to speciation (Miller and Brannon, 1982). Homing to the natal habitat was a characteristic thought to have been acquired early in the development of the family Salmonidae as the decisive trait that permitted adaptive synchrony with the local environment in the evolution of the salmonid reproductive system. Also early in their origin, the adoption of anadromy was necessary to permit the incipient oncorhynchid to leave freshwater and exploit the more abundant nutrient resources of the marine environment to markedly increase their reproductive capacity through enhanced growth and fecundity. However, it would appear that anadromy had its most far reaching influence by allowing the incipient oncorhynchid to concentrate limited freshwater resources just on the production of juvenile biomass for temporary freshwater residence and thus greatly leverage their diversity and numerical potential in freshwater systems before emigrating to richer marine resources for post-juvenile growth.

Speciation among the eastern Pacific oncorhynchids, therefore, was promulgated by the distinct delineation of freshwater habitats, and greatly assisted by the oncorhynchids

[1] In this paper the Columbia River Basin is divided into the lower Columbia, mid-Columbia, and Snake River regions, each of which is further subdivided into several sub-basins. We define the lower Columbia as the region extending from the mouth of the Columbia to the confluence of the Snake River. The mid-Columbia is that region extending from the confluence of the Snake River upstream to the Grand Coulee Dam. The Snake River region encompasses the entire Snake River basin.

being free of dependence on long-term freshwater residence. As divergence and speciation transpired, diversity within species further evolved against the background of spatial and temporal variation of the environmental template over the latitude and elevation of their range. The short, steep, hydrologically variable streams flowing into the Northeastern Pacific basin, with precipitation cycles and a temperate climate resulting in both fall and spring flood patterns, characterized the coastal zone. In contrast was the drier interior zone with better defined seasons that varied with elevation and distance from the coastal area.

In the broader definition of the oncorhynchids, chinook and steelhead are unique by their similarities. They are sympatric throughout much of their Pacific range except for the northern-most extremity. They share the common trait of penetrating far into the freshwater systems along the Northeastern Pacific. As anadromous forms, chinook and steelhead coinhabit most of the extensive freshwater rivers, from the lower reaches of major trunk streams clear to the headwaters feeding the systems. Their juveniles are stream dwellers, show territoriality, and depend on benthic and drifting food sources.

Among the differences that set them apart as distinct species, however, are their reproductive strategies and temporal distributions. Steelhead maintained the repetitive spawning characteristic of their iteroparous relative, *Salmo*, while semelparity evolved in chinook that consolidated the entire procreative energy into the one-time production of offspring. Except in the southernmost part of their range, chinook spawn in the fall, with juveniles migrating to sea in their first and second year. In contrast, steelhead are late winter and spring spawners, with progeny that remain in freshwater at least two years before migrating to sea. The Columbia Basin represents a microcosm of environments that have been most conducive to the elaboration of very different life history forms within and between the species that elucidate the biological foundations that separate chinook salmon and steelhead.

Columbia Basin Chinook Salmon Biology

Chinook represent the most diverse anadromous life history patterns of all the Pacific salmon. They show the greatest variability in size, enter freshwater over the most variable temporal pattern, penetrate into the most variable freshwater habitats of the system, and show the greatest temporal range in spawning. Chinook are classified by the seasonal timing of their freshwater entry (Burner, 1951; French and Wahle, 1965) and by their stream residence behavior (Healey, 1991). Columbia River returning adults have thus been referred to as spring chinook, summer chinook, and fall chinook from the early years of the fishery (Cobb, 1930). Chinook fingerlings show a high degree of variation in stream residence time, extending from a few weeks to over a year (Healey, 1991). Gilbert (1913) first identified chinook based on their length of stream residence. Sea-type, later referred to as ocean-type (Healey, 1991), were those entering marine waters in their first year (age-0), while those fingerlings that remained in freshwater and migrated as yearling smolts were referred to as stream-type chinook. Spring chinook generally assume the stream-type life history form, and fall chinook generally demonstrate ocean-type life history, although exceptions are numerous. However, in the general perspective, migrating smolts are found leaving the river nearly every month of the year (Dawley et al., 1984, 1985), with a discontinuity during winter months that separates what is viewed as the two life history forms.

Adult Columbia Basin chinook return to spawn primarily in their third to sixth year of life. Fecundity ranges from 3000 to 12,000 eggs, and averages around 5,000 (Healey, 1991). Chinooks spawn over larger gravel in deeper water than other oncorhynchids and

generally select sites associated with downwelling or upwelling riffle areas in the mainstem or larger tributary streams. They spawn in late summer, fall, and early winter. The progeny incubate until early spring, and after emergence reside initially in the security of their natal stream.

This diversity in timing and location of spawning is matched by diversity in the life history traits of juvenile and sea-going stages. Reimers (1973), Schluchter and Lichatowich (1977), and Healey (1983) have recognized numerous life history forms based simply on where and how much time juveniles spent in freshwater before entering the sea. Diversity in freshwater life history is the consequence of chinook evolution as a stream resident generalist during their juvenile stages. As with all stream dwelling salmonids, chinook have had to contend with the limitations of the carrying capacity of stream environments, which meant that stream habitat ultimately controlled their abundance (Bjornn and Reiser, 1991; Chapman et al., 1995). The multiplicity of forms that chinook life history has assumed, therefore, can be viewed as the result of adaptive strategies selectively maximizing their opportunities under population numerical pressures in these nutrient limited systems (Stearns, 1976, 1977; Real, 1980).

Given the variability in life history strategy, fry emerging from incubation show high diversity in stream residence patterns. Emerging fry seek cover in shallow areas next to shore (Hillman et al., 1989a, b). Some take up residence and feed in a three-dimensional territory, while others follow a feeding migration downstream over successive weeks. Length of residence is also variable (Reimers and Loeffel, 1967; Bjornn, 1971; Reimers, 1973). Some migrate immediately, while some remain in the locality of their natal stream only a short time before moving (Lister and Walker, 1966). Others will remain until the following spring and migrate rapidly downstream and immediately out to sea. The pattern of residence and migration is influenced by growth rate and other environmental factors, and has become embedded in the genetics of the different stocks.

Young chinook, therefore, are found migrating to sea any time during the first 18 months of life (Rich, 1920; Reimers, 1973; Dawley et al., 1984). Young chinook show a high tolerance for serum chlorides, and they can rapidly acquire a tolerance for water of high salinity (Weisbart, 1968; Wagner et al., 1969, Whitman, 1987), which gives them the ability to enter marine waters over an extended period of time. Many juvenile Columbia chinook move to the estuary after about 3 months of residence in the river (age-0), and inhabit the marine environment in the littoral areas closer to shore (ocean-type) as they move northward along the coastline (Dawley et al., 1981; Healey, 1991). Those that migrate as yearling (age-1^+) are larger at the time of marine entry (stream-type) and these fish make a more rapid transition out to sea, migrating northward further offshore (Dawley et al., 1981; Healey, 1991). The young feed mainly on terrestrial and aquatic invertebrates throughout their freshwater residence (Chapman et al., 1994a), and become predominantly piscivorous as they grow into adults (Keeley and Grant, 2001).

Juvenile salmon imprint on their homestream site (Hasler and Scholtz, 1983), and apparently in their seaward migration (Quinn, 1982), to establish the route of the adult return journey; the provision that permits adaptation with local environments to maximize fitness. Columbia chinook migrate north as far as the Bering Sea, while others remain off the coasts of Washington, Oregon, and California (Hartt, 1980; Healey, 1991). Columbia chinook range from 1 to 7 years in age at return (Healey, 1991), which appears associated with differences among river systems (Rich, 1925), but most chinook return to spawn at 3 to 5 years of age. Their marine life is spent feeding along ancestral migratory circuits specific to stock origin (Brannon and Setter, 1989), preparing for the trek home and ultimately reproduction.

Columbia Basin Steelhead Trout Biology

Steelhead are considered to show the most life history diversity among the salmonids because of the options they have in anadromy and resident life history patterns (Barnhart, 1986). As anadromous forms, they demonstrate different life history patterns from that of chinook salmon. Adult steelhead returning to the upper Columbia River basin migrate long distances and overwinter to spawn the following spring. They face different overwintering conditions than steelhead in coastal regions west of the Cascade Mountain crest, which contribute to the distinctiveness between the coastal and inland forms (Allendorf, 1975). In both coastal and inland areas, adult steelhead enter freshwater and migrate upstream in fall and spring of the year, and in the Columbia are designated as summer-run and winter-run fish with regard to the timing of freshwater entry.

Two major lineages of *O. mykiss* are presently recognized in North America: the coastal—*O. m. irideus* and inland—*O. m. gairdneri* groups (Behnke, 1992), generally separated in the Columbia River Basin by the Cascade crest (summarized in Busby et al., 1996). Steelhead can be divided further into two basic reproductive ecotypes based on the state of sexual maturity at the time of river entry and duration of spawning migration (Burgner et al., 1992; Busby et al., 1996). Stream-maturing (commonly known as summer-run) steelhead enter freshwater from May-October in a sexually immature condition and remain in rivers all winter, spawning the following spring. In contrast, ocean-maturing (also known as winter-run) steelhead enter freshwater from November to April with well-developed gonads and spawn shortly thereafter. Winter-run distribution tends to be low in the Columbia River drainage with only a few populations existing above the Bonneville Dam, and predominate in coastal rivers. Summer-run steelhead are a little smaller and usually return to cooler streams further upstream than winter steelhead (Busby et al., 1996), and constitute most of the inland steelhead of the Columbia River Basin.

However, it should also be pointed out that the differentiation between summer-run and winter-run steelhead is not as clear as one might assume from descriptions in the literature. The maturation schedule might better be viewed as a continuum based on geographical and temporal criteria. Streams that are on the coast have short migration times to spawning grounds, and thus the maturation process may need to begin in the ocean, whereas the migration times to spawning grounds inland are much greater, and the fish would begin maturation on their way to the spawning ground. There may not be a clear and clean breakpoint between stream and ocean-maturing ecotypes, but rather a continuous distribution. In the Columbia River Basin, there is a fairly clear line between coastal and inland drainages, and the observed break in the maturation forms may only reflect the physiogeography.

In addition to the ocean- vs. stream maturing forms (i.e., winter vs. summer dichotomy), summer steelhead in the Columbia River basin, particularly the Snake River sub-basin, are commonly referred to as either A- or B-run. These designations are based primarily on a bimodal distribution of migration by adults, noticeable at Bonneville Dam, and also a difference in body size. A-run fish are younger and smaller and found throughout the range in the Columbia Basin, and B-run fish, which are larger and tend to be a year older, are only found in the Clearwater Sub-basin and the North and Middle Forks of the Salmon River in Idaho. There is some uncertainty about the genetic basis for these groupings, and the classification system separates them by the date they pass Bonneville as they migrate upstream. A-run steelhead pass Bonneville Dam from June to August 26, whereas B-run pass the dam from late August to October (Busby et al., 1996, 1999). In addition, the A-run fish generally spend one full year at sea and average about 75–100 mm smaller than the B-run fish, which tend to spend two full years at sea before returning (Busby et al., 1996).

Although steelhead may have spawned in some areas of the mainstem Columbia, adults are most generally associated with tributary streams. Summer-run fish that spawn in the upper and mid-Columbia tributaries enter the system months earlier between May and September [Washington Department of Fisheries (WDF) et al., 1990]. They pass Rock Island Dam from July through the following May, with the peak occurring between August and September (Craig and Suomela, 1941; Fish and Hanavan, 1948; Peven, 1992), and overwinter in the mainstem of the Columbia or tributaries (French and Wahle, 1959). Although summer-run fish spawn a little later than winter-run fish, all steelhead spawn in the late winter and spring months, generally from December to June, and well isolated from most chinook spawning times.

Steelhead fecundity covers a range of 2500 to 10,000 eggs, with an average around 3500 eggs (Shapovalov and Taft, 1954; Bulkley, 1967; Pauley et al., 1986; McGregor, 1986). In the mid-Columbia region, however, steelhead fecundity has averaged as high as 5,300 eggs (WDF, 1938). Steelhead fry emerge from their incubation streams in late spring to August. Fry and small fingerlings may disperse downstream in late summer and fall. Juvenile steelhead rear all year in freshwater, migrating seaward as smolts in March to early June after 2 years of stream residence. However, stream residence can range from 1 to 7 years before fingerlings get large enough (>170 mm) to smolt. It is interesting that A-type steelhead juveniles appear to have adapted to high summer temperatures and can be found rearing in water that exceeds 22°C during summer months, as is also characteristic of redband trout, their freshwater resident form (McCullough, 1999). Smoltification among steelhead appears to depend on the size of fish rather than age (Elson, 1957; Fessler and Wagner, 1969; Ward and Slaney, 1988). Naturally produced steelhead smolts average between 143–207 mm fork length (Chrisp and Bjornn, 1978; Peven, 1989; Mullan et al., 1992).

Steelhead have been known to migrate well into the Northwestern Pacific, making long treks out to sea (Hartt, 1980), but others also are more closely associated with waters offshore of Washington and Oregon. Marine age in fish of the Columbia Basin is generally 2 years, but can range from 1 to 4 years. For example, in the Snake River drainage, a portion of the steelhead from the Clearwater River smolt at age 2, but spend only 1 year in the ocean, returning at age 3, and spawning at age 4. In contrast, South Fork Salmon River steelhead smolt at age 3, return to freshwater at the end of their sixth year, and spawn at age 7. Mid-river female smolts tend to be older than males (Peven et al., 1994), and females also tend to remain longer in the ocean than males. In general, data reported on Columbia stocks (Howell et al., 1985) show the prevalent age of naturally-produced steelhead in the mid-Columbia region is 4 years, 2 years in freshwater, and 2 years in marine waters.

As a species with both anadromous and stream resident forms, *O. mykiss is* rather unique compared to the other oncorhynchids, with strong representation of both life history forms throughout their range. Resident forms occur in most areas occupied by steelhead, especially in inland drainages, but the proportion of the two is not well documented. It is possible that the fitness advantages of anadromy decrease with increasing migration distance, but cold temperatures appear to diminish the anadromous life history option (Mullan et al., 1992) as is apparent north of the Aleutians (Van Hulle, 1989), confounding the influence of distance with elevation. Most interesting, however, is the evidence of gene flow between life history forms (Busby et al., 1996), although the magnitude is unknown. Recent genetic analyses have demonstrated that rainbow trout and steelhead from within the same basins are more closely related to each other than steelhead or rainbow trout populations across basins (Busby et al., 1996), and, in some cases, these sympatric forms cannot be differentiated genetically from one another (Leider et al., 1995).

Ecological Diversity

Based on evolutionary theory, speciation arose in isolation by accumulation of selective traits compatible with the defining environmental template (Mayr, 1966). As geographic barriers fell and species commingled, interactive pressures would have further defined species around ecological parameters, with more specific differentiation concurrently evolving at the population or stock level. Population structure of a salmonid species is defined by the life history strategies that evolved to maximize fitness under the variety of environmental conditions delineated within their geographic range. Chinook salmon competition for rearing habitat with chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), and sockeye (*O. nerka*) doesn't occur because chum, pink, and sockeye juveniles are not stream resident. Juvenile coho salmon (*O. kisutch*) are stream resident, but spawn later than chinook and utilize tributaries and smaller streams that overlap with chinook primarily at lower elevations. Steelhead and cutthroat trout (*O. clarki*) are spring-time spawners, which separates them from salmon. Cutthroat are generally in higher elevation streams than steelhead, which leaves chinook and steelhead as the primary species that are integrated in similar habitat over the same geographic range.

Species integration under diverse and dynamic environmental conditions is complex, involving temporal patterns in flow, temperature, nutrient base, interactive competition, predation, and the numerical abundance. We suggest that the evolution of chinook life history occurred with chinook as a dominant species among the salmonids, and thus their life history strategy was probably not markedly influenced by interaction with steelhead of comparable age (Miller and Brannon, 1982). In contrast, steelhead life history is presented as having evolved under a greater influence of other salmonids, and assumed their present pattern in the Pacific salmonid ecosystem in large part from interaction with the more numerous members of the salmon community. Life history strategies of chinook and steelhead as sympatric species, therefore, have taken different pathways in response to the complex environment confronting them.

Most revealing among the differences separating chinook and steelhead was the manner in which they accommodated sympatry, and the decisive influence this had on life history options between the two species. Interactive encounters among sympatric salmonids would have been common with the rapid expansion of habitable territory from the recession of the continental glaciers. Overlapping demands for food and space are suggested to have promoted interactive competition, resulting in the displacement of congeners by the dominating species in a given area (Allee, 1982). Interactive aggression, therefore, would have created dominance hierarchies, specific to environmental circumstances and the size of interspecific competitors. Interactive segregation, however, would also have been under selective pressure to minimize the cost of aggression on fitness, encouraging genetic tendencies to segregate volitionally in the presence of the more aggressive forms (Brian, 1956; Michod, 1999), referred to as selective segregation. Under such a scenario, hierarchical patterns supposedly evolved that left the competitively less dominant salmonids in successively less productive sites in order of the degree of submission among congeners.

Where sympatric with chinook, steelhead are reported to use different daytime and nighttime habitats throughout the year (Chapman et al., 1995), consistent with the concept of selective segregation. Hillman et al. (1989a, b) observed such segregation in the Wenatchee River where juvenile steelhead occupied shallower and slower water than chinook in summer months. Steelhead stations were near cobble and boulder cover, while chinook were associated with brush and woody debris cover. During the winter, steelhead and chinook used similar habitat, but segregated to different reaches. In studies of certain

Idaho streams, Everest and Chapman (1972) and Hillman et al. (1987) also found that steelhead and chinook selectively segregated to different habitats. Whether such distribution is displacement from more productive feeding sites by the dominant resident as the theory implies, or related to the evolution of habitat preferences, is uncertain. However, in the presence of chinook salmon, it appears that steelhead segregate to different habitat or cover to reduce aggressive encounters.

A more decisive strategic difference between chinook and steelhead was the temporal evolution of spawning times. Spring-time spawning among trout in general is uncommon except within the geographic range of Pacific salmon where *O. mykiss* and *O. clarki* are spring-time spawners. Miller and Brannon (1982) suggest that steelhead evolved from the fall spawning pattern, characteristic of most other Pacific salmonids, to a late winter and early spring spawning time to avoid overlap with fall spawning salmon. The motivation for such temporal differences in spawning time is speculative, but spring-time spawning of steelhead served to reduce competition with salmon for spawning area, and it also positioned fry emergence at a time when the shallow feeding areas were being outgrown and evacuated by salmon fry.

However, such temporal adaptation also permitted *O. mykiss* to more effectively colonize cooler headwater streams and habitat available at higher elevations. Headwater streams probably challenged fall spawning species because freezing and or desiccation of otherwise suitable habitat during winter would cause higher risks to incubating eggs and alevins in that environment. By adapting to spring-time spawning, incubating progeny of steelhead were far less susceptible to such adverse conditions, and by exploiting higher elevation habitat, they avoided having to compete with young salmon in those areas. Therefore, although the evolutionary motivation for spring-time spawning of *O. mykiss* is uncertain, the opportunities available to steelhead by such adaptive strategy appear to be significant in the evolution of a life history that provided a measure of segregation from competing salmon.

In the process of salmonid evolution, chinook salmon appear to occupy the principal mainstem and tributary habitats of the freshwater system at the most favorable temporal setting for maximum fitness of progeny. By the apparent absence of modified behavior and distribution in the presence of other salmonid species, we conclude that chinook salmon are a dominant form in the mainstem and tributary streams they occupy over their range. Conversely, by the opportunities that steelhead have through altered timing and behavior over that same geographic range, we conclude that the presence of chinook salmon at least exerted an interactive influence on steelhead integration within the salmonid ecosystem. Steelhead accommodated sympatric residence with chinook by having different spawning times, different emergence times, slight differences in preferred habitat, and use of different stream reaches during rearing (Hillman et al., 1989a, b). These differences, therefore, are apparent from the biology of the species, their ecological interactions, and the population structure that each species has assumed to maximize survivability.

Life history forms, therefore, are genetically predisposed to strategies that optimize survival under the restraints of local stream environments. When referring to life history strategy, we are describing a behavioral repertoire that has proven successful for a particular population of the species under given environmental constraints. For example, fall chinook that utilize a stream for incubation and early rearing that is unsuitable later in the summer or winter will acquire a short-term pattern of residence and disperse downstream before unsuitable conditions arise (Bjornn, 1971). Others may experience less productive rearing conditions upon emergence in their stream and disperse immediately downstream (Lister and Walker, 1966), while others that find sufficient nutrient resources in reservoirs remain in

residence for a full year before emigration (Murdock and Petersen, 2000), similar to spring chinook.

O. mykiss has retained the resident life history option (Burgner et al., 1992) or the rainbow phenotype that plays a major role in the life history of this species. In several instances, steelhead may also show a distorted sex ratio in favor of females. Peven et al. (1994) reported that 63% of the smolts sampled at Rock Island Dam in 1988 were female. In at least one assessment on the Thompson River, adult females were much more numerous than males (McGregor, 1986) and reports have been made on the predominance of females in high sea samples (Burgner et al., 1992). As Chapman et al. (1994b) commented, it may be more important for females to become anadromous because of the physiological cost of maturation, which might help explain the differences in sex ratios observed in the mid-Columbia region.

These different patterns of behavior, therefore, are referred to as life history strategies that represent various options that have been selectively successful over the broad geographic range of the species. In combination, the life history strategies of a species represent multiple options, but a given population may have but one option under specific circumstances unique to its habitat. We believe the variability in life history strategy of steelhead and chinook salmon associated with the freshwater habitats is dominated by water temperature as the defining environmental characteristic of stock evolution. As temperature influences the age at which juveniles emigrate, and even the annual variability in the period of residence before emigration (Roper and Scarnecchia, 1999), we argue it also determines the life history forms they assume. This results in a population structure, therefore, that is determined by the various life histories of the component parts.

Herein rests the problem in describing the population structure for chinook salmon and to some degree for steelhead. The two theories on the origin of chinook life history have a major influence on the definition of population structure, and what actions are taken to preserve their contribution to the Columbia Basin ecosystem. The racial model implies a polyphyletic lineage of chinook, which represents a markedly different perspective of population structure having evolved as separate "races," which subsequently distributed faithfully to their prototypes. We argue that separating chinook into two racial forms masks the interpretation of life history phenomena and tends to leave management and recovery approaches less flexible than looking at life history as a response to the nature of their habitat experiences. Population structure is determined by the genetic elements associated with the member populations but, more importantly, by the life histories of the populations contributing to that structure within the respective river system. Life histories are defined by the adult return, spawning, incubation, rearing and marine phases that are expressed by the species in the river system, and can be roughly divided into spawning/incubation and the rearing/emigration profiles. The racial model emphasizes the juvenile rearing/emigration phase of their life history and tends to ignore the major influence of the spawning/incubation profile on life history. Resolution of this issue is fundamental in understanding the evolution of population structure and, therefore, is given attention here to establish the basis of this assessment.

The Origin of Life History Forms

Life history theory on chinook salmon centers around two fundamentally different perspectives: one of existence and expansion as separate subspecies (racial model), and one simply of environmentally induced forms (temperature model). The racial theory is based on the isolation and evolution of two life history types from which all subsequent populations were

derived. Counter to that argument is the theory that life history forms are the result of ongoing natural selection in response to environmental forces, principally temperature, evident in early life history behavior patterns during freshwater residence and shortly thereafter.

The Racial Model and Chinook Life History

In discussing the racial model on life history of chinook, it is necessary first to define the term race, which has assumed various meanings in the fisheries literature. Race has been used synonymously with the terms population, run, deme and stock as discussed by Meehan and Bjornn (1991). Thompson (1945) used such a definition of race to describe the separate runs of sockeye returning to streams of the Fraser River, and thus as distinct sub-units or breeding populations within a run returning to an individual river basin. In that instance, the term is clearly used as a synonym of stock, and thus even temporal segregations within a returning salmon or steelhead run could qualify under such a definition of race.

However, race may be defined in the broader context as a genetically distinct group within the species that is carried across and identifiable throughout the geographical range of the species. Merrell (1981) defined races as "geographically distinct aggregates of breeding populations that differ genetically from one another and between which gene flow is restricted." He used the term race congruently with the term subspecies. For purposes of this discussion, race is used in this broader context, as a geographically distinct group or subdivision of the species, and in contrast to stock that in this discussion will represent a segregated unit of the breeding population or run returning to a given stream. Race defined in the broader context, therefore, is consistent with the definition of Myers et al. (1998), in which races represent separate monophyletic evolutionary lineages, as "types" of chinook salmon.

Chinook were first classified as two different types by Gilbert (1913), who based the separation on scale analysis. Gilbert considered those chinook with scales showing wide growth rings around the nucleus as having entered the marine environment shortly after emergence, and he referred to these as "sea-type." In contrast, those with scales having crowded or narrow rings around the nucleus representing slower growth were assumed to have spent their first year in freshwater residence before entering marine waters, and those Gilbert referred to as "stream-type." Healey (1983, 1991) expanded on the nomenclature and included with the contrasting residence patterns the differences in marine distribution between chinook of ocean-type (formally sea-type) versus stream-type forms. The primary element in Healey's premise was that these types were segregated across the range of the species and paralleled the subspecies classification conforming to Merrell's (1981) definition of race. Therefore, ocean-type and stream-type were presented as separate races, independent and geographically isolated from one another except in the southern part of their range where they are sympatric within river systems but separated temporally (Healey, 1991).

The evidence that Gilbert, and later Healey, used for classification of chinook salmon as two different types, and supposedly genetically discrete, was based on the contrast between two obvious juvenile behavioral forms. In the racial model, the two races were contrasted (Table 1), but the primary differences were related to length of stream residence and marine distribution, including the length of time spent in near-shore waters and age at return. The stream-type form was shown to rear for 1 or 2 years in freshwater before migrating to sea, and making extensive offshore migrations in the North Pacific. Geographically, this race was associated with that area of the North Pacific coast above 56°N latitude and in headwater systems in areas south of 56°N at higher altitudes (Figure 2). The sea- or ocean-type form was associated with the rest of the area located south of 56°N latitude.

Table 1
Life history structure of chinook salmon showing division of two races: ocean-type and stream-type, and the characteristics of each race (Healey, 1991).

Race: stream-type	Race: ocean-type
Adults runs in spring and summer and enter freshwater months before spawning	Adults run in summer and fall, and spawn soon after entering freshwater
Long freshwater residence as juveniles	Short freshwater residence as juveniles
Variation in seaward migration in years	Variation in seaward migration in weeks
Variation in time of return to natal stream—February through July	Variation in time of return to natal stream—July through December
High fecundity	Low fecundity

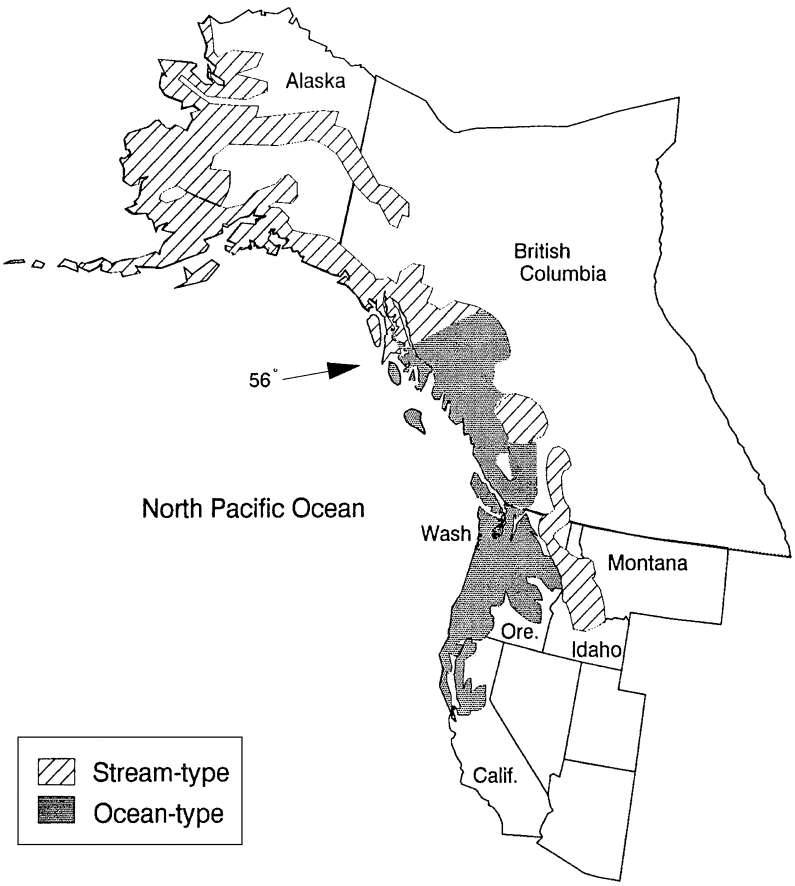


Figure 2. Map showing the distribution of chinook salmon populations on the Northeastern Pacific coast and Bering Sea under the racial model.

Juveniles of the ocean-type form enter marine waters in the first few months after emergence from incubation, and remain longer in near-shore waters with less extensive migrations into the North Pacific. Under the racial model, the types were derived through allopatric evolution during continental glaciation (Healey, 1983), and following glacial recession, they independently colonized new habitat similar to that of their founding sources.

Post-glaciation colonization of two distinct forms was consistent with the hypotheses of McPhail and Lindsey (1970, 1986), Lindsey and McPhail (1986) and Taylor (1990a), suggesting evolutionary origin of ocean- and stream-type chinook could have occurred in isolated refugia during the extensive Pleistocene glaciation period of the northern continent, the Beringia in the north and the Cascadia in the south. The implication, therefore, was that 56°N on the Pacific Coast is the general boundary between the areas recolonized from the two refugia, stream-type to the north and ocean-type to the south. Taylor (1990b) also showed genetic differences between ocean- and stream-type chinook salmon populations in a comparative study, and such evidence could be used to support separate origins under allopatric evolution, corresponding to the broad definition of race as subspecies. Myers et al. (1998) used the racial classification of chinook in their status review and suggested the genetic data supported the concept of two races by reporting "clear evidence" of genetic separation between ocean-type and stream-type life histories, compatible with separate monophyletic lineages.

We disagree that the racial theory provides a viable model for the present chinook salmon life history patterns observed, and we suggest that the genetic data is not as decisive as originally thought. Geographically, both life history forms overlap throughout much of the chinook salmon range, and 56°N latitude does not represent a clear boundary above which ocean-type chinook are absent (Delaney et al., 1982; Johnson et al., 1992). Sufficient time has elapsed over the 10,000+ years since glaciation to have permitted introgression of forms in areas where ocean- and stream-type chinook overlap, if life history differences were simply the result of founding types. Moreover, the behavioral differences reported by Taylor (1990b) were from comparative observations and involved behavioral patterns that would be expected to arise independently if they were of selective advantage under the respective circumstances (Linley, 2001). Therefore, rather than chinook salmon life history forms originating from different founding types as races or subspecies, we propose the alternative model where life history forms are primarily the result of environmental temperatures related to latitude and elevation. In support of the broader theory, corroborating ecological and genetic evidence is presented with implications on life history strategy of both chinook and steelhead.

The Temperature Model and Chinook Life History

Consistent with evolutionary theory to include the adaptive maintenance of behavioral variation, we propose that the different life history forms of chinook salmon can be explained by their interactions with the environmental template where temperature is the primary influencing mechanism. Although we don't address the McPhail/Lindsey hypothesis that chinook salmon may have segregated in isolation during continental glaciation, we argue that the phenomenon most responsible for such adaptive strategy was not isolation, but rather the more basic and continuing influence of water temperature, suggested by Miller and Brannon (1982) and implied by Taylor (1990a), using air temperature as the comparative parameter.

Understandably, poikilotherms salmonids are completely dependent on temperature, which affects metabolic rate, growth, and other physiological characteristics of the species

(Groot et al., 1995). In retrospect, however, its role in life history and ultimately population structure has not been sufficiently regarded. Karr (1994, 1995, 1997) has been a consistent advocate of river health, and has identified primary classes of water resource attributes through which human activities can alter biological integrity. In these fundamental works, temperature has been included among other environmental parameters grouped together under the general classification of water quality. However, when the biological entity is a poikilotherm, temperature needs to be given separate and special recognition. Water quality constituents such as sediments, nitrates, and even pesticide levels have thresholds in concentration below which little or no effect can be demonstrated on the biological activity of the organism. There is no comparable lack of affect on poikilotherms that accompany changes in temperature. Even minor temperature shifts have an influence on life processes among the salmonids, and can impose substantial alterations over life history patterns demonstrated at the population level (Brannon, 1987; McCullough, 1999).

Most concerns about temperature in the ecological literature seem to be identified with increases that approach the lethal extremes. However, the far more profound impacts of temperature are related to the changes that occur well within the tolerance range of the species. A change in mean incubation temperature of 1°C, for example, can alter the period of incubation and emergence timing by more than a month (Miller and Brannon, 1982; Brannon, 1987; Táng et al., 1987; McCullough, 1999). These otherwise forbearing differences in finite temperature regimes, therefore, have major influences on the synchrony between life history and the environment, which we have referred to as life history strategy (Stearns, 1976, 1977).

We propose that life history strategy of chinook salmon evolves under the influence of temperature along two different avenues. The first is its general influence on the timing of adult return to freshwater, and thus the classification of what has traditionally been referred to as spring-, summer-, and fall-run chinook in the Columbia Basin. The second avenue is its influence on the age of emigrating juveniles and the classification of what has been referred to as ocean-type and stream-type life history forms.

1. The Basis of Spring, Summer, and Fall Chinook Life History Forms. Spawning times, and thus return patterns that facilitate getting fish back to their natal streams on time, are indirectly determined by (a) the influence of temperature on migration and spawn timing, and (b) the relationship between spawning and incubation temperatures. Both of these factors are under the controlling influence of the fitness of emerging fry.

a. The influence of temperature on chinook return migration and spawn timing. Columbia River adult returning chinook salmon are referred to as spring-, summer-, and fall-run fish (Burner, 1951; French and Wahle, 1965). The designation is based almost arbitrarily on the times they enter freshwater. Chinook in the lower and mid-Columbia are presently designated by the date they pass Bonneville Dam (Table 2), and subsequently as they pass

Table 2
Identification of spring, summer, and fall chinook based on passage dates.

	Spring-run	Summer-run	Fall-run
Bonneville Dam	3/15–5/51	6/01–7/31	8/01–11/15
McNary Dam	4/01–6/08	6/09–8/08	8/09–10/31
Rock Island Dam	4/13–6/17	6/18–8/17	8/18–11/15

dams further upstream, such as at McNary and Rock Island, respectively [Fish Passage Center (FPC), 2001]. Returning chinook are thus identified as three different runs. This is an unfortunate classification system because it has implications on managing Columbia chinook as three separate groups. For example, Ricker (1972) identified Columbia River runs to include a spring run (early spring entering the river in February to mid-April that headed for the Willamette and Klickitat Rivers and a late spring main river run migrating upriver from late March to May), a June and July summer run migrating to the middle and upriver spawning tributaries, and a fall run of mainly lower river fish entering the system in August to November. In reality the Columbia River chinook salmon run is made up of many different sub-units that contribute to a near continuum of returning fish over the return year. Although much reduced from their historical abundance, we argue that the pattern represents a cline or continuous return from February to December with multiple peaks of abundance that at any given time represent the combination of several populations, each destined for a different natal stream. Therefore, we argue that rather than three distinct spring-, summer-, and fall-chinook segments or "races" entering the river, the migratory return pattern represents a continuum of many different populations of a single race passing up through the mainstem river in sequence based on their predetermined travel optima and spawning times.

Adult chinook start their migration at different stages in reproductive advancement. Those fish migrating greater distances, or experiencing a more difficult journey, enter freshwater at an earlier stage of sexual maturity. The temporal difference between migration and maturation is much exaggerated among the early returning fish because of the environmental conditions that must be accommodated for the early spawning segment to successfully reach their native habitat. The early return time is related to river temperatures, flow, and migratory distance. Many spring chinook populations return months before maturation to enhance their access upstream, and we speculate to minimize energy requirements needed to sustain them until spawning. With the high summer temperatures in the Columbia, it is suggested that returning upper river spring chinook evolved an earlier freshwater entry timing to pass through the mainstem early enough to avoid the negative affects of the warmer temperatures (Berman and Quinn, 1991). Similar to all salmon, chinook fast upon return to freshwater, which makes energy conservation a high priority. Early entry allows chinook to avoid warmer temperatures with net energy savings applied to spawning needs. For example, if late August chinook spawners in the Wenatchee River were returning through the mainstem of the Columbia during late July and August, they would have to confront temperatures in excess of 20°C (Figure 3). Estimated active energy needed to negotiate the 800 km distance would be nearly twice the calories required over the same distance during early May when mainstream temperatures are 10°C (Brett, 1995). Wenatchee chinook appear to enter the Columbia well before the high temperatures occur to conserve energy for the spawning event.

The difference in energy use while holding is markedly different than energy expended for active migration. Applying the same standard (resting) metabolic rates for sockeye (Brett and Glass, 1973) to chinook, 10- to 15-fold less energy would be used to hold in warmer temperatures compared to actively swimming. By migrating earlier in cooler temperatures and holding during the warmer period, a net savings in energy occurs even with the extra holding time required until spawning. Berman and Quinn (1991) demonstrated that early returning Yakima River chinook thermoregulate by seeking refuge in cooler, lower velocity water while fasting, as part of the energy conservation strategy during the holding period.

Avoidance of high temperatures also circumvents other related problems. Any effect that prolonged exposure to high temperatures has on maturation schedules (McCullough,

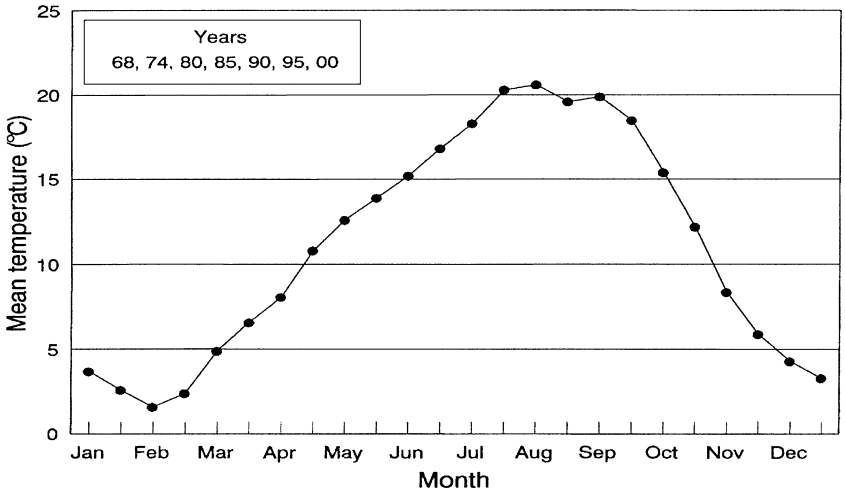


Figure 3. Columbia River mean biweekly temperatures measured at The Dalles Dam.

1999) can disrupt the temporal synchrony with the environmental timetable. High temperatures can also affect gamete viability, increasing egg mortality as temperatures elevate above 13°C (Leitritz and Lewis, 1980). The disadvantages of high temperatures enroute to the spawning grounds are believed great enough that chinook experiencing those conditions have adapted to earlier freshwater entry, weeks and months before maturation, to secure a more optimal thermal regime, and then hold in proximity of their destination several weeks until spawning.

Among the late returning stocks of chinook, the difference between return time and maturation is most compressed. Late stocks characteristically enter freshwater shortly (<1 month) before spawning in the late fall and are not challenged by high summer temperatures. The timing patterns demonstrated among and within different segments of the Columbia River chinook run are stock specific, as with other salmonids (Thompson, 1945; Ricker, 1972; Miller and Brannon, 1982), and thus critical to stock identity in the return migratory continuum and to the diversity of chinook in the system. Therefore, even with the lower numbers of fish migrating during summer months, once migration is initiated, return time should be viewed as a continuous variable that reflects the ecological differences among the temporal segments of the chinook run. The assumption is that selection has identified the timing of return among chinook stocks within the system to optimize fitness, and if that pattern is altered significantly beyond the normal range of variability, we expect that it would have a negative effect on survival as shown in various studies (Chilcote et al., 1986; Hulett et al., 1996; Reisenbichler and Rubin, 1999).

Factors other than temperature also have major effects on the timing of adult return. Flow, in many cases, is a decisive factor associated with travel time, getting past areas that have very low summer flows, and partial barriers. An example is the return timing of the early Puntledge River chinook that allows them to take advantage of higher flows to facilitate passage over the Puntledge River falls on Vancouver Island. Two populations are identified in the Puntledge system, an early returning population that spawns above the Stotan Falls (Figure 4), and a later run that spawns below the falls (D. Lister pers. comm.). Spawning grounds are separated by the falls, and temperature regimes of the upper and lower river spawning areas are nearly the same. However, the summer-run enters the Puntledge in

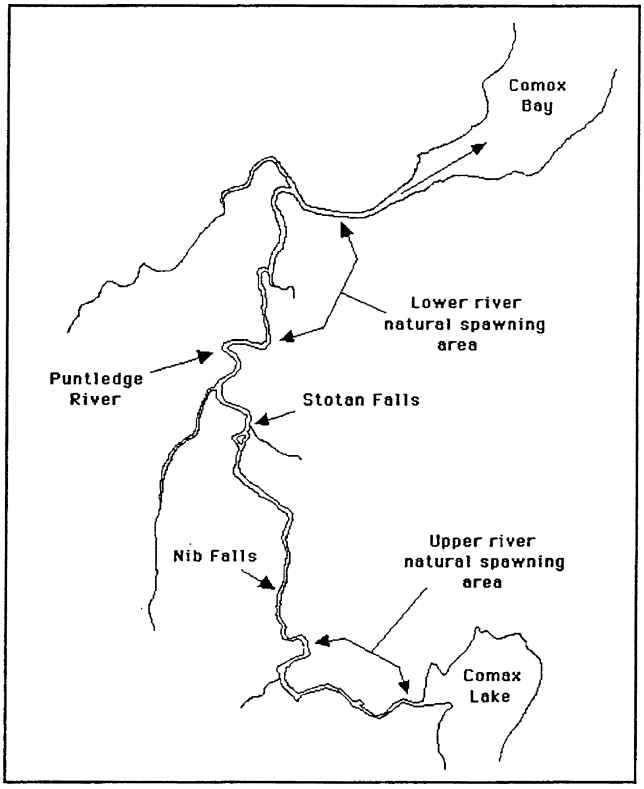


Figure 4. Puntledge River showing locations of upper river June/July returning summer chinook spawning area and lower river October returning fall chinook spawning area. Both populations spawn in October.

June and July, negotiates the falls and then waits three months to spawn in mid-October at the same time as the fall-run that enters the river in September/October. Negotiation of the falls in October is not possible because flows are too low to allow passage. Although the populations have the same spawning times, the opportunity to reach the spawning area above the falls is permitted only by returning early when flows are sufficient to provide access. These populations have adapted to the circumstances that satisfy their individual access and spawning requirements, each with very different return times but similar spawning times.

Therefore, in the ecological framework, the more informative point of reference to classify adult chinook salmon is spawning time, which is the origin of temporal differences associated with migratory behavior. The advantage of including spawning time in stock classification nomenclature is that it provides a maturation standard that allows accurate comparisons of temporal differences among stocks. Therefore, we propose that stocks should be identified by a three-letter abbreviated stream, return time (S, Su, F), median spawning date, and smolt age (0 or 1) rather than simply time of return. For instance, spring chinook spawning in the Upper Salmon River in mid-August would be designated as [USa-SA15-1], or summer-run in the Wenatchee River that spawn between September 2 and October 9 designated as [Wen-SuS21-0], or fall chinook spawning in the Lewis River in late November as [Lew-FN25-0]. This would provide the identity and the comparative

Table 3
Observed peak spawning dates of chinook in sub-basins of the Yakima River. (Data from Yakama Tribe spawning ground summaries).

Sub-basin	Early peak	Late peak
American river	August 8	August 15
Naches river	September 8	September 18
Little Naches river	September 1	September 11
Bumping river	September 6	September 8
Yakima river	September 15	October 5
Cle Elum river	September 16	October 5

temporal patterns among stocks to clarify life history relationships, and to identify stocks more accurately for management purposes.

Yakima River returns are a good example of how classification based simply on migratory timing can be deceptive. Chinook in the Hanford Reach of the Columbia, off the mouth of the Yakima, are arbitrarily classified by the date they pass McNary Dam (Table 2). Spring chinook passage corresponds with the period from April to June 8, summer chinook from June 9 to August 8, and everything passing the dam after August 8 are considered fall chinook (FPC, 2001). Based on those dates, fisheries managers consider the primary production in the Yakima to be from spring chinook. Summer chinook have been declared extinct because there is a gap in river entry corresponding to the June 9—August 8 period associated with summer chinook passage at McNary Dam (Table 2). Fall chinook make a relatively minor contribution on account of high temperatures in the lower Yakima River, and the high occurrence of exotic predators may also be limiting to fall chinook juveniles passing through the lower river. However, if one examines the distribution of spawning times of the component segments of chinook in the Yakima River (Table 3), September spawners are well represented in the system. Based on spawn timing, therefore, it appears that some of what has been classified as spring chinook in the Yakima are really summer chinook that demonstrate a migratory pattern specific to their needs in that particular river.

Water temperatures in the Yakima as well as other rivers are ultimately a function of air temperature (Sinokrot and Stefan, 1993, 1994; Johnson and Jones, 2000). With the length of the Yakima River and the hot summer weather in the Yakima Basin, the lower Yakima has probably always been too warm in July and August for good adult migratory conditions based on temperature models by Vaccaro (1986) and Lilga (1998). We would argue that the Yakima summer chinook adapted to earlier migratory timing in cooler temperatures, with a concurrent extension of the holding period (Berman and Quinn, 1991) until ready for September spawning, because of the selective benefit in energy efficiency that such behavior provided. Their absence in the July/August migratory slot passing McNary Dam, therefore, may not be from extinction, but rather ancestral selection for earlier stream entry to reduce the high-energy cost associated with migrating in warmer water. They avoid the negative effects of high temperature on spawner survival and egg viability by adapting to migrate up the Yakima River earlier than in other systems, but they show the same September spawning pattern demonstrated by other summer chinook.

More importantly, as demonstrated in Table 3, designations based on spawning times allow the components of the returning run to be classified as temporal segments within the seasonal maturation continuum of the Yakima subpopulations, and thus provide more precise

recognition of specificity in temporal identity than what is shown by migratory timing. Six segments are represented in the Yakima return population, separated geographically by location of spawning areas and by substantial temperature differences. We suggest that such differences are evidence that distinct temporal units are also represented in this system. Such specific criteria is important because it represents the biological diversity and synchrony that each of the many populations along that continuum has with its natal environment. They should not be lumped into broad categories where they lose recognition as specific units.

b. Relationship between spawn timing and incubation temperature. Chinook salmon spawning times in the Columbia Basin are related to thermal profiles of the natal stream. Spring chinook are those stocks destined for cold winter streams and enter freshwater in the spring, but spawn in the late summer. Summer chinook homing to progressively warmer streams spawn later, and fall chinook still later in the autumn. The controlling mechanism in spawn timing, however, is the timing of fry emergence, which translates into fitness. It is here that temperature is first demonstrated as a major influence on life history. Embryo development rate is a function of environmental temperature, with yolk stores sustaining development and growth until the fry emerge in the spring. The length of the incubation period is determined by the mean temperature (Figure 5). Incubation can take as little as three months at mean temperatures above 10°C or as long or longer than eight months as mean temperatures drop below 3°C.

The critical element that ensures high fitness of the progeny is the temporal position of emergence to maximize the subsequent survival of the newly emerged fry (Miller and Brannon, 1982; Brannon, 1987). Fry that emerge at the appropriate time for initial feeding opportunity, predator avoidance, and the temporal integration with other life history needs, have the selective advantage in subsequent survival over those fry emerging too early or

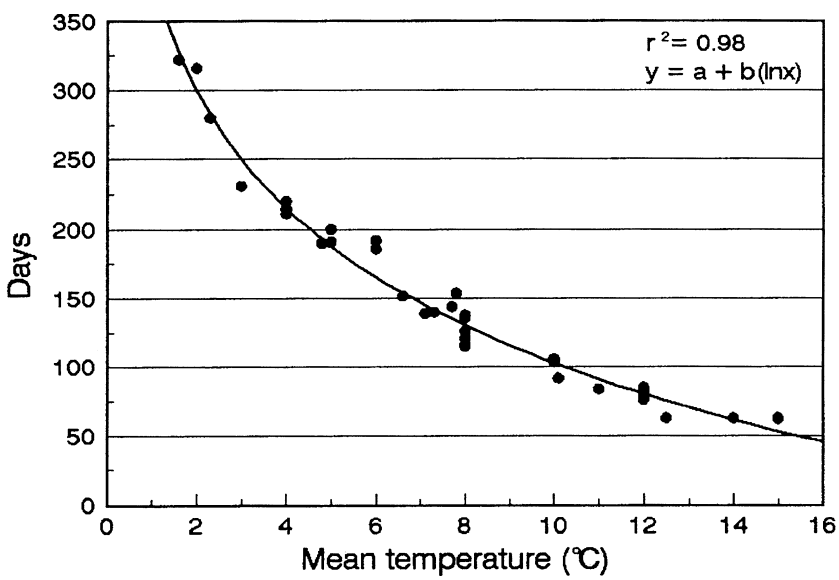


Figure 5. Relationship between mean incubation temperature and length of the incubation period in days to yolk absorption for chinook salmon (Seymour, 1956; Graybill et al., 1979; Alderdice and Velsen, 1978; Heming, 1982; Rombough, 1985; Murray and Beacham, 1987; Murray and McPhail, 1988; Crisp, 1988; Beacham and Murray, 1990).

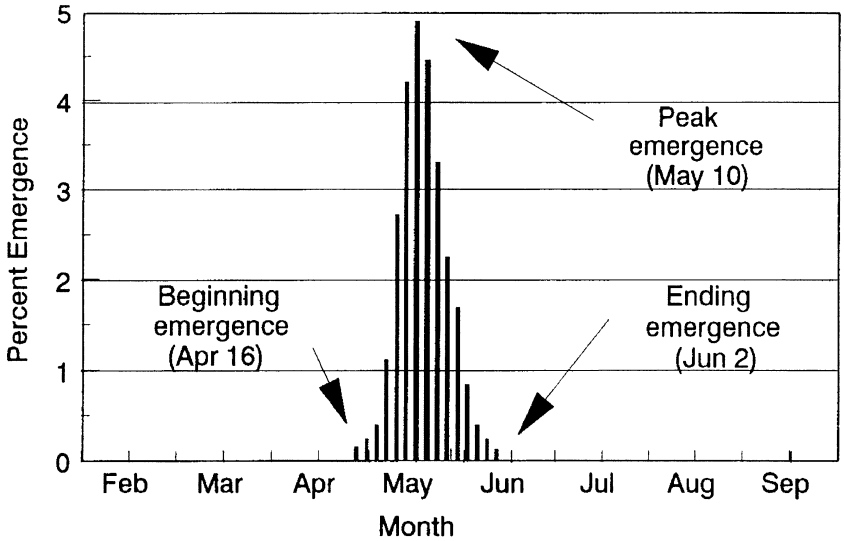


Figure 6. Emergence pattern for a hypothetical chinook salmon fry population with optimum timing demonstrated by the peak abundance on the emergence curve.

late in the cycle. Hypothetically, the process is illustrated in Figure 6, where the long-term average pattern of emergence starts on April 16, with the peak occurring on May 10 and terminating by June 2. In this example, therefore, the average peak emergence timing (May 10) represents the optimum temporal synchrony between emergence and the productivity of the receiving environment because it represents the highest spawner abundance, and thus selectively the segment of the run that is most successful.

Given that emergence is timed for maximum fitness, and that mean incubation temperature determines the length of the incubation period, then feed-back from the selective advantage of emergence timing establishes the point at which incubation must begin, and thus the most favorable point when spawning should occur. Natural selection positions spawning to correspond with the optimum time for fry emergence in the particular stream environment. Progressing from the lower reaches of the mainstem to its headwaters, mean incubation temperatures generally follow a decreasing trend, and because the rate of embryo development is slower at lower temperatures, spawning must occur correspondingly earlier to synchronize emergence with the optimum time in the spring for survival opportunity.

Plotting mean incubation temperatures against spawning times of various run segments in the Columbia Basin demonstrates how selection has positioned spawning in relation to mean incubation temperature (Figure 7). Temperature data were taken from USGS (1980–2001), USDOE (1960–77), USFWS (1969–73), Lindsay et al. (1986), Hillman et al. (1989b), Mullan et al. (1992), Petersen et al. (1995), Homolka and Downey (1995), IDFG (2000) and LaRiviere (2001). Peak spawning times are based on reports (regional biologists, Howell et al., 1985; Myers et al., 1998) and emergence based on agency reports or temperature analysis. Essentially, the relationship corrects for the effect that temperature has on the length of the incubation period. Cooler mean incubation temperatures select for earlier return and spawning characteristics of the early spring chinook, and progressively warmer temperatures select for correspondingly later spawners, forming a clinal pattern over time with the latest spawners returning to the warmest stream reaches.

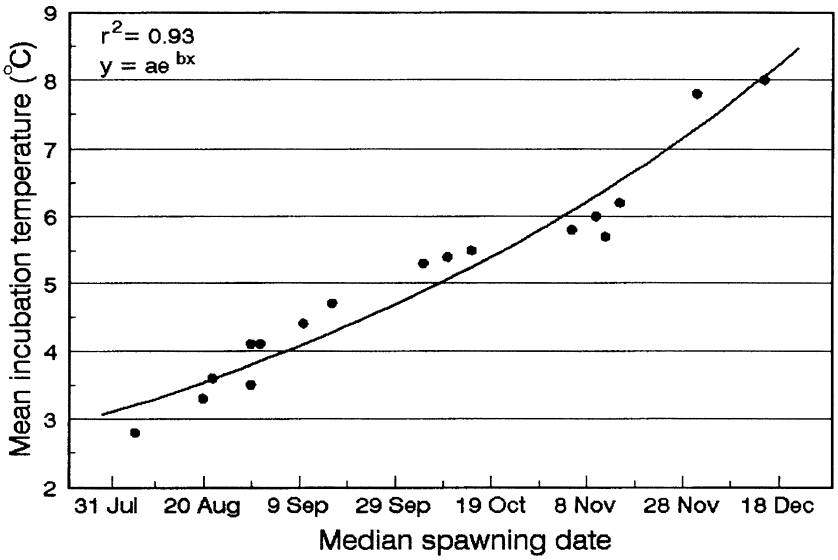


Figure 7. Relationship between mean incubation temperature and chinook salmon spawn timing of 17 chinook populations in the Columbia Basin (data sources reported in text below).

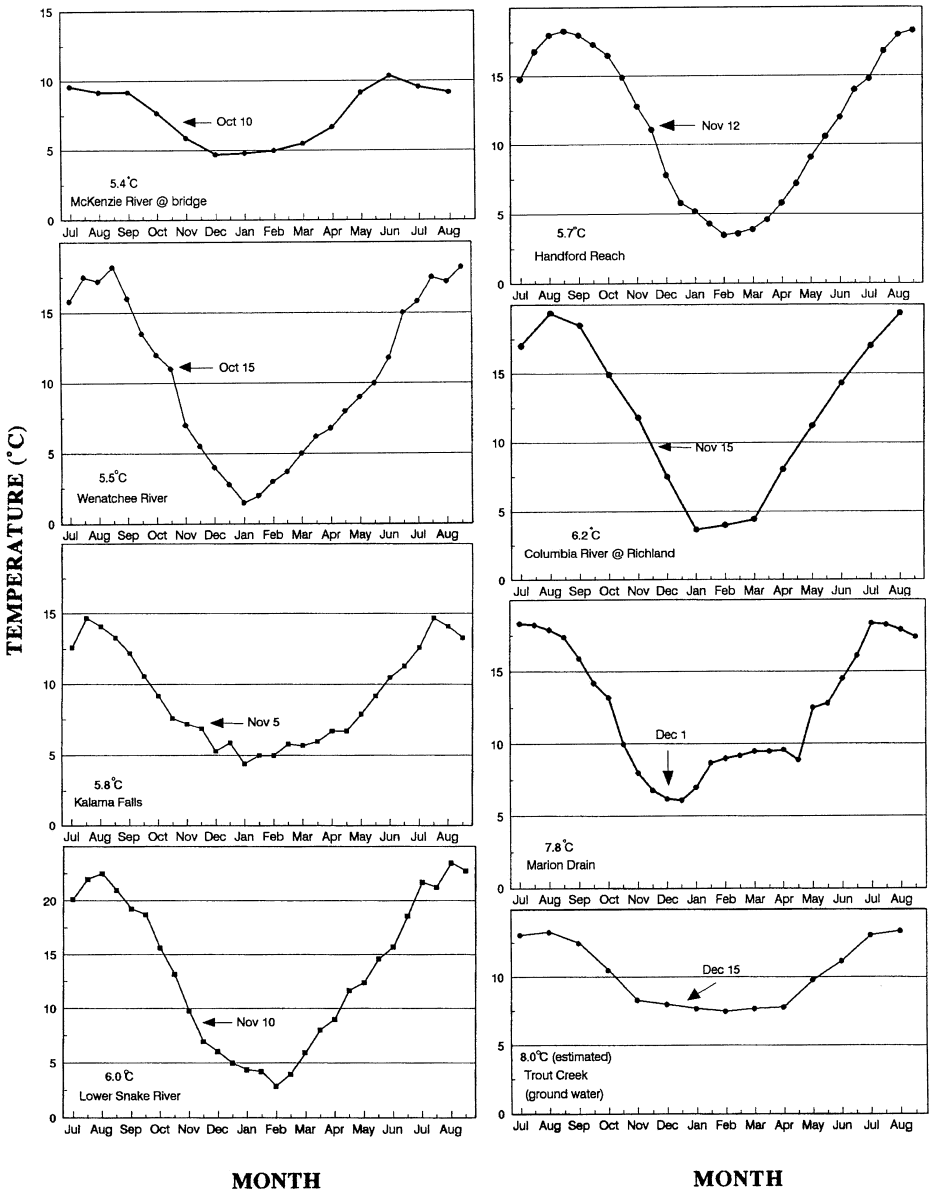
This is best demonstrated in the Columbia Basin by looking at the temperature regimes of various rivers in which chinook spawn (Figure 8). Seventeen chinook spawning streams representing areas from the American River, upper Salmon River, Snake River and mid-Columbia River down to the lower-Columbia are included. Early, middle and late spawning populations are represented. The rivers are aligned in the figure from coolest to warmest, with the estimated monthly incubation temperatures shown from the mid-point of spawning in late summer and fall seasons to spring for the respective chinook salmon populations. Temperature data were taken from USGS (1980 –2001), USDOE (1960–77), USFWS (1969–73), Lindsay et al. (1986), Hillman et al. (1989b), Mullan et al. (1992), Petersen et al. (1995), Homolka and Downey (1995), IDFG (2000), and LaRiviere (2001) and represent only approximations because the number of years varies among data sources. Peak spawning times are based on reports (regional biologists, Howell et al., 1985; Myers et al., 1998).

It is apparent from these graphs showing temperature regimes and peak spawning periods from the coolest to warmest rivers, that spawning progresses later in time along a temporal cline from early August to December as mean incubation temperatures become increasingly cooler. Although a level of variation occurs in incubation time related to egg size and oxygen concentration, the differences attributed to genetic variation in spawn timing among the populations are quite extensive. The mechanism that establishes and hones their genetic predisposition is feedback from the optimum performance of emerging fry. The survivors perpetuate the timing pattern responsible for their success, and that pattern on the average will also serve the needs of the successive brood years under that environmental template.

The importance of emergence timing in the ecology of chinook salmon is thus underscored by the degree that adult return and spawn timing has been altered to accommodate the length of the incubation period experienced by the progeny exposed to different temperatures among their respective natal streams. To successfully target a particular spawning time within a season that ranges from late summer to winter, each adult population must

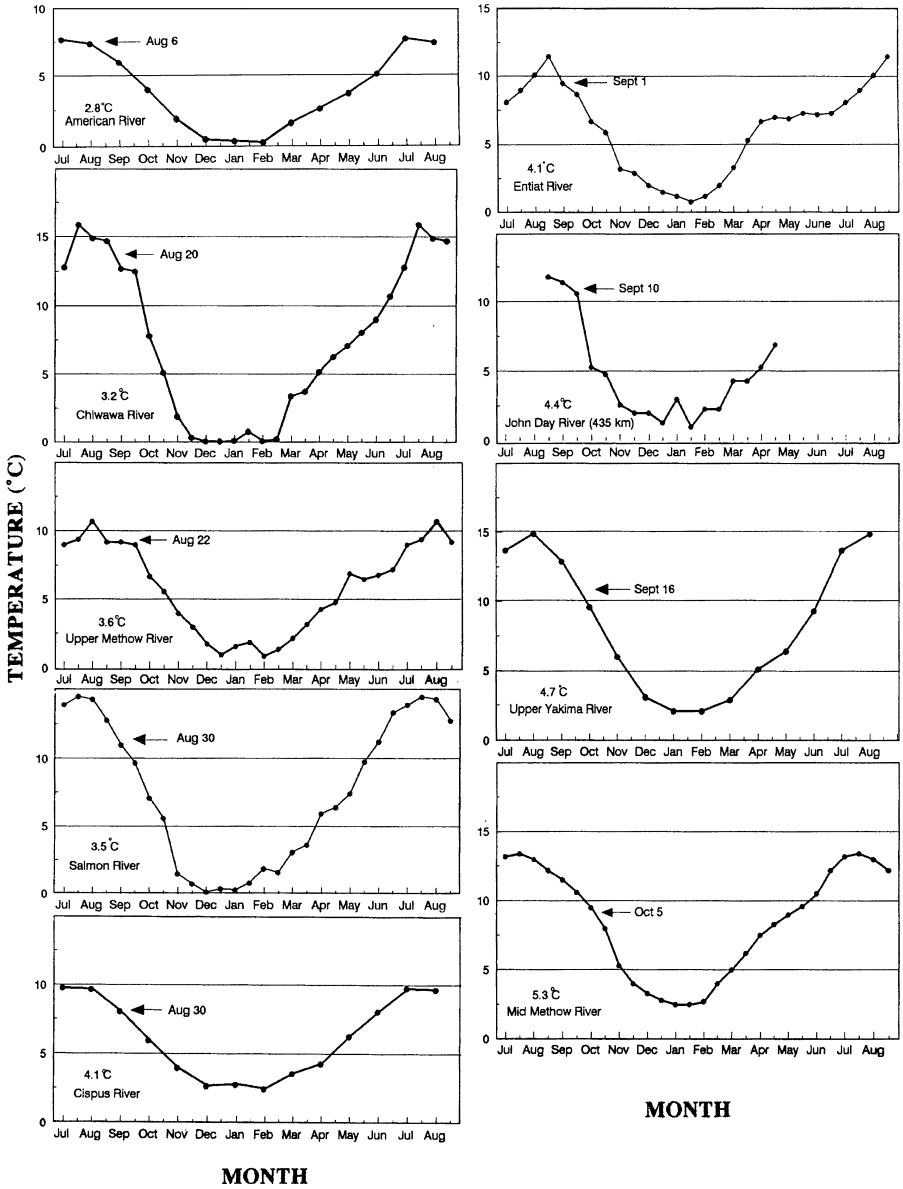
have a specific transit timetable along their marine migratory circuit, freshwater entry timing, freshwater stream transit timing, and homing to assure arrival on the spawning grounds and allow them to meet their spawning schedule. Consequently, emergence time is a critical event that has a decisive influence on the elaboration of life history.

An uncertainty with the relationships presented is that annual temperature regimes, spawning times and incubation periods can vary markedly from year to year. Also the temperature-recording locations are most often not directly associated with the spawning



(a)

Figure 8. Mean monthly temperatures in 17 Columbia Basin chinook salmon streams with median spawn timing and estimated incubation temperatures. *(Continued)*



(b)

Figure 8. (Continued)

grounds. The incubation temperature regime of Trout Creek is a good example of the uncertainty associated with temperature data and even population identity. Trout Creek, a tributary of Sandy River, is reported to be used by December spawners listed among indigenous stocks in the Columbia (Myers et al., 1998). However, temperatures in the Sandy Basin are not warm enough to support December spawners unless they selectively spawn on groundwater irrigated reaches. Groundwater temperatures are spotty, and although the estimated regime in Figure 8 would support December spawners, groundwater doesn't appear very extensive. Another tributary of the Sandy reported to be used by the late

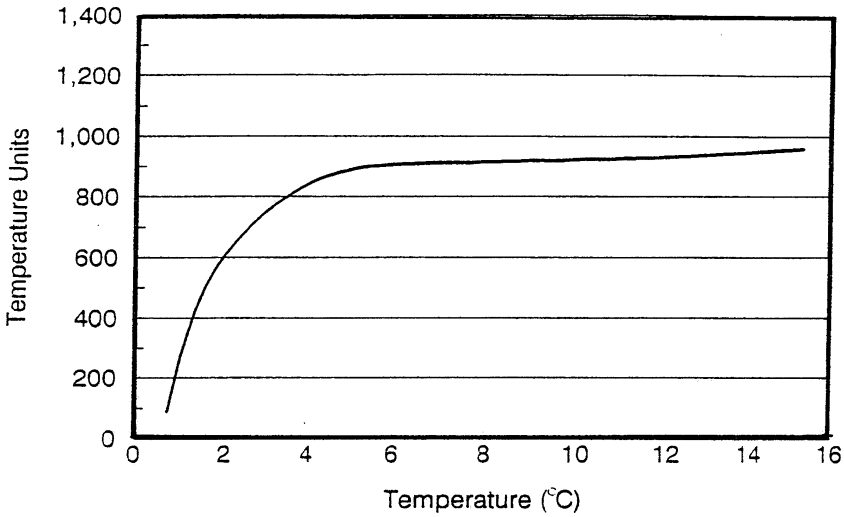


Figure 9. Relationship between temperature and the number of temperature units (degree-days) required for chinook salmon embryos to complete yolk absorption (converted from Figure 5).

spawners is Bull Run, but temperatures in that river remain below 5°C from November to March, a pattern appropriate only for October spawners. It is uncertain, therefore, whether Sandy River late-fall chinook are native or remnants of an introduced run originating from outside the Basin. The relationships shown in Figure 8, therefore, represent only the best approximations from the data available.

The importance of emergence timing is also demonstrated in how the embryos accommodate variability in incubation temperatures that occur over the incubation period beginning in the fall at temperatures generally above 10°C to mid-winter when temperatures fall to near 0°C. As demonstrated in Figure 5, chinook embryos require more time to reach yolk absorption as mean incubation temperatures decrease. However, the nature of the relationship between time and temperature is not linear. By converting time and temperature in Figure 5 into degree days (°C > 0°C/24 hr) and plotting degree days against temperature (Figure 9), it demonstrates that fewer degree days are required to reach yolk absorption at lower temperatures, and thus rate of development per unit of temperature increases as temperatures decrease. In essence, embryo metabolism helps compensate for the length of time that would otherwise be required to complete development when confronted with decreasing temperatures. The level of compensation shows a four-fold decrease in the number of degree days required by chinook embryos when incubated at 1°C compared to those incubated at 15°C (Figure 9).

The extent of such metabolic compensation is apparent when contrasting thermal unit sums without compensation. If the number of temperature units required from fertilization to exhaustion of the yolk stores were constant, then embryos incubating in cold streams would require proportionally more time to complete incubation. For example, if 1000 degree days were required to utilize their yolk stores, regardless of temperature, then embryos experiencing a mean of 10°C would require 100 days of incubation compared to 333 days for embryos at a mean of 3°C. However, because of metabolic compensation, embryos incubating at 3°C require about 240 days to utilize yolk stores, or an incubation rate 30% faster than predicted without compensation. Proportionally fewer temperature units for

incubation at cooler temperatures permit fall spawning salmon to avoid the problems that would accompany deviations in spawn timing when confronting abnormal temperatures in the absence of any compensatory ability.

The compensating mechanism also helps address the problems from unpredictable deviations in seasonal climate patterns after the spawning event, which could hasten or delay embryo development and distort emergence timing. For example, if winter is early and temperatures drop rapidly, thus decreasing the number of temperature units accumulated per day, compensation helps reduce the delay in emergence that would otherwise occur.

In this regard, we view the temporal range in emergence timing of fry as an expression of temporal fitness when taken over the combined timeframe of several years. Understandably, the emergence curve represents the accumulative effects of slight differences in spawning times experienced among brood year spawners, differences in egg size, variations in embryo development rates, and differences in irrigation efficiency through the redds. However, given such variance, the mean peak of the emergence curve represents the segment that contributes most effectively to the sustained reproduction of the population under that environmental template, demonstrated hypothetically in Figure 6. The accumulative effect of those factors responsible for peak abundance in the emergence curve translates into the temporal segment of the run with the highest fitness. We argue that elements left and right of the peak have not been as successful or emergence would have shown a much broader peak in timing, such as observed in Cedar River sockeye (Stober and Hamalainen, 1979, 1980). Spawning extends over seven months because Lake Washington is highly productive (Edmondson and Abella, 1988), allowing good fry survival over a much extended emergence period.

Similarly, in British Columbia, Cultus Lake is productive enough to promote sockeye spawning and emergence over 3-month periods in contrast to shorter durations in most other less productive lakes in the Fraser River system. The influence of selection on incubation rates is demonstrated by the sockeye fry from the late segment of the Cultus Lake run requiring about 150 degree-days less incubation time at constant temperatures than the early segment (Brannon, 1987), and thus converging on optimum timing. Therefore, in moving away from the peak, whether broad or narrow, the tails of the curve represent the pattern of diminishing fitness among those members of the population as they deviate further from central timing. The total absence of emerging fry beyond the tails of the emergence curve underscores the disadvantage to fitness if emergence timing deviates too far from the optimum pattern, and the critical nature of timing synchrony in the evolution of life history strategy.

It is important to reiterate the dynamic nature of this process. Every year there will be some level of variation in the spawning time, incubation temperature regime, and the receiving environment from that experienced by the parental brood year. The expected outcome associated with such environmental change is that slightly different temporal optima will be formed around emergence. Those components of the population that are most in synchrony with the optimum timing will be selectively favored on that given year. The genetic variability in a population, therefore, is present in part because the natural variability in the environmental conditions has been repetitious enough to maintain representation of the phenotypic variations. The process is dynamic and probably the best example of ongoing adaptive evolution. As suggested by Hendry et al. (2000), some population characteristics can demonstrate rapid evolution, and we argue that because life history strategy is so responsive to different temperature profiles, changes among clinal elements of the life history forms can occur in a relatively short timeframe, with concurrent implications on population structure.

Therefore, the first major influence of temperature on chinook life history demonstrated in this review is the very complex and puissant effect it has on adult migration and maturation through the feedback of optimum emergence timing. The synchrony of fry emergence with optimum conditions in the nursery environment is the functional element that establishes the most favorable point of spawn timing, and thus the driving influence on the adult return migratory schedule. The relationship clearly shows that stock evolution occurs through temporal segregation along differences in mean incubation temperature regimes over the length of the river continuum. In essence, selection positions spawning times to maximize fry survival under the environments specific to each population. Fry emergence is timed to correspond with the optimum feeding opportunity and to minimize losses during other life history phases. Optimum emergence timing is thus the basic determinant in the adult migratory return schedule and spawn timing.

2. *The Basis of Stream-Type and Ocean-Type Life History Forms.* The length of the juvenile chinook stream residence period has been a criterion used to classify the species into what is called stream-type and ocean-type forms (Healey, 1991). Most Columbia River stream-type juvenile chinook remain in freshwater at least a year before migrating to sea at an average length of >90 mm (Dawley et al., 1981). Stream residence of ocean-type chinook is characteristically less than a year, with juveniles migrating to marine waters within a week or two up to seven months following emergence (Lister and Walker, 1966), at a size <75 mm in length. Life history types are also associated with differences in marine residence patterns. In marine waters, stream-type chinook do not remain very long in nearshore areas, but move offshore and make distant feeding migrations, extending as far north as the Bering Sea. In contrast, ocean-type chinook remain closer to shore for their first year, and do not venture as far offshore or as far north as stream-type chinook (Healey, 1991). As summarized in Table 1, ocean-type chinook adults are younger upon return, are larger for their age, and also carry larger eggs than stream-type chinook (Linley, 1988; Lister, 1990). Therefore, the second avenue through which temperature has been the determining factor on life history strategy has been (a) its influence on length of stream residence before emigration, and (b) its affect on marine residence location.

a. Influence of temperature on length of stream residence before emigration. Although some of these differences have evolved around genetic associated phenomena (Taylor, 1990b; Linley, 2001), we argue that the basic differences that separate ocean- and stream-type chinook can in essence be reduced to the influence of their age and size at marine entry. The freshwater growth continuum of chinook during their residence in freshwater is interrupted by winter, and those conditions will separate juveniles of different sizes into pre-winter (0-age) and post-winter (age-1^+) seaward migrants, and thus create ocean-type and stream-type life history forms. Adaptation will then facilitate those characteristics that enhance fitness.

We conclude, therefore, that given sufficient food availability, the mechanism determining age and size at marine entry is the effect of temperature. Growth rate determines which of several life history strategies young chinook will assume, and thus the temperature associated with that phenomenon becomes the critical component dictating life history options. As pointed out by Taylor (1990a), the typical habitat associated with stream-type chinook life history forms is the cooler upper river reaches where lower temperatures require longer rearing periods before juveniles reach migratory size. Cooler headwater systems can limit growth, regardless of the nutrient base (Brett, 1995), and if chinook juveniles are unable to reach the migratory size at age-0, they will remain in freshwater and emigrate the following spring as larger smolts. In contrast, ocean-type chinook rear in habitats with higher

temperatures that encourage greater stream productivity and promote more rapid age-0 growth, and these fish enter marine waters in their first year of life. We submit, therefore, that the dichotomy between ocean- and stream-type phenotypic expression has its origin with fingerling growth phenomena related to temperature, as suggested by Rich (1920, 1925). The larger of the first year juveniles migrate at age-0 as ocean-type chinook, and those remaining migrate as stream-type age-1 smolts.

As with all life history traits, fitness will increase through selection for those characteristics that are successful under the constraints present in the particular habitats. With ocean-type chinook, those characteristics include elements that enhance early marine entry (Taylor, 1990b). Because growth opportunity during winter months will be much reduced and thus delay size related emigration, selection for higher growth rates under summer growing conditions would benefit presumptive age-0 smolts, and thus genetic selection for inherently higher growth rates would be an advantage to ocean-type juveniles. And in those coastal streams where habitat variability transcends both stream- and ocean-type environments, populations may express more than one life history type.

Ocean-type chinook also have larger eggs compared to stream-type chinook (Taylor, 1991; Lister, 1990). Smirnov (1975) hypothesized that because yolk conversion efficiency was lower at higher temperatures, greater yolk stores were required at warmer temperatures to complete development. However, the more important element of larger eggs is the larger fry (Fowler, 1972) they produce. Fry from larger eggs start feeding as larger individuals in the subsequent growth regime. This would have little benefit if larger eggs simply required proportionally more time for the embryos to absorb the yolk, but larger chinook salmon eggs also have a larger initial embryo mass (Linley, 1988), which helps offset the greater assimilation time that greater yolk stores would require. Larger eggs, therefore, appear as part of the adaptive mechanism to promote early marine entry among ocean-type chinook by starting at a larger size, as suggested by Taylor (1991) and Kreeger (1995).

Chinook salmon alevins also have the ability to utilize ingested food items before yolk stores are completely absorbed (Hopely, 1974; Heming et al., 1982). This is in contrast to other salmon species that don't begin feeding until yolk stores are nearly exhausted (Harvey, 1966; Hurley and Brannon, 1969; Roley, 1974). Hopely (1974) showed that chinook salmon alevins not only benefit from feeding at an early stage, they can attain a size at yolk absorption well over twice that of unfed alevins. Heming (1982) demonstrated that the growth response was accentuated at warmer temperatures. The net benefit of early feeding among ocean-type chinook, therefore, is that it promotes early growth and thus prepares them for early marine entry. Because growth rate is temperature limited (Brett et al., 1982), early feeding opportunity would have less benefit for stream-type life history forms that are associated with cooler temperatures and overwinter in freshwater before migrating to sea.

Linley (2001) demonstrated that the alevin growth response from precocious feeding was stock specific. Under identical laboratory conditions, alevins from Andrew Creek on the Stikine River in Alaska grew markedly better than alevins from Tahini River in Alaska under identical laboratory conditions. Andrew Creek fish come from a background of warmer temperatures than Tahini River chinook, and Linley suggests that growth differences were related to the evolution of life history strategies encouraged by the different environmental templates of the respective streams. Andrew Creek chinook have adapted to maximize their size at emergence and to facilitate early dispersal downstream by starting with larger eggs and alevins that benefit from early feeding. Tahini chinook don't have the option of early distribution in the cooler temperatures of Tahini River where such adaptations would serve little purpose in promoting early migratory opportunities. The Andrew Creek/Tahini River chinook example demonstrates that where opportunities exist, selection

from among the genetic variability present will produce life history forms that optimize their circumstance.

To rationalize the interplay between temperature and growth in formulating life history strategies, it is instructive to refer to the sockeye work of Brett et al. (1969). Brett suggested that sockeye, as lake-dwelling salmonids, were most frequently confronted with a ration insufficient to meet their scope for growth. Sockeye, therefore, were thought to assume a dispersal pattern in lake systems that could compensate for limited food by descending to the temperature strata where the scope for growth was optimized on the ration size consumed. The rationale was that smaller rations induced a retreat to greater depths where cooler temperatures would provide greater growth benefit from the limited food available. However, stream-dwelling salmonids are confronted with very different circumstances from that experienced by sockeye. Unlike lacustrine systems, variable temperature regimes are not readily available in stream environments. Rather than being able to easily retreat to cooler temperatures to optimize efficiency of food consumed, stream resident salmonids must attempt to optimize growth by increasing food consumption (Figure 10).

Chinook juveniles are territorial, which at least functionally works as a strategy to aggressively secure proportionally greater food resources in an attempt to satisfy their scope for growth at the temperature regimes they experience. We believe that until chinook reach migratory size, the readiness of juveniles to disperse locally or distribute further downstream is inversely proportional to that economy.

Carrying capacity and density of juveniles/m^2 of habitat has been described by various authors (Cederholm and Reid, 1987; Bjornn and Reiser, 1991; Mullan et al., 1992). Density dependent dispersal of newly emerged fry has been described by Lister and Walker (1966) in the Big Qualicum River. They suggested the habitat could support only a certain number of fry and the excess would disperse downstream. Habitat involves the physical space, the food resources necessary to sustain the resident population and the competitive interactions of the community depending on those resources. It is reasoned, therefore, that where food

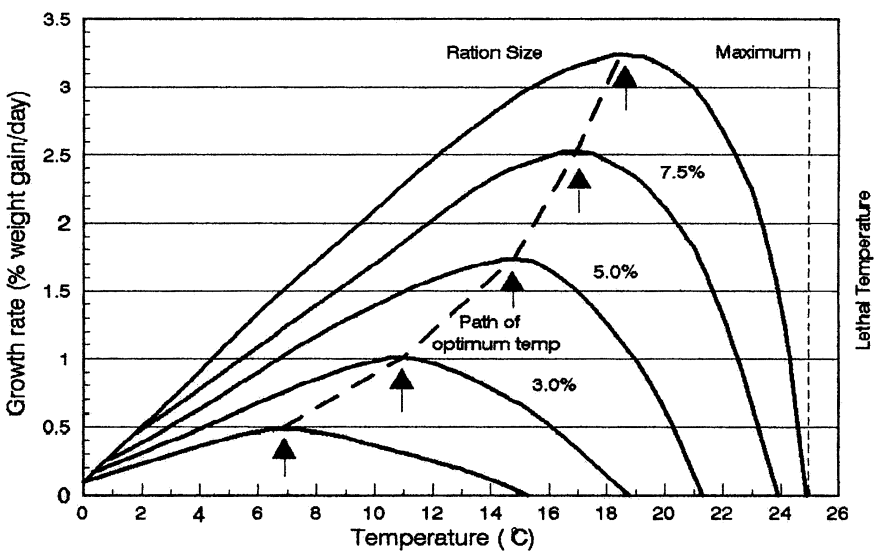


Figure 10. Scope for growth of chinook salmon at different ration sizes and environmental temperatures (developed from Brett et al., 1982).

resources are sufficient to provide for energy demands, young chinook fingerlings will remain in the stream area originally colonized or show limited dispersal based on physical constraints of the habitat, as theorized by Mason (1975) for coho. However, where food resources are insufficient to meet energy needs, dispersal downstream to other feeding areas would be expected to occur until the juvenile finds sufficient resources or enters marine waters. Such behavior again would be stock specific based on stream temperature and productivity.

Chinook populations that show dispersal downstream during their first year of residence are primarily juveniles of fall and late summer chinook populations, and those juveniles would have a higher scope of growth because of the warmer temperatures that characterize their habitat. Basal metabolic demands increase at a rate proportional to temperature (Brett, 1995), but in addition to the increasing needs with higher temperatures, there are the collateral energy needs associated with the growing fish, as well as the enlarging biomass of recruits funneling into the mainstem from the tributaries. These circumstances exaggerate the demands on food resources, and if juvenile chinook are not able to satisfy that demand in their natal stream, greater dispersal would be expected to secure better feeding opportunities.

These differences in stream habitats play a major role in the elaboration of stream-type and ocean-type life history strategies. Although the seasonal scope for growth, and thus instantaneous growth, of juvenile chinook increases with temperature, growth of the food supply doesn't necessarily follow the same pattern to meet that demand. Studies by Nightengale (1998, 1999) on the Yakima River is a case-in-point. Macroinvertebrate samples were taken from several sampling stations over the length of the river in the spring, summer, and fall of 1997 and 1998. Results from three of the stations are shown here as examples of stream productivity (Figure 11); one at Easton, 315 km from the river mouth characteristic of stream-type chinook habitat, the second near Selah, midpoint down the Yakima River, and the third near Benton City, 40 km from the mouth and in ocean-type chinook habitat.

The macroinvertebrate biomass was substantially lower in June than it was two months earlier in April at all three locations, with subsequent increases occurring in August and continuing into October, similar to what is often observed with plankton biomass in lake systems (Baldwin et al., 2000; Goodlad et al., 1974). The diversity of organisms was highest in the upper basin, and tended to increase with the seasons. Total biomass was much higher in the lower river, and composition did not appear to be biased against preferred food items for salmon. We can conclude from this study that macroinvertebrate standing biomass does not necessarily follow the pattern of increases with temperature, or at least biomass may not increase proportional to temperature, until some time after the beginning of summer. The June reduction in macroinvertebrate biomass may have been caused by their exodus from the stream, recession between reproductive cycles, cropping by predators, and/or exhaustion of their own nutrient base, but the point is that the pattern of the initial spring bloom in the benthic community was followed by a substantial reduction before rebuilding during the summer and fall. The reduction of the macroinvertebrate community occurring concurrently with the increase in stream temperatures and the increasing demand of juvenile chinook for food over that particular period is important in considering the distribution response of fry and fingerling chinook, and thus the elaboration of life history strategy over the long-term.

At the lower station, characteristic of fall chinook habitat, temperatures increased from 7°C in April to 16°C in June, corresponding with an increase in scope for growth among chinook salmon from 1.5 to 3.1% weight gain/day (Figure 10), or a substantially increased food demand to satisfy growth potential. Therefore, although scope for growth was elevated by over 100%, the standing crop of macroinvertebrates descended by at least 50% over the

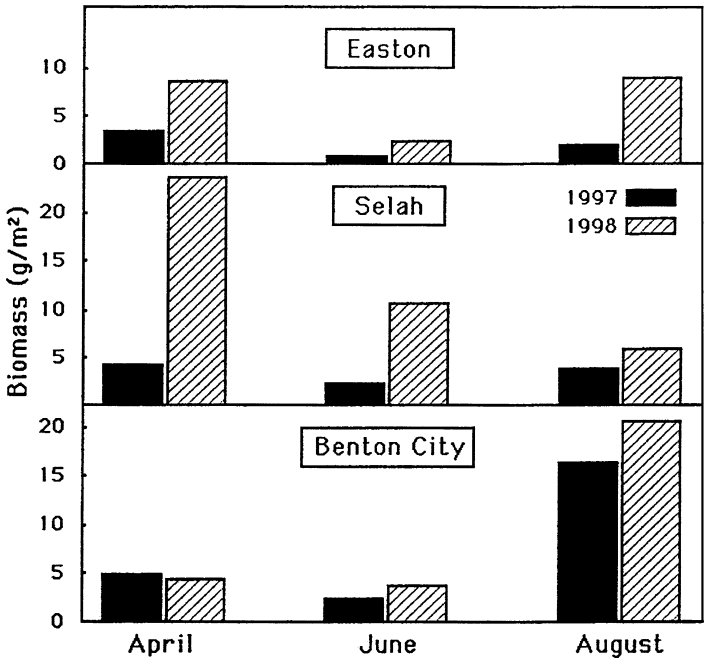


Figure 11. Mean biomass of benthic invertebrates at Easton, Selah, and Benton City in the Yakima River, Washington, 1997 and 1998 (Nightengale, 1998, 1999).

same time period, which would be cause for concern about the sustaining ability of the food supply if the population is near carrying capacity. Given the high June temperatures and the increasing metabolic demands of the growing population, a reduction in the standing crop of macroinvertebrates at the onset of summer represents a potential risk of a shortage of nutrient resources, which we reason would motivate juvenile chinook to disperse downstream in search for better feeding opportunities, consistent with ocean-type life history.

However, the situation is different for spring chinook juveniles in the upper river because of cooler temperatures. Emerging fry would experience an increase in temperature from 4°C in April to only 8°C in June. Although food resources also dropped in the upper river between emergence in April and the June rearing period, the lower temperatures would be expected to limit growth before exhausting nutrient resources, and the fry would not be as inclined to disperse downstream in search of other food sources. By the time temperatures increased to 15°C in August, macroinvertebrate resources had more than doubled over the June level and would better support energy demands of the growing population. Similar to the view on dispersal of juvenile coho (Mason, 1976), stream-type chinook that rear in cool environments will most likely be confronted by temperature limits on growth before limiting effects of the food supply, and thus consistent with stream-type chinook life history strategy.

The magnitude of nutrient resources available also changes from year to year, which could explain the variability in the annual ratio of age-0 and age-1 migrants that occurs in some streams. In 1998 for instance, Nightengale showed a six-fold increase in macroinvertebrate biomass at some stations over that measured in 1997. Although the change in biomass followed the same pattern of substantially lower biomass in June samples and the

rebound by late summer, the total magnitude of nutrient resources was markedly different. Food supply and size of the juvenile population on any given year are the variables that would be expected to influence the pattern of juvenile dispersal. In the long run, we would expect adaptive evolution to establish the point in nutrient availability at which young chinook disengage from their residence behavior and disperse downstream. We would expect the dispersal tendency to be higher among fall chinook because of the metabolic demands at higher temperatures. From the evolutionary perspective, the risk of not achieving their growth objectives in warmer waters as age-0 migrants would have to be measured against the hazard of predation and other losses when proceeding through unknown waters.

It is suggested that dispersal behavior, therefore, is governed by the relative abundance of food resources and hence an age-0 migrant size-related objective, because fall (ocean-type) chinook are targeting late summer or fall marine entry timing in the first year. Dispersal motivation can be expressed as a function of the difference between the fingerlings scope for growth and its instantaneous growth, expressed as:

$$D(t) = L(t)/S(t)$$

where : D = dispersal index
L = length/day (mm) increase
S = maximum scope for growth in mm/day
t = temperature

If D is less than the threshold growth rate encouraging continued residence, juvenile chinook would be expected to disperse, and this would be a trait independent of life history type. Moreover, the readiness to disengage and drop downstream would also be expected to develop a genetic basis for that performance if that option proves selectively beneficial over time. We are suggesting that the readiness to remain in residence and delay movement, such as most spring (stream-type) chinook, or the tendency for age-0 emigration such as fall (ocean-type) chinook is food (growth) related.

Among chinook that would normally disperse, the tendency for volitional residence when in the presence of adequate food resources is demonstrated by the behavior of fall chinook reared in hatcheries. For instance, fall chinook that would normally disperse downstream in the natural system within the first couple of months after emergence show no tendency to work the outlet screens of rearing ponds in an attempt to escape, as long as feeding levels are sufficient. As examples from personal experience, summer chinook from the Elwha River on Washington's Olympic Peninsula, and fall chinook at the University of Washington hatchery would remain in their respective rearing ponds until feeding was terminated before they would volitionally emigrate. Prior to the termination of dispensing feed and with the retaining screens removed from the pond outlets, little tendency to migrate was detected over the several years of such observations.

The influence of the environmental template in life history options is demonstrated in work with spring chinook in the Squamish River (Schubert, 1993). Prior to enhancement programs the Squamish chinook were stream-type life history forms where juveniles migrated predominantly at age-1. However, after culturing the fish at the Tenderfoot hatchery and providing higher growth rates through hatchery feeding, smoltification among the spring chinook changed to the ocean-type life history pattern and juveniles migrated at age-0. Similar results from culturing fall chinook (Donaldson and Manasveta, 1961) and coho (Brannon et al., 1982) have been shown. By accelerating growth through warmer

temperatures and high feeding rates, emigration was stimulated to occur from a few months to a year earlier than what occurred in these populations as wild stock.

An interesting alteration in migratory patterns among chinook juveniles is also demonstrated in the mid-Columbia River (J. Sneva pers. comm.). The typical downstream movement of age-0 Wenatchee summer chinook has had a major change in the form of extended reservoir residence above McNary, adopting an age-1 migratory pattern. This now involves over 60% of the Wenatchee summer run population (Murdock and Petersen, 2000), and is common in both the mid-Columbia summer/fall run chinook and the Snake River fall chinook, noted as residuals in Lower Granite by Bennett (1992). The size of age-1 migrants can exceed 190 g compared to age-0 migrants of less than 75 g. The change suggests that because the major reservoirs have been created in the Basin, feeding levels in those systems are favorable enough to have extended juvenile residence to age-1 emigrants. It appears that the altered residence behavior has been selectively favored and the frequency of age-1 ocean-type life history forms are increasing to become a dominant pattern in those reservoir sections of the Basin.

Analogous with the variability in fall chinook dispersal by remaining for a year in freshwater before emigration, some Columbia Basin spring chinook populations also show variability as age-0 migrants (Serl and Morrill, 1999, 2000), especially in the lower river. Most spring chinook typically have a significant portion of their populations dispersing downstream as fry and fingerlings (Chapman and Bjornn, 1969; Bjornn, 1971; Mullan et al., 1992). The Yakima spring chinook population averages 25% age-0 downstream migration on the way to the Columbia (Berg, 2001). These and other examples show that alternative age-0 or age-1 migratory behavior is not atypical for either juvenile spring or fall chinook. Consistent with the temperature theory, we suggest that regardless of life history type, variations in migratory behavior is influenced by energy needs, and growth conditions (productivity and temperatures) under given environmental templates. The pattern and genetic predisposition that evolves will vary within stream- and ocean-type life history forms, but such variability forms the basis for the multiplicity of life history options in the species.

Therefore, although ocean- and stream-type chinook show differences in their general life history and distribution patterns, we believe the differences have their origin based primarily on the environmental template. Those environments define what optional strategies will be successful, and the resulting life history forms occur through selective adaptation to the different ecological niches. Observations by Taylor (1988) on differences in rheotactic behavior among chinook life history types, and by Linley (2001) on differences in growth potential, and by Unwin et al. (2000) on stream-type chinook evolving from ocean-type, are consistent with this concept. Perpetuation of selectively advantageous traits is the natural consequence of adaptive evolution and would be expected to occur under any environmental setting. In warmer stream environments where growth is more rapid and food resources become proportionally more limited for the biomass present, we consider dispersal as the strategy to access feeding opportunity and achieve optimum size for marine entry. Although ocean- and stream-type life history forms are not exclusive, age-0 migration is most often not an option for slower growing stream-type chinook that rear in cooler temperatures. Ocean- and stream-type chinook, therefore, have different dispersal patterns within their respective life history forms, but both patterns are observed among what is referred to as summer chinook in the Columbia and Snake rivers (Chapman et al., 1994a; Myers et al., 1998) where exposure to intermediate temperatures provide the transition zone between the two life history forms. We agree in concept with Miller (1970) that dispersal is an adaptive behavior related to resources for sustaining juveniles in residence, and we

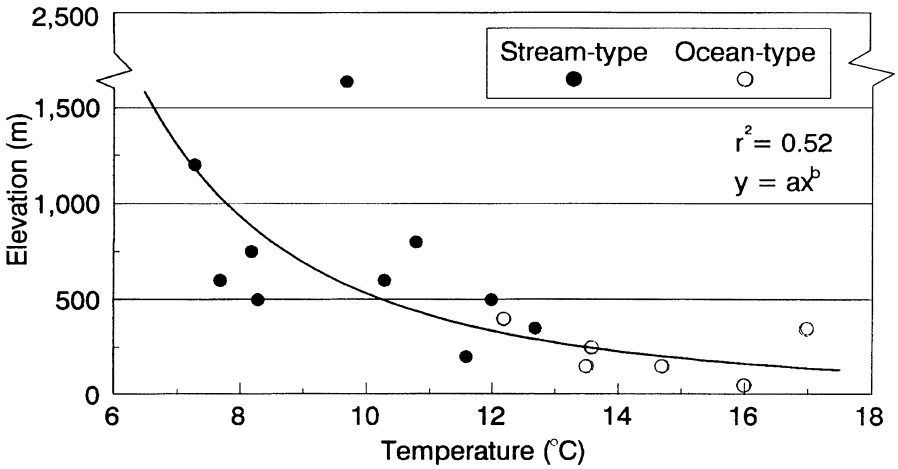


Figure 12. Relationship between Columbia Basin stream-rearing temperatures and elevation from April 1 through September 30; relationship associated with juvenile chinook salmon at migration (age-0 and age-1). Information on life history types was taken from agency records and published data. Temperature data was collected from USGS (1980–2001), USDOE (1960–77), USFWS (1969–73), Lindsay et al. (1986), Hillman et al. (1989b), Mullan et al. (1992), Petersen et al. (1995), Homolka and Downey (1995), IDFG (2001), and LaRiviere (2001).

argue that this temperature-related phenomenon is the mechanism around which ocean- and stream-type life history strategies of chinook salmon have evolved and through which phenotypic-defining genetic traits have been selected.

The relationship between rearing temperature and life history form is best demonstrated by the mean rearing temperatures associated with the different life history types (Figure 12). Although many juvenile chinook do not remain in their natal stream for the entire rearing season, and the duration of higher temperatures is a major influence, we have used the temperatures of their natal stream from April 1 through September 30 as the general indicator of life history segregation. As demonstrated, those populations experiencing mean temperatures below 11°C tend to remain in residence for a year or more. In contrast, those populations rearing in stream reaches with mean temperatures above 12°C show a greater tendency for ago-0 migration. Although the migratory behavior is size-related (Reimers and Loeffel, 1967; Dawley et al., 1981; Taylor, 1990b), we argue that temperature's role in determining size potential (Brett et al., 1982) makes temperature a primary factor in the origin of the two different life history types. We conclude, therefore, that phenotypic differences observed among stream- and ocean-type chinook are the result of natural selection enhancing the ability of the life history forms to accommodate the respective environmental templates.

b. Relationship between freshwater temperature and marine distribution. As previously discussed, we suggest that temperature-based freshwater life history strategies have translated into different marine habitat options, consistent with size-related distribution behavior among other salmon fry in marine waters. Pink and chum fry that migrate to sea at <35 mm remain in littoral marine habitats and feed on smaller marine plankton abundant in those waters (Heard, 1991; Salo, 1991) until they reach approximately 120 mm in the southern part of their range and 90 mm in the north (A. Hartt pers. comm.). When they grow beyond those lengths, they seek food resources associated with areas more distant

from shore where it is suggested they are less vulnerable to predation (Hartt and Dell, 1986), similar to the behavior of yearling sockeye (Burgner, 1991) and later migrating coho migrants (Sandercock, 1991) that have attained fingerling size in freshwater before entering marine waters. We assume that food resources in near-shore habitats become limiting to the increasing size and total biomass these species would accrue if they didn't migrate to conditions more favorable for larger fish. The biological costs of remaining in near-shore waters is demonstrated by coho that stay in Puget Sound for extended rearing, resulting in an average of two or more pounds less weight at maturation than coho migrating off the coast (Feldmann, 1974).

The smaller ocean-type age-0 chinook($<$75) and the larger age-1 stream-type chinook smolts ($>$90) demonstrate life histories apparently reflecting trophic differences in distribution related to size. Based on the pattern of emigrating juvenile pink and chum salmon, one can conclude that it is more beneficial for the smaller ocean-type emigrating juveniles to initially occupy the littoral habitat. This is especially true because many age-0 chinook are emigrating at a time when pink and chum salmon fry have grown to the fingerlings stage and are leaving the littoral marine habitat for open water, providing a competitively more favorable opportunity for chinook to occupy the niche in their absence. Fry and small fingerling (age-0) chinook feed on plankton and chironomids among other things in near-shore waters (Dunford, 1975). Larger stream-type yearling smolts (age-1^+), on the other hand, move offshore after marine entry (Dawley et al., 1981; Healey, 1991; Fisher and Pearcy, 1995) and follow a marine size-related feeding pattern different from that of ocean-type chinook by targeting larger food resources such as larval and juvenile fish in their diet (Dunford, 1975).

Consequently, we suggest their patterns of marine distribution and the origins of stream- and ocean-type marine life history forms are indirectly related to the influence of freshwater temperature on juvenile growth and age of emigration. The subsequent patterns of ocean migration that are related to size upon marine entry are suggested to be adaptations resulting from the natural progress of exploiting size-related opportunities. Given the different initial sizes at marine entry, genetic predisposition would be expected to evolve to facilitate the feeding circuits each life history form follows. Once chinook have committed to a pattern of near-shore residence until they reach a size compatible with off-shore movement, they also have committed to a timeframe that limits the range of their annual feeding circuit. Because the circuits that populations follow are different by location of their marine entry points and are annually repetitive in nature (Hartt, 1980; Brannon and Setter, 1989), we suggest that marine distribution patterns are stock/type specific within those size/time restraints.

The Temperature Model and Evolution of Chinook Life History Forms. We propose, therefore, that life history of chinook salmon may be described by the working model that is based on the dominant influence of temperature on nearly every aspect of chinook freshwater ecology (Figure 13). The first avenue of influence is shown on the left of the diagram with regard to the timing of adult returns. As discussed previously, based on ancestral performance there is an optimum time in the spring for chinook fry to begin their rearing phase to maximize subsequent survival. Given that temperature determines the length of the incubation period, spawning times are synchronized by feed-back to target the optimum time of emergence for each respective population. Concurrently, return times evolve to accommodate the migratory restraints experienced in meeting the spawn timing objectives.

Consequently, as shown with an increase from lower to higher mean incubation temperatures across their range, what traditionally has been referred to as spring, summer, fall, and winter chinook spawning times should be viewed as a cline or continuous pattern associated

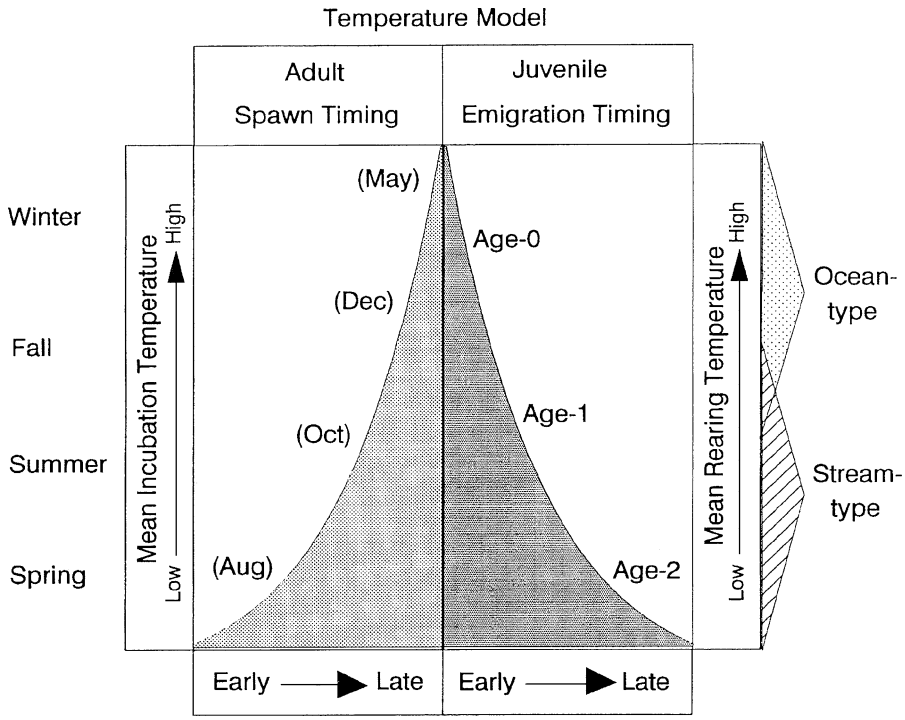


Figure 13. Chinook salmon life history model in which mean incubation temperature determines early (spring) to late (fall) spawning times, and mean rearing temperatures determine age-0 (ocean-type) and age-1 (stream-type) marine entry forms.

with the increase in mean incubation temperatures. Those fish representing the early part of the cline (spring-run) are shown in the model to start very early (July) in streams that have low mean incubation temperatures to accommodate the greater number of days required for incubation. As mean incubation temperatures increase, adult return and spawning times become progressively later in the season because fewer days are required for incubation at warmer temperatures. For a given brood year, spawning can extend into the following year, and is at least as late as May for Sacramento River winter chinook.

The second avenue of temperature's influence on life history strategy depicted in the model is its determination of ocean- and stream-type life history forms, identified on the right of the figure. The rationale is that as mean rearing temperatures decrease, growth rates correspondingly decrease along a cline associated with the incremental reduction in temperature. Because juvenile growth rate affects foraging strategies (dispersal), migratory patterns, marine entry timing, size-related early marine residence area, and thus marine migratory distribution, we argue that the evolution of ocean- and stream-type life history forms has been based on the associated differences in temperature. The demarcation between life history types is the interruption or termination of growth among those populations residing in cooler stream environments with the onset of winter, which sets the stage for subsequent differences in size-related distribution and migratory behavior. Consequently, we propose that the contrasts between the life history types shown earlier in Table 1 can be explained by freshwater rearing conditions that have resulted in those life history strategies.

The overall basic mechanism demonstrated by this model, therefore, is the influence of temperature on life history strategy. Recognizing the selective compromises that chinook have made to accommodate the limitations of freshwater stream environments is the key to understanding the strategies around which life history differences evolved. The genetic traits that reinforce life history forms with different return, spawning, distribution, and emigration strategies originate as the consequence of temperature's influence on embryo incubation rate and juvenile freshwater growth. Temperature creates the environmental template around which life history synchrony evolves. The multiplicity of life history strategies that have evolved in *O. tshawytscha*, therefore, have been created by specific circumstances in the natal streams in which the selected genotypes are perpetuated as separate populations. Generally, one primary temporal pattern will be associated with a particular stream, but secondary options can no doubt coexist where diverse opportunities occur. Most certainly, depending on the environmental variability present, more than one life history strategy can be accommodated over the length of a stream where different temperatures occur along predictable patterns. We conclude, therefore, that survival pathways selectively reinforced over time have created genetically distinct temporally specific stocks distributed along a temporal cline, with two principal life history types distinguished through juvenile freshwater growth as age-0 emigrants separated from age-1 emigrants by winter low temperatures. Corroboration of the temperature model is shown by the pattern that life history forms along the Northeastern Pacific (Figure 14), which has evolved under the influence of the environmental temperatures characterized by differences in the latitude and elevation over their geographical range.

Application of the Temperature Model on Chinook from California to Alaska. Distribution of chinook populations along the coast from California to Alaska (Figure 14) demonstrate the influence of temperature on the life history forms when spawning time is plotted against mean incubation temperature (Figure 15). In a classical clinal variation (Mayr, 1966) the temporal distribution of spawn timing aligns graphically from the lowest to the highest mean incubation temperature. Populations at the lowest temperatures are associated with highest elevations and latitudes and are the earliest spawners (spring-run chinook). Spawning becomes later (spring- to summer- to fall- to late-fall- to winter-run chinook) with warmer temperatures associated with lower latitudes, until late-fall and winter-run chinook are present at the lowest latitudes, consistent with the temperature model.

The influence of rearing temperature on the life history types is also demonstrated from Alaska to California. It is apparent that age-0 emigrants are the most prominent life history form at warmer rearing temperatures and age-1^+ emigrants are the most prominent at cooler temperatures (Figure 16), as one would expect from the influence of temperature on growth. Although age-0 migrants dominate in the south and age-1^+ migrants dominate in the north, there is no fixed latitude where a transition between ocean- and stream-type takes place because day length can increase summer rearing temperatures in the more northern latitudes.

Figures 15 and 16 show that spawning/incubation and rearing/emigration profiles are influenced by temperature, and in similar ways, but those temperatures have distinctly different effects in their manifestation on life history because of the season when their influence is exerted. The spawning/incubation phase begins around the fall equinox and proceeds through the winter solstice. Lower incubation temperatures are thus accentuated in the more northern latitudes by the exaggerated decrease in day length, while longer winter days in the southern latitudes provide a broader spectrum of incubation temperatures and thus increased flexibility in spawn timing. In contrast, the rearing/emigration phase

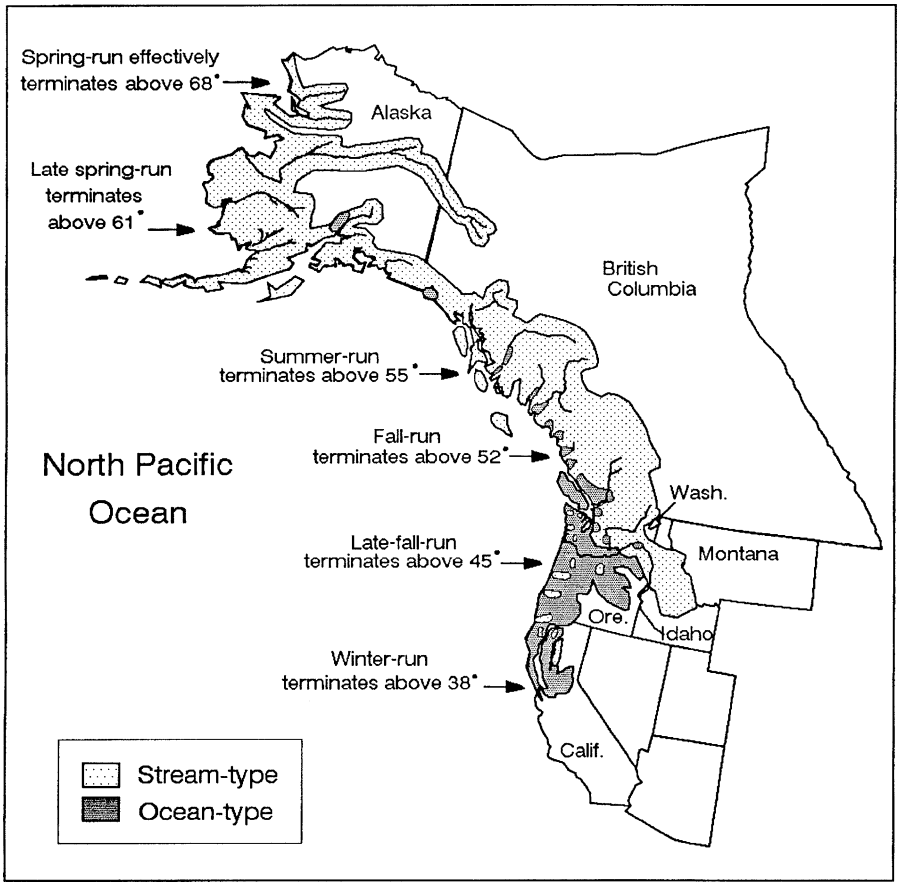


Figure 14. Map of chinook salmon population distribution and life history in the Northeastern Pacific range. Distribution of ocean- and stream-type life history forms is shown by differences in shading. The general northernmost distribution of winter-, fall-, summer-, and spring-run chinook is indicated by the °N latitude and arrow associated with the life history form.

begins near the spring equinox and proceeds through the summer solstice when day length is greatest in the north. The influence of the sun on rearing temperature is thus exaggerated in the north, overcoming some of the cooling affects of the higher latitudes. Therefore, the relationships between spawning life history forms and latitude, and rearing life history forms and latitude are different because of the time of year when incubation and rearing take place.

It is important to take time to clarify the details around these temporal relationships over the geographical range of chinook salmon to appreciate the major influence that temperature has had and will continue to have on the evolution of life history form. At the southern extreme of their freshwater distribution, around 38°N latitude, the Sacramento River chinook demonstrate the most extensive range of timing within the species, historically returning to the Sacramento nearly every month of the year (Healey, 1991). The historical temporal succession in spawning events in the Sacramento River followed from the coolest to the warmest mean incubation temperatures. Spring chinook were historically reported to spawn in the upper cool reaches of the basin such as the McCloud River in late summer (Hedgpeth,

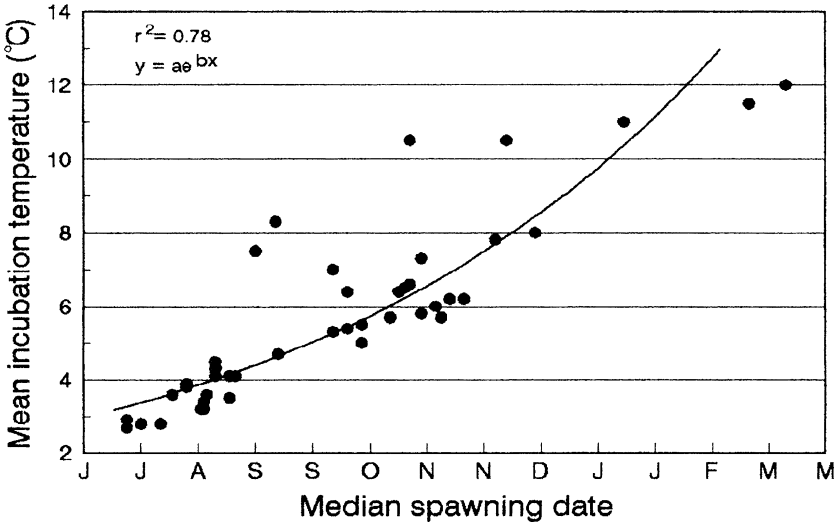


Figure 15. Mean incubation temperatures and spawn timing of chinook salmon in streams from Alaska to California. Spawning times were based on agency records and Myers et al. (1998). Temperature data were taken from USGS and state or provincial agency records, and only approximate the temperatures associated with incubation sites.

1944; Moyle et al., 1995). The Sacramento fall run spawned lower in the mainstem and tributaries primarily from October to December (Fisher, 1994). Most notable among the temporal segments, however, were the late-fall- and winter-run that returned very late in the year and extended spawning over January to May of the following year (Fisher, 1994; Moyle et al., 1995).

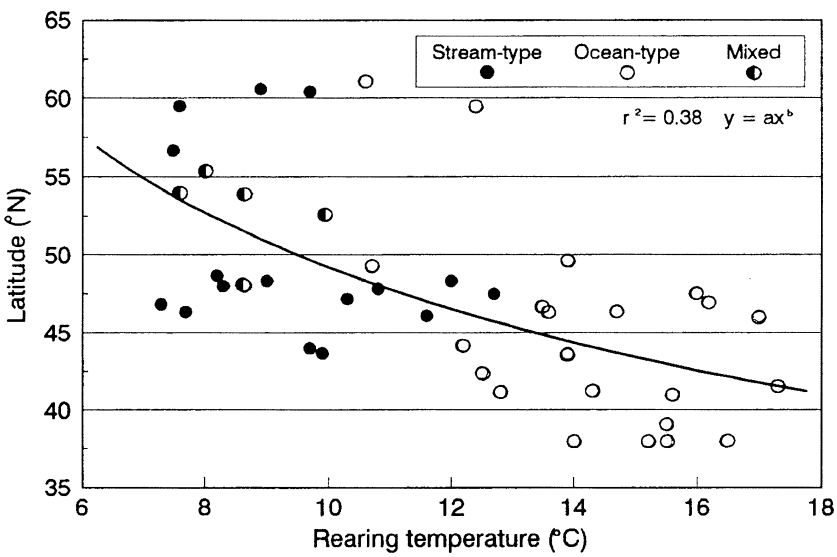


Figure 16. Relationship between mean rearing temperatures from April 1 to September 30 and latitude, associated with juvenile chinook salmon age at migration (age-1 and age-0) from Alaska to California. Information on life history types was taken from agency records and published literature.

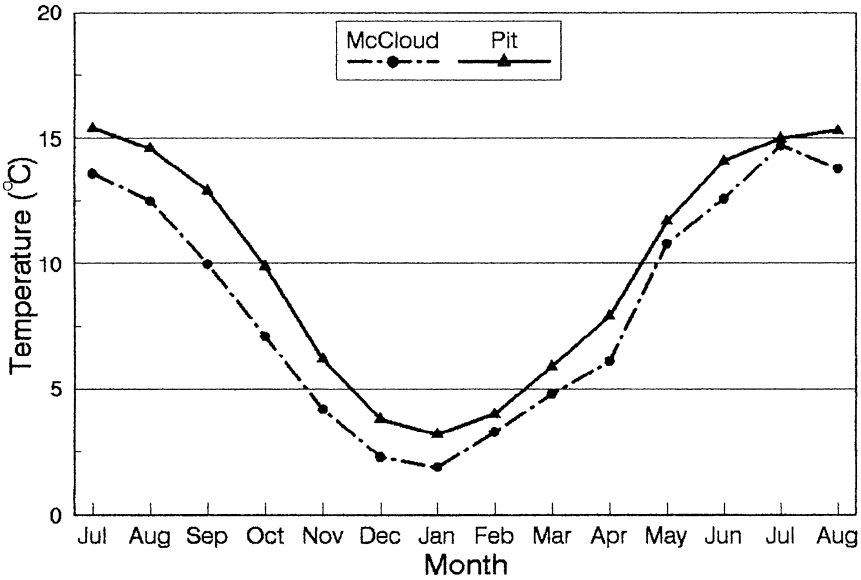


Figure 17. Mean daily incubation temperatures of the McCloud and Pit rivers in the upper Sacramento River Basin, 2000, adjusted for elevation of spawning grounds.

Based on the recent temperature regimes (Figure 17), the chinook that returned to the Pit and McCloud rivers would have been expected to spawn in late August or September as temperatures decreased from 12°C to 10°C. Incubation temperatures appear to remain near 2°C during the winter, which would have resulted in fry emergence sometime in mid-April, with subsequent juvenile rearing in temperatures from 6°C in April to 14°C through July. Based on such a scenario, these fish would have been considered late spring or summer chinook and could have emigrated to the marine environment as age-0 smolts ([Pit-SS15-0], [McC SS8-0]), especially if they distributed downstream and experienced warmer temperatures during the early freshwater rearing phase.

Although ocean-type subyearlings represent the majority (>90%) of emigrants in the Sacramento River (Myers et al., 1998), stream-type yearling chinook are still reported to come from the Deer and Mill creek basins (C. Harvey pers. comm.) and Butte Creek (Hill and Webber, 1999). Butte Creek chinook show a mixture of ocean-and stream-type life histories.

Fall-run populations spawn in October, November and December in the tributaries such as the Yuba River, and fall under the general classification of fall chinook based on those spawning times. These fish incubate from 13°C down to 8°C, and emergence from most of the Central Valley streams is reported to begin in December through March (S. Cramer pers. comm.), which conforms to the incubation periods at those temperatures. Fry that rear in the Central Valley can exceed 60 mm in length by May 1 and emigrate downstream during April to mid-June (Kjelson et al., 1982), which would allow passage through the delta before mean daily temperatures exceed 21°C. Smolt size leaving the estuary is reported >75 mm (Kjelson et al., 1982). The upper limit for optimum growth reported by Brett et al. (1982) and Armour (1990) is 19°C, and while chinook withstand higher temperatures, feeding diminishes and mortality starts increasing above 20°C (Brett, 1952; Beacham and Withler, 1991).

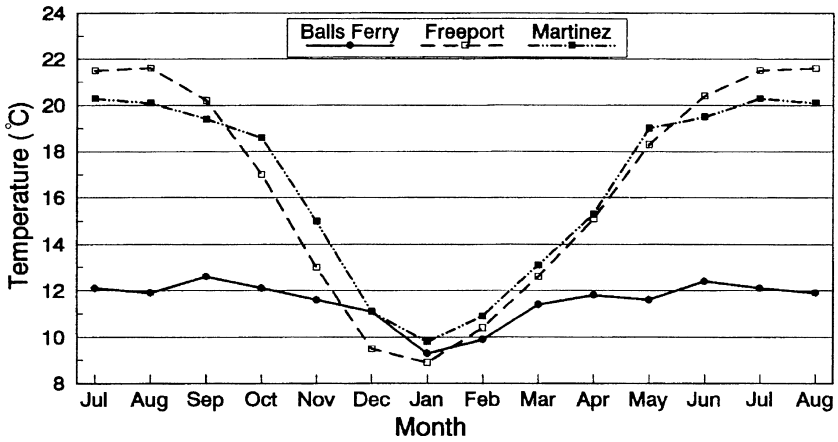


Figure 18. Mean daily temperature of the Sacramento River at Balls Ferry Bridge, Freeport, and the estuary in California. Temperature records from USGS, CWR, and CDFG.

Late-fall chinook generally spawn in the mainstem well into January and February. Synchronized with optimum emergence timing, incubation historically would have been at temperatures averaging around 10°C with fry emerging before May. The mainstem Sacramento River at Balls Ferry Bridge, south of Redding, reaches 11°C by the first of April (Figure 18), and averages over 12°C for May and progressively higher downstream, which engenders a high scope for growth after emergence. With temperature control now operating at Shasta Dam, temperatures at Balls Ferry Bridge are lower than the historical regime, but the lower river still equilibrates close to the historical pattern by the time flow reaches the delta. The delta is an extensive area and, with the estuary network, appears to offer considerable habitat for rearing, with suitable rearing temperatures persisting well into May.

The winter-run chinook are unique to the Sacramento and represent the evolution of an even later spawning strategy than what is exercised by late-fall chinook, and one that truncated the entire freshwater experience from spawning to smolt marine entry within a period of less than a year. This was possible because while winter-run chinook spawned as late as May in McCloud River (Williams and Williams, 1991), they appear to have used reaches irrigated with springs or groundwater that permitted them to avoid the potentially lethal range in temperature reported by Murray and McPhail (1988) that would have been present in surface water. The ground water reaches would have been the unique environmental characteristic that induced winter chinook to evolve separate from other chinook life history forms.

It appears that winter-run chinook were also able to take advantage of good rearing temperatures that occur later in the year and to utilize a fall window of opportunity through the estuary (Kjelson et al., 1982). May spawning would result in August emergence timing when river temperatures were starting to decline into a favorable range for rearing. Reaching the extensive delta and estuarine area from September to December would have exposed them to rearing temperatures ranging from 17°C down to the 10°C (Figure 18) and sufficient conditions to attain >70 mm in length for late fall marine entry. The environmental template that encouraged winter-run life history was unique. Without the cool late summer incubation temperatures and exposure to suitable fall rearing temperatures of the Sacramento River

meandering through the long and sunny Sacramento Valley, there would have been no opportunity for the winter-run chinook life history form to have developed.

As one progresses north beyond 38°N latitude along the coast, the winter-run chinook life history pattern disappears, leaving the summer, fall, and late-fall runs represented along the coastal rivers of northern California and Oregon (Myers et al., 1998). Late-fall chinook are reported to extend as far as the Klichis River in northern Oregon (Nickolas and Hankin, 1988). The incubation temperature regime from December to March, and the warmer rearing environments available appear to be the primary habitat characteristics that provide the window of opportunity for late-fall chinook. Although not as rare as the winter-run, late-fall life history forms are not common, and they disappear a little north of 45°N latitude. Except for spring chinook that remain in the Butte, Deer, and Mill creek basins (C. Harvey pers. comm., Hill and Webber, 1999) and some along the Oregon coast that show stream-type life history residence to age-1 before migrating to sea, ocean-type chinook appear to have been and continue to be the dominant form in California and Oregon (Healey, 1991). Facilitated by warmer weather associated with those latitudes, streams are warm enough and growth rates high enough to generate age-0 smolts even among spring-run chinook.

Based on return times, it is noteworthy that what is referred to as the spring chinook such as in the upper Trinity, Klamath, Umpqua, and Nestucca rivers on the coast, could be classified as summer- or even fall-run populations as far as spawning times are concerned. September is generally the earliest spawning date among these populations (Myers et al., 1998) and spawning occurs well into November. Therefore, biologically what would be referred to as spring chinook with July and August spawning dates are nearly absent along the coast of California and Oregon until reaching the Columbia Basin.

The more typical spring-run, stream-type chinook are well represented in the Columbia as presented earlier, and are associated with the interior of that part of the range where lower temperatures at higher elevations require earlier spawning and longer freshwater residence of juveniles. Stream-type life history patterns among spring chinook along the coast begin in earnest around 47°N latitude and appear related to streams that originate from higher elevations of the Olympic Mountains in Washington and the coastal range in British Columbia. The elevations of that region result in the low winter incubation temperatures and cooler summer rearing temperatures typical of stream-type life history forms. Although stream-type life history patterns increase in frequency as one proceeds up the coast, age-0 juvenile migrants are still well represented along Washington's coast and in Puget Sound where higher summer rearing temperatures occur.

Spring chinook populations associated with coastal climate influences show both ocean- and stream-type juvenile migratory patterns in streams that have no more than 45 km of functional length, but fall from several thousand feet elevations to extensive floodplains just above sea level. Spring chinook are generally associated with the upper reaches of these streams, and summer and even fall chinook are associated with mid or lower reaches.

Consistent with the temperature theory, the presence of age-1 and age-0 juvenile chinook would be expected in the temperate coastal climate where temperatures are highly variable from year to year. A good example is the Dungeness River flowing from the Olympic Mountains into Juan de Fuca Strait, with the typical variability in coastal temperature patterns from the influx of the temperate marine air masses mixing with the cold air at higher elevations in the headwater areas. Annual mean temperatures during incubation can vary by as much as 2°C (WDFW, 2001), representing markedly different incubation rates and thus highly variable emergence timing (Figure 19). A 2°C difference in mean incubation temperature among brood years would result in a six-week difference in emergence timing, and thus very different opportunities for early growth from year to year. Moreover, in warm

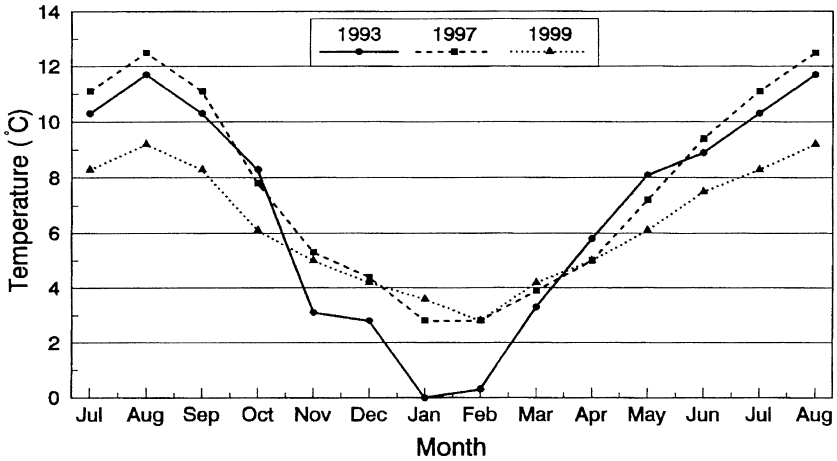


Figure 19. Mean temperatures of the Dungeness River, Washington, 1993, 1997, and 1999 (Dick Rogers, Manager, WDFW Dungeness Hatchery).

years, fry will be exposed to substantially warmer spring rearing and midsummer rearing temperatures that can average as much as 3°C higher (12°C) than on cool years (<10°C). Under such conditions with temperatures reaching 12°C by mid-August, fry would have an opportunity to migrate as age-0 smolts. On cold years, fry would emerge later, grow slower with mid-August to September temperatures averaging less than 10°C, and emigration delayed until the spring.

The variability in migrant patterns among Dungeness River spring chinook was apparent from downstream migrant trap records (WDW, 1952) taken from about 18 km upstream of the river mouth. Records show both age-0 and age-1 chinook migrants. Fry started showing in March and were apparent in some years until October, with size increasing from 38 cm to 100 mm over the seven-month period. Yearling chinook were intercepted beginning in May with some at sizes >120 mm. The immediate destination of the age-0 fish was unknown, and may represent only local dispersal, but we assume some were headed to marine waters. The interesting aspect of the behavior is that it can change from year to year in terms of the percentage of age-0 and age-1 migrants, and may be representative of chinook in many coastal streams in response to the variability in coastal climate.

The variability in temperatures in the Dungeness River shown in Figure 19 is a good example of coastal temperature variations compared to the headwater streams in the interior of the Columbia Basin. Icicle Creek flowing into the Wenatchee River has a flow similar to the Dungeness and follows a similar mean temperature pattern, with July/August temperatures a little warmer and midwinter temperatures a little colder than the Dungeness (Figure 20). However, common to the interior east of the Cascade Crest, the annual variability in temperature is lower than on the coast, which we suggest my provide the explanation for why spring chinook under coastal temperature influences demonstrate a more variable pattern in age of marine entry than populations of springs in the upper interior of the Columbia Basin.

In much the same manner that winter-run chinook discontinued north of 38°N and late-fall chinook discontinued north of 45°N, the extent of fall-run chinook tends to drop off at ≈52°N as the mean winter temperatures decrease further with latitude. It is here that the disjunction between spawning patterns (spring, summer, and fall life history forms) and juvenile emigration patterns (ocean- and stream-type life history forms) is more easily

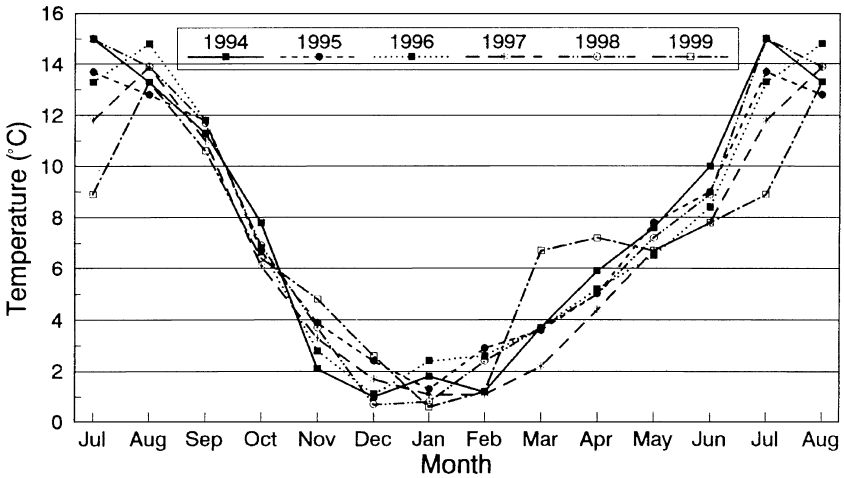


Figure 20. Mean temperature of Icicle Creek, Washington, 1994 to 1999 (data from Dan Davies, Manager, USFWS Leavenworth Hatchery).

differentiated. As discussed earlier, incubation conditions associated with winter temperatures, and rearing conditions associated with summer temperatures work on different phases of chinook life history. Generally in the midrange of the species, the low elevation environments that encourage late spawning (fall chinook) also encourage age-0 (ocean-type) emigration because at that range in latitude temperatures are moderate, and differences in the incubation and rearing conditions are less extreme, such as in Puget Sound and on Vancouver Island.

However, as one progresses further along the British Columbia coast, the disparity between incubation and rearing temperatures increases, influenced by the complexity of the region with the extensive assortment of low elevation islands, deep inland fjords, and steep elevations of the British Columbia coastal mainland. Excluding the Fraser River that shows stock diversity similar to the Columbia, fall-run chinook occur at least as far north as Rivers Inlet along the coast of British Columbia (R. McNicol per. comm.). Further up the coast, summer-run chinook (September spawners) also tend to phase out north of Skeena/Nass River (≈54°N), leaving spring-run chinook remaining in the North as the primary temporal form associated with run timing.

Mean incubation temperatures also influence spawn timing among spring chinook populations. Systems like the Kenai River Basin (Figure 21) are vast enough to have a variety of temperature regimes among the various streams (Burger et al., 1985). Large lakes and several smaller ones in the Kenai River Basin act as heat sinks and have a decided influence on temperatures over the ensuing winter. For example, in a 1979–1982 study by Burger et al. (1985) the succession of chinook populations returning to the Kenai River Basin showed progressively earlier spawn timing associated with successively cooler mean incubation temperatures. The Funny River chinook [Fny-SJ17-1] and the Killey River chinook [Kly-SJ22-1] were exposed to cooler temperatures from surface runoff and showed a midpoint in spawning time as early as July 17 and July 22, respectively. Juneau Creek chinook [Jnu-SA1-1] spawn in a stream with two small lakes on the system, and had an August 1 midpoint in spawning. Chinook in Quartz Creek [Qtz-SA6-1], downstream from midsized Crescent Lake, showed a midpoint in spawning time of August 6, Kenai

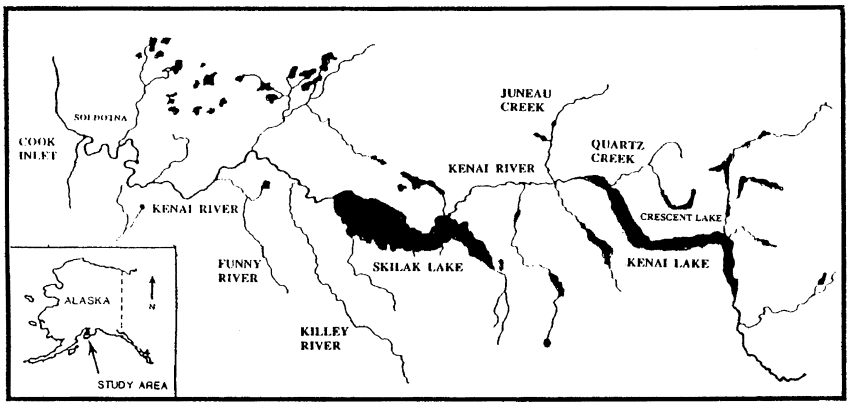


Figure 21. Kenai River Basin showing major streams and lakes (Burger et al., 1985).

River chinook [Kai-SA21-1), spawning in four reaches of the river from the large Kenai and Skilak lakes, had an August 21 mean midpoint in spawning.

These data relate spawn timing of Kenai River spring chinook with the absence or presence of a lake and the size of the lake. Occurring shortly after the summer solstice, spawn timing is influenced by the amount of lake surface area that has absorbed and stored radiant energy. As the late summer and early fall temperatures decrease, stream temperatures reflect the influence of the thermal reservoir in the respective lake basins. Compared to surface runoff streams, temperature regimes of streams coming from the lake basins are warmer in proportion to the stored energy of the water-mass. Incubation temperature, and thus spawn timing, is influenced by the percentage of the total flow contributed from those sources (Burger et al., 1985), and spawning becomes later as the respective mean incubation temperature regimes increase among the various streams in the Kenai system.

The effect of the lake basins as heat sinks during the winter months is most evident on the Kenai River by the differences in temperature between the outlet of Skilak Lake and the mouth of the same river at Soldotna (Figure 22). River temperatures at Soldotna

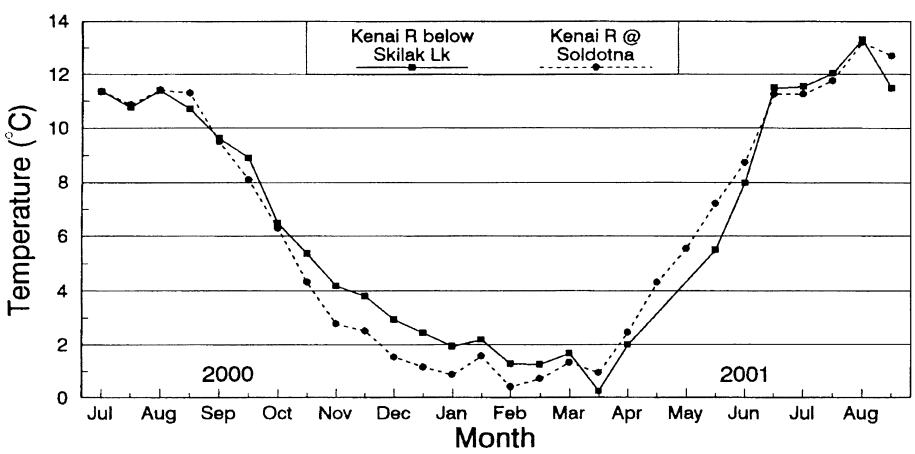


Figure 22. Kenai River temperatures in the outlet of Skilak Lake and at the river mouth at Soldotna (USGS).

from the end of September to March average at least 1°C lower than the lake outlet over the same period. The pattern changes during the spring months with surface waters heating more quickly compared to the lake where the water-mass acts as a buffer against rapid increases in temperature. Further west and north along the Alaska peninsula, the streams drop to 0°C for several weeks during the winter, such as the Terror River on Kodiak Island, and the Nushagak and Kuskokwim rivers further north (USGS), with only the earlier spring chinook remaining above 61°N.

In contrast to the decrease in winter incubation temperatures as one progresses north, the change in summer rearing temperatures over that range is not as decisive. The longer summer day length associated with the north tends to overcome the effect of latitude, and rearing temperatures can be relatively warm and more comparable to summer temperatures at lower latitudes. Consequently, there is no defined latitude where the transition between ocean- and stream-type life history patterns occur. Although winter incubation temperatures are cool enough to require very early spawning to synchronize emergence with the environmental template, rearing temperatures during the summer months can still be warm enough to encourage age-0 emigration. Ocean-type life history forms are represented among some of the chinook populations of the Bella Coola (52°25′N), the Kitimat River (54°N), the Skeena (54°20′N), and the Nass River (55°20′N) (Healey, 1991).

However, immediately to the north of Nass River, there appears to be a change in the coastal environment extending along the entire Alaska panhandle to Glacier Bay, excluding ocean-type chinook until again reaching the lower coastline influence along the Yakutat peninsula (59°30′N). The major drainages, on the mainland northwest of Misty Fjords National Monument, including the Stikine (56°40′N), Whiting (58°05′N), Taku (58°30′N), Alsek (59°10′N), and Chilkat (59°15′N) rivers, are surrounded by glaciers and peaks several hundred meters higher than the mountain ranges along the coast to the southeast. These northern basins are incised valleys with extensive glacial melt creating a greater reduction in temperature than in the lower topography immediately to the south, and suitable primarily for stream-type chinook. For example, the lower Stikine and Taku rivers appear to show summer rearing temperatures (April through September) only 1–2°C cooler than the Nass and Skeena rivers, but the duration of warmer temperatures are diminished in the former compared to the Nass and Skeena (Figure 23). Ocean-type chinook are present in the Nass and Skeena rivers, but absent in the Stikine and Taku (Healey, 1983). The relationship is based only on generalizations because the rearing distribution patterns of juvenile chinook in these systems are unknown, and thus the rearing temperature history is only surmised. However, summer rearing in the Stikine and Taku rivers occurs at lower temperatures and of less duration than in rivers along the northern British Columbia coastline, especially in the lower river reaches.

The reoccurrence of ocean-type rearing conditions along the Yakutat peninsula appears in the Situk River (59°30′N) (Johnson et al., 1992) and also further north under similar circumstances in the Deshka River (62°N) (Delaney et al., 1982). The Situk River drains low elevations with ground water and lake sources. The Deshka River is tributary to the Susitna River and courses over 75 km of extensive low elevation bog and wetland areas north of Cook Inlet.

Consistent with the ocean-type life history, both these river systems have warmer summer temperatures associated with ground water or lower elevation wetlands that sponsor rapid growth and age-0 migration patterns. As demonstrated in Figure 24, winter temperatures in Situk River drop below 2°C by November and remain there until mid-April, which requires early spawning times, and thus the classification of the population as spring chinook [Sit-SA25-0]. However, rearing temperatures reach 10°C by June and remain above

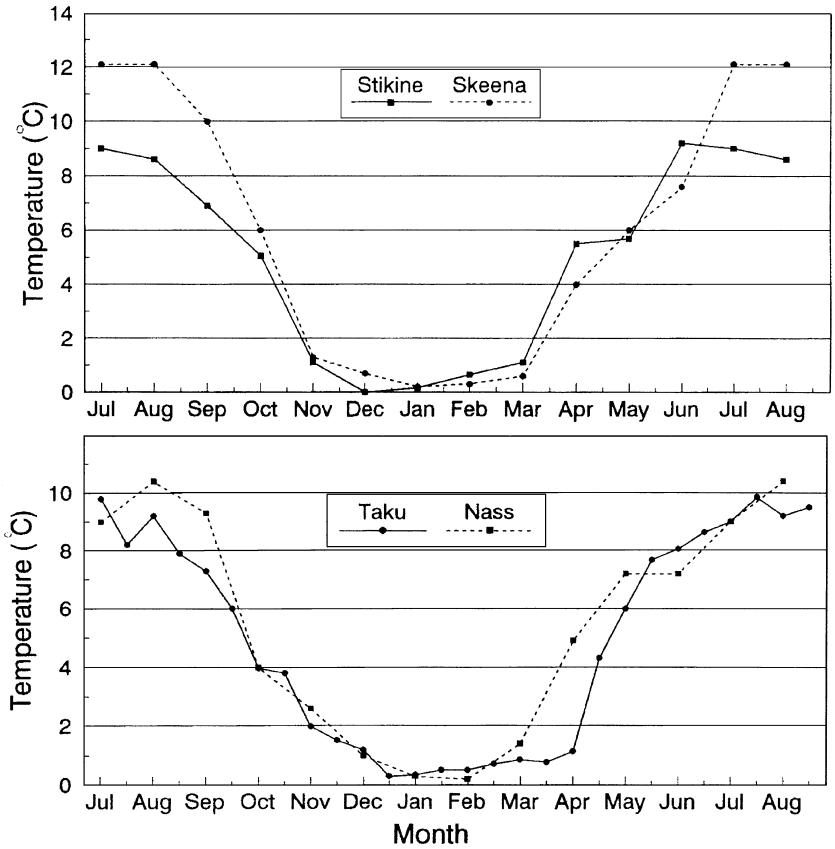


Figure 23. Mean temperatures of the Skeena, Nass, Stikine, and Taku rivers from 55° 20′N to 58° 30′N, in British Columbia and Alaska (USGS and DFO).

12–14°C until after September, which allows juveniles to evacuate the system as age-0 emigrants at a size >70 mm before September.

In the Deshka River, chinook spawn earlier than in the Situk because of cooler temperatures, remaining near 0°C from October until May. Deshka chinook, therefore, would also be classified as spring chinook because of the early spawning in response to the very cold winters (Des-SJ30–0]. Rearing temperatures, however, also reach 10°C by June and climb as high or higher in the summer than the Situk River temperatures, with age-0 juveniles emigrating by August at a length >80 mm. Although both of these systems are somewhat unique in Alaska, chinook spawning behavior in these streams follows the typical pattern for the North because cold winter incubation temperatures drop to near freezing at those latitudes. In essence, this means that alevins need to be well advanced by the end of October to emerge by the middle of April, similar to other chinook in cool incubation environments of Alaska. Therefore, their uniqueness is not related to incubation temperature, but instead to warmer rearing temperatures that promote age-0 juvenile emigration. Age-0 emigrants may be found among other Alaska chinook populations in smaller rivers draining extensive low wetland areas close to the coast that provide warm rearing environments.

The curtailment of winter-run chinook above 38°N, of late-fall-run above 45°N, of fall-run above ≈52°N, of summer-run generally above ≈54°N, and late spring-run above

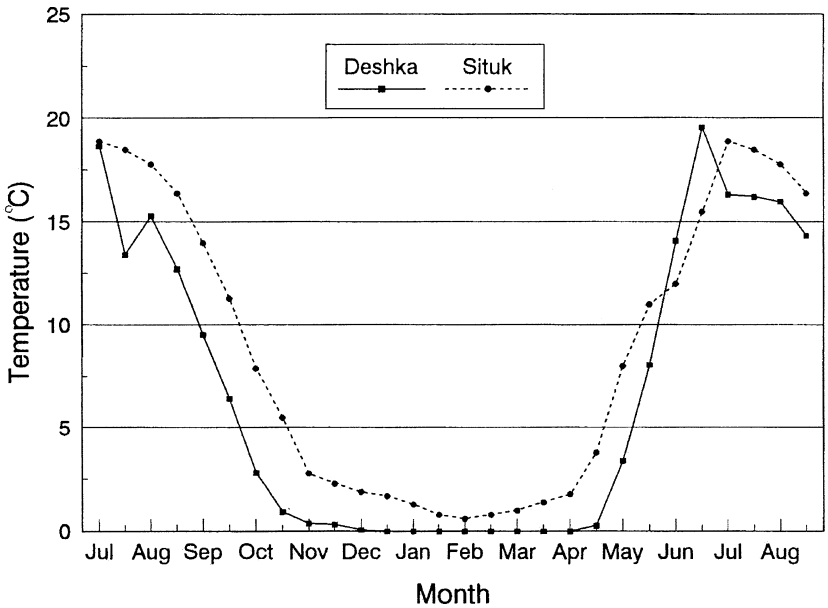


Figure 24. Mean temperatures of the Situk and Deshka rivers, Alaska, where ocean-type chinook dominate compared to the Taku River where stream-type chinook persist (USGS).

60°N latitude, demonstrates the influence that incubation during the fall equinox and winter solstice has on limiting spawner/incubation life history options. As latitude and elevation increase, stream temperature regimes decrease and temporal compensation to synchronize emergence timing moves spawning forward until the only functional option that remains is the early spawning, spring-run strategy, as shown earlier in Figure 15.

The inverse frequency of ocean- and stream-type life history forms from southern to northern latitudes and low to high elevations, respectively, shows through growth responses the similar influence that decreasing rearing temperatures have on life history types. Although inversely distributed, the forms are more ubiquitous because rearing temperatures can be low at high elevations in the south, and high in northern latitudes during the spring equinox and summer solstice, which permits ocean-type chinook to exist even in the northern latitudes, as shown in Figure 16.

We reiterate that the rearing environments and the corresponding temperature profiles in which juvenile chinook are exposed to in most river systems is unknown. Variability in annual temperature patterns and juvenile behavior occurs which makes the relationships more difficult to ascertain. Unlike the spawning, incubation and emergence behavior of chinook salmon, the rearing phase is not site specific and juvenile chinook have the freedom to remain in the area of the home reach or to venture some distance away. The growth continuum among slower growing individuals is disrupted to different extents by termination of growth during winter conditions. The influence of temperature on chinook salmon life history as the foundation of population structure, however, is demonstrated consistently over the latitudes and elevations that characterize the geographical range of the species. Rather than four temporally separated spawning segments or two discrete racial types, chinook life history strategy is best described as a continuum of spawning and stream resident forms determined by environmental temperature. The multiplicity of life history strategies

that define the population structure of the species are thus determined by temperature profiles peculiar to the specific stream systems as one progresses over the chinook salmon geographical range of latitude and elevation.

The Temperature Model and Steelhead Life History

Steelhead have assumed a very different ecological strategy than chinook salmon as late winter and spring spawners. Steelhead embryos develop much faster than salmon embryos, with emergence in the late spring of the same year they are spawned. Moreover, like many of the trout species and Atlantic salmon, steelhead maintained iteroparity. By retaining successive interannual breeding opportunities, it helped prevent extinction through calamitous losses of young due to floods or drought in lightly populated more tenuous habitats. These traits segregated steelhead from chinook in spawning ground and early rearing environments, but also allowed them to be geographically sympatric with chinook by exploiting temporally different incubation and juvenile feeding opportunities (Miller and Brannon, 1982).

Another strategic characteristic of steelhead life history is retention of the stream resident life history form, and both forms have continued in sympatry (Rounsefell, 1958; Chrisp and Bjornn, 1978; Burgner et al., 1992; Mullan et al., 1992). In contrast to other stream dwelling oncorhynchids that diversified life history options around anadromy, steelhead retained their total freshwater option and gene exchange with the resident form, rainbow or redband trout (Shapovalov and Taft, 1954; Busby et al., 1996). This strategy appears to give steelhead a definite advantage where harsh environmental circumstances or limited access may occur in their more isolated habitats. Moreover, interbreeding with and retaining the resident life history form maintains a preadaptive gene pool for security of the respective anadromous population under conditions of variable reproductive success, as suggested by Leider et al. (1994). This is similar in evolutionary strategy to that suggested in the sockeye/kokanee relationship, and helps insure against loss of the adaptive traits when conditions preclude the anadromous form from successfully reproducing in some years. The degree of interbreeding between resident and anadromous forms of *O. mykiss*, and their general genetic and evolutionary relationship to one another, however, are still largely unknown. Savvaitova et al. (1999) concluded that steelhead and rainbow in the Utkholok River in western Kamchatka were one interbreeding population. However, the Zimmerman and Reeves (2000) evidence from the Deschutes River, Oregon, suggests that in some cases sympatric steelhead and rainbow populations remain reproductively isolated.

The Basis of Summer and Winter Steelhead Life History Forms. Similar to other salmonids, anadromy evolved among *O. mykiss* to take advantage of the relative productivity of the marine environment for growth, while still having the security of freshwater breeding sites (Northcote, 1979; Miller and Brannon, 1982; Gross et al., 1988). Despite the advantages that large size conveys for egg production and competition on spawning grounds, some populations of steelhead leave the ocean many months prior to spawning, foregoing prime feeding opportunities at sea in the summer to make their migration upstream. However, in contrast to the spawning cline displayed by the chinook, early returning steelhead spawn at about the same time or even later than the late returning populations.

Early return behavior is somewhat curious when several stocks of Columbia River steelhead (especially Snake River stocks) have sizeable proportions of the run remaining below mainstream dams during the winter months. Shapovalov and Taft (1954) observed

that some steelhead don't migrate (even if sexually ripe) unless specific environmental conditions are met. For example, tagged steelhead remained in the Deschutes River for 198–233 days before returning to spawn. Steelhead bound for the Umatilla River pass Bonneville Dam by July, but may not pass John Day Dam until the following March (Howell et al., 1985), a distance <75 km. Furthermore, different parts of the same spawning stock may migrate through the Columbia drainage in a disjunct manner. For example, steelhead from the Grande Ronde and Asotin drainages pass through the lower Snake River drainage in two parts; the first peaking in mid- to late-September and the second from April to early-May (Howell et al., 1985). Analysis of the early- and late-runs suggest they behave differently in the reservoir above Bonneville Dam, resulting in markedly different timing at The Dalles and John Day dams. This behavior is consistent with the common impression that steelhead hold in drainages, such as the White Salmon or Deschutes rivers, tributaries of the Columbia between Bonneville and John Day dams (L. Beck pers. comm., ACOE) before ascending to spawning sites in the upper Basin.

Personnel at several dams have also reported semiresident steelhead living in and around the fish ladders. For example, during dewatering at McNary Dam in December of 1954, 1571 steelhead were removed from the deep water in the upper portions of the fish ladder. This number exceeded the count of 1,527 steelhead ascending that ladder during the entire month of November. The "holding" between dams, nonlinear migration rates and complex life history of summer-run steelhead prevented calculation of accurate travel times upriver; the peak count at one dam might be earlier than the peak downriver.

Movement of these steelhead resumes again the following spring when warming water temperatures are thought to trigger upstream movement. Disorientation of adults as they negotiate the ladders around specific dams may affect observed migration timing. Leman and Paulik (1966) demonstrated a strong relationship between the ability of salmonids to locate fish passes and manipulation of spillway gates at Rock Island Dam. In response to these relationships, the design and engineering of fish ladders have changed over time. Improved salmon passage was also apparent at Priest Rapids Dam after improvements were made to facilitate passage in 1977. Modifications at both of these dams may have resulted in earlier passage. Dams themselves may have improved passage on some sections of the Columbia River. Inundation of Celilo Falls in 1957 created a large increase in upriver summer escapement for several species, including steelhead (ODFW/WDFW, 1995) and shad (Quinn and Adams, 1996) for at least the subsequent 10 years, suggesting the falls had been a partial barrier to some species.

Ocean distribution and population dynamics of steelhead may be influenced by thermal regimes (Welch et al., 1998) and large-scale climate stochasticity that affect the eastern rim of the North Pacific (Welch et al., 2000). Thus, there may be some correlation between ocean temperatures and the timing of the return to coastal areas, as Blackbourn (1987) reported for sockeye salmon. However, we expect that timing of upriver migration (e.g., counts at dams) will be controlled primarily by genetic factors. Adults should return at the long-term average optimal date, with some interannual variation in response to environmental changes (see similar arguments for sockeye: Quinn and Adams, 1996). As many as 11 different age classes have been observed among returning steelhead (Howell et al., 1985; Mullan et al., 1992), with the most predominant spending 2 years in freshwater and 2 years in saltwater. Repeat spawners among mid-Columbia steelhead is lower (2 to 4%) than winter-run steelhead (6 to 12%) throughout their range (Withler, 1966; McGregor, 1986) and may never have been high in the Basin (Long and Griffin, 1937), although recent evidence from interceptions of spent-fish at the dams suggests their historical contribution may be underestimated (P. Anders, pers. comm.).

Steelhead have also segregated from salmon in their return migration, most pronounced among summer-run fish. Winter-run steelhead ascend river systems after fall returning chinook and coho are already on the spawning grounds, and only a month or two before spawning. Summer-run steelhead enter the river months in advance of spawning, but after most spring chinook have ascended the system and well before late returning salmon enter the river. Although higher flows are targeted, which we associate with providing migratory access to areas that won't be as readily negotiated during low flow periods, a significant portion of their migration occurs at the highest temperatures, and thus occurs at a time when the migratory energy cost is the highest. As discussed earlier, summer-run steelhead can hold in the mainstem river for several months, which may reduce migratory energy losses at high temperatures, but at least a significant portion of their presence in the Columbia mainstem occurs during the period of highest temperature. The pattern appears counter-intuitive except that the more distant migrating fish must get within reach of their spawning areas before late summer flows become low for passage or winter temperatures drop below the migratory threshold.

The causal influences on the temporal and spatial changes in steelhead migration patterns (e.g., changes noted in the l950s) are most likely attributable to a suite of environmental and engineered alterations in the river rather than to natural variability. The Columbia River now has markedly altered temperature and flow regimes. Modified fish passage facilities at dams also contribute to changes in timing patterns, as well as changes in stock structure from the differential fishing mortality. However, summer steelhead migrations are clearly defined by entering the river long in advance of spawning, holding in winter during the period of coldest water and lowest flows, and then ascending tributaries to spawn at specific times to facilitate emergence of juveniles in favorable conditions. Steelhead have made an evolutionary compromise between feeding at sea to store energy for migration and reproduction, and accessing distant spawning locations in the late winter and spring. This compromise is comparable to the tradeoffs made by other salmonids that return to freshwater long in advance of spawning. The challenge is to explain the long-term natural riverine conditions that favored such a life history pattern and to estimate the effects that river modifications have had when considering recovery options.

The increased number of storage dams in the upper reaches of the Columbia and Snake rivers have significantly altered the natural river hydrograph and enabled a great increase in flow control. By storing water, naturally high summer flows from snowmelt are reduced and low winter flows are increased, allowing for a more even hydropower production throughout the year. Peak flows at Rock Island Dam increased from 1933 until the early 1950s, but Bonneville, McNary, and Rock Island dams all experienced a substantial decrease in flow since the 1950s (Quinn et al., 1997). At Bonneville, decreased summer flow since 1950 has paralleled increasing summer water temperatures. Furthermore, spring warming has become earlier, and fall cooling has become later for the Bonneville to McNary section of the Columbia River (Quinn et al., 1997). Further up the river, temperatures at Priest Rapids have warmed, whereas those at Rock Island decreased until the 1960s and have since steadily increased. Temperatures at Ice Harbor on the Snake River have decreased. It is instructive, therefore, to look more closely at the affects these environmental changes have had on steelhead migration.

a. Effects of altered temperature. Throughout the last 60 years, both early and late portions of the summer steelhead run have migrated past Bonneville Dam at close to peak summer temperatures. However, during the cooler temperatures of the 1950s, early run steelhead migrated earlier, but have became progressively later during the subsequent warming years. The early run has been ascending Bonneville Dam later in the summer (roughly

mid-August rather than early August), which has minimized the changes experienced in the thermal regime. Greater delay by the late run would also cause them to experience somewhat cooler temperatures at Bonneville Dam, but this has not been observed, which suggests that the extent of that change biologically has not been too significant.

Elson (1969) demonstrated increased migration intensity for Atlantic salmon with increasing water temperature up to a temperature within 5°C to 6°C of the upper lethal limit (about 30°C). Steelhead may also favor warmer temperatures for their initial upstream migration, prior to "holding" for cooler water above Bonneville Dam (USCOE, various reports). Seeking cooler water would reduce energy loss (as for spring chinook salmon, Berman and Quinn, 1991) during migration through the upper river regions. Although there have been shifts in migration timing and temperature, it does not appear that the timing of steelhead migrations has fundamentally evolved to avoid peak temperatures in the lower river. They could migrate later in the fall if necessary. However, river temperatures are now warmer during the migratory period than in past years, and this raises the energy cost during migration (Brett, 1995). Moreover, warmer water during the spawning run may decrease weight, reproductive output, and perhaps survival (Gilhousen, 1990). However, this may be offset to some extent by the lower water velocities in the reservoirs, which have been associated with more rapid upstream migration by sockeye salmon (Quinn et al., 1997).

In addition to summer peak temperatures, cold winter temperatures may play a role in controlling the evolution of migratory timing in steelhead. Thompson et al. (1958) reported that steelhead in the Snake River drainage stopped migrating when temperatures declined below 3°C and resumed in the spring when temperatures exceeded 4°C. Swimming performance declines at very low temperatures (Brett, 1995), and tributaries at high elevations may partially freeze in winter, reducing flow to impassable levels until the spring. This has been suggested to result in later spawning in the upper portions of the Columbia and Snake River drainages compared to lower elevations (Howell et al., 1985). However, later spawning at high elevations also occurs with resident *O. mykiss* and is more likely related to less favorable incubation conditions during early spring. Movement by summer steelhead is minimal during winter in the Skeena and Chilcotin rivers in interior British Columbia, where less than 0.1 km per day is reported (Spence, 1981; Lough, 1983). By overwintering in freshwater, steelhead lose some growth opportunities at sea in late summer. However, winter growth at sea is slight (Burgner et al., 1992), and, by entering freshwater early, they are near the spawning grounds when spring temperatures increase and timing is suitable for reproduction. Furthermore, the cold, low-flow conditions in deep pools could facilitate an effectively dormant winter condition, minimizing loss of energy reserves that may not be possible at sea.

b. Effects of altered flow. Flow regimes of the Columbia River have changed since construction of mainstem dams. The most obvious has been the reduction in summer peak flows and increase in winter flows, but the peak is now somewhat earlier than historical pattern (Figure 25).

The natural pattern of summer steelhead has been to migrate during the late summer and early fall (Figure 26), when flows are declining from their peak in May and June. Except for the Snake River run, the demonstrated historical bimodal pattern also seems to have become a unimodal pattern in the mid-Columbia by the 1980s and in the rest of the system by the 1990s.

The record at Bonneville Dam shows early run steelhead, which migrate in higher flows than late-run fish, migrating earlier as peak flows increased into the 1950s and progressively later since that time, when peak flows have decreased (Figure 27). Little variation in the pattern for late-run steelhead may be a result of migrating at discharge levels that are lower

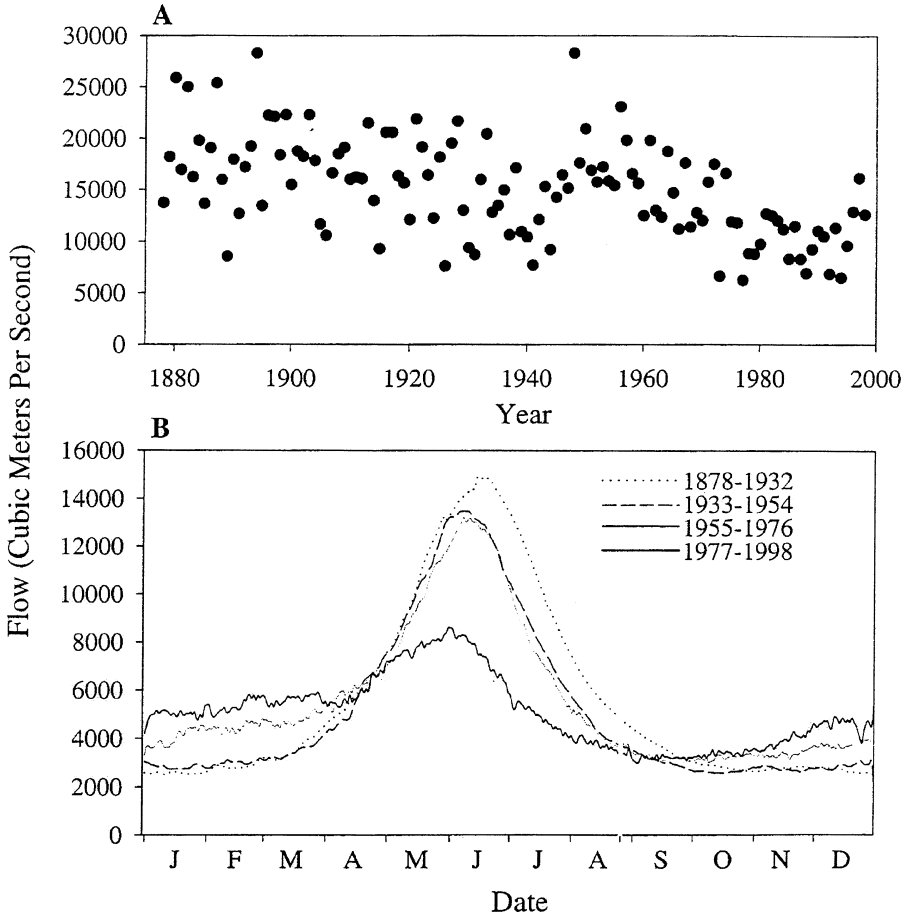


Figure 25. Effect of reservoir operation on the Columbia River flows at The Dalles, Oregon. Data from USGS-National Information System Files, station number 14105700. A: Annual peak flows; B: Seasonal patterns of flow for predam (prior to 1932), and the three subsequent 21-year periods to present.

on average and have changed less than those experienced by the early run. The pattern further up the river is different, indicating some change in behavior above Bonneville and The Dalles Dam.

Flow is the factor most frequently cited as controlling the rate of upstream migration of salmon in rivers. Jensen et al. (1989) indicated that adult Atlantic salmon in Norway could only migrate at river flows below a certain level to allow passage over several waterfalls. Banks (1969) also indicated that Atlantic salmon prefer moderate rather than high or low flows. Furthermore, lower flow in itself may slow passage of salmon (Banks, 1969; Liscom et al., 1985). Observers at Bonneville Dam observed less hesitation at flashboards during periods of greater flow (April 11, 1939, USCOE, 1939). It is difficult to understand the detailed hydraulics of passage around rapids and falls that no longer exist, such as at Celilo Falls (inundated by The Dalles Dam), but passage of steelhead is believed to have evolved to balance the need to feed and grow at sea during the summer and the need to get upriver at flows that facilitate easier passage. For example, the tendency of steelhead to "hold"

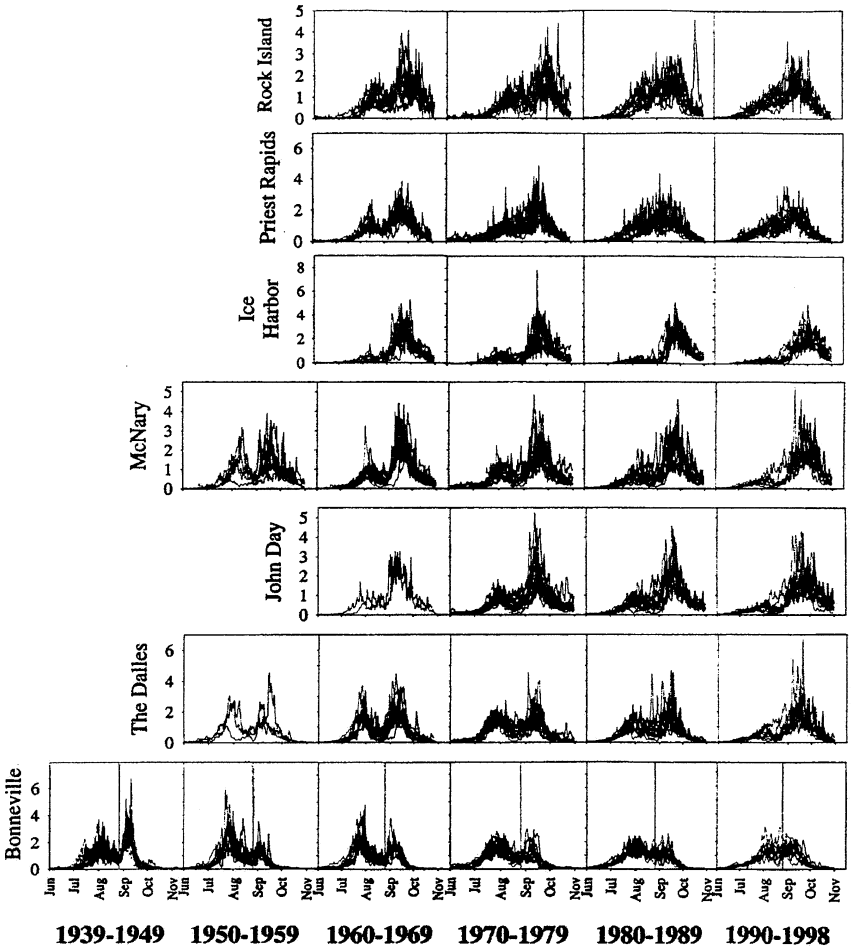


Figure 26. Percent daily-runs, grouped by decade for mainstem dams and salmonid counts on the Columbia River and Ice Harbor on the Snake River. Graphs are plotted from June 1 (start of fish year) to October 31 except for Bonneville plotted unit November 15. Each decadal graph consists of 10 (annual) lines, each representing 150 data-days (16 hrs/day). Black vertical lines on Bonneville plots represent arbitrary split between A- and B-runs.

between Bonneville Dam and the historic location of Celilo Falls may, in part, be indicative of such as adaptive balance.

Mean flow alone does not appear to explain their early migration into the river system some 8 months prior to spawning. Flows in the early spring are similar to those in the fall at the time of the summer-run migration. Steelhead could thus leave the ocean in February or March and swim as far as their spawning grounds, arriving at the same time as if they overwintered in freshwater. However, this neglects the role of low temperature in swimming performance and also the uncertain variation in river flow. Migration would occur in water temperatures less than half those in the fall (Figure 28). Furthermore, summer-migrating steelhead that arrive early, when flows are still too high to negotiate an area of difficult passage, can wait and ascend later. On the other hand, if they migrated in spring and encountered excessively high flows, they might be unable to reach spawning grounds in

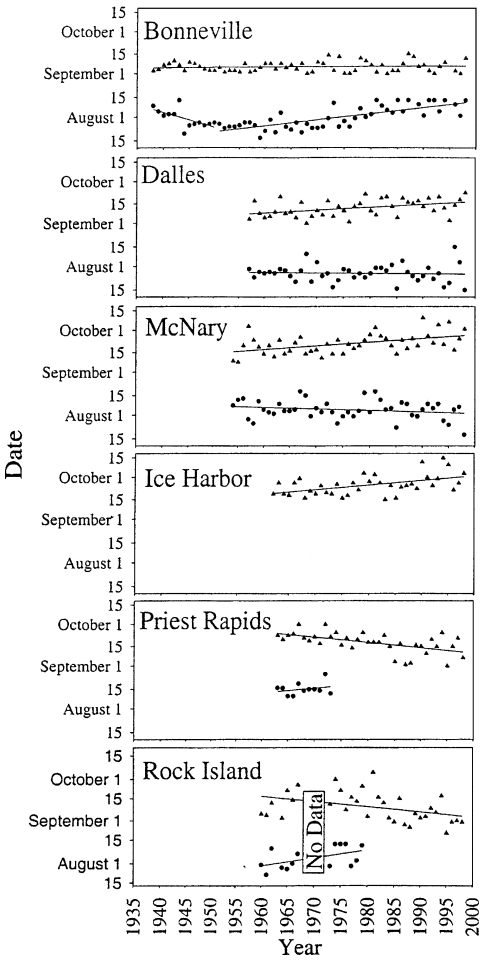


Figure 27. Peak migration date of early-run (circle) and late-run (triangle) steelhead passing mainstem dams in the Columbia River system.

time. This pattern of peak flows was also observed on the Salmon River above dam projects. In addition, the interaction between flow and passage may also be most critical in the spring at the spawning grounds, particularly those at high elevations where conditions might lower flows to impassable levels. In these cases, steelhead appear to wait for increased flow rather than using a specific temperature cue (Spence, 1981; Lough, 1983).

c. Relationship between steelhead spawning and fry emergence timing. Steelhead spawn from late January to July with winter-runs spawning somewhat earlier than summer-run populations. Summer-run fish start their migration in close temporal proximity to that of spring chinook, but they hold in freshwater several months longer than chinook, spawning in late winter and spring months. *O. mykiss* probably evolved largely in the headwaters of the larger streams (Miller and Brannon, 1982) but where residence was possible year round. In colonizing headwater streams, they confronted low enough temperatures to forestall their progeny from leaving the natal system in some cases (Mullan et al., 1992).

Rainbow trout, the nonmigratory form of *O. mykiss*, are generally small and less fecund, but we believe they provide the security of maintaining the adaptive gene pool from which anadromous forms can be reinitiated given the right opportunity, much like the relationship

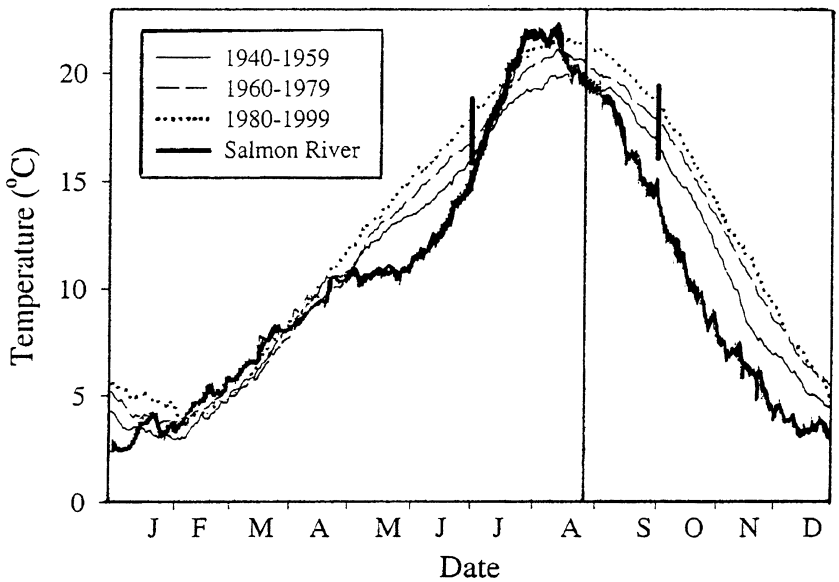


Figure 28. Seasonal pattern of water temperatures at Bonneville Dam over three equal periods since construction. Thick vetrtical black bars on chart depict the general boundaries of the summer-run steelhead migration period; the thin vertical line indicates the cut-off between the arbitrarily defined A- and B-runs.

between sockeye and kokanee mentioned previously. Also, by retaining iteroparity, the losses of juveniles due to chaotic floods alternating with near droughts help provide the security of maintaining the brood line for subsequent generations. Steelhead also may delay maturity to acquire the size and energy stores for long migrations and lengthy residence before spawning, especially when they need? to maintain sufficient health to return to sea after spawning. Shaffer and Elson (1974) suggested that delayed maturation among Atlantic salmon correlated with extensive migratory journeys similar to what steelhead experience.

Major physiological changes were required for *O. mykiss* to evolve away from the fall spawning pattern of other oncorhynchids into late winter or spring spawning forms. Because emergence timing among steelhead also targets a favorable growing environment in the spring or early summer, late winter or spring spawning steelhead had to shorten incubation time to synchronize fry emergence. Therefore, as spawning time evolved from a fall to spring pattern in this species, there had to be a concurrent selection for an accelerated rate of embryo development. Steelhead require a little more than half the number of days to reach yolk absorption at given temperatures compared to that of fall spawning chinook (Figure 29), which represents a significant difference from that of their salmon relatives.

Spring-spawning strategy is believed to have evolved partly as a result of competition with the more numerous salmon (Miller and Brannon, 1982). However, the movement to more headwater habitats also meant the steelhead had to endure the harshness of the winter to gain the selective advantage over salmon in those locations. By evolving spring-spawning time and a compressed incubation period, they were able to avoid freezing winter temperatures and low flows at higher elevations, which were clearly advantages in those environments.

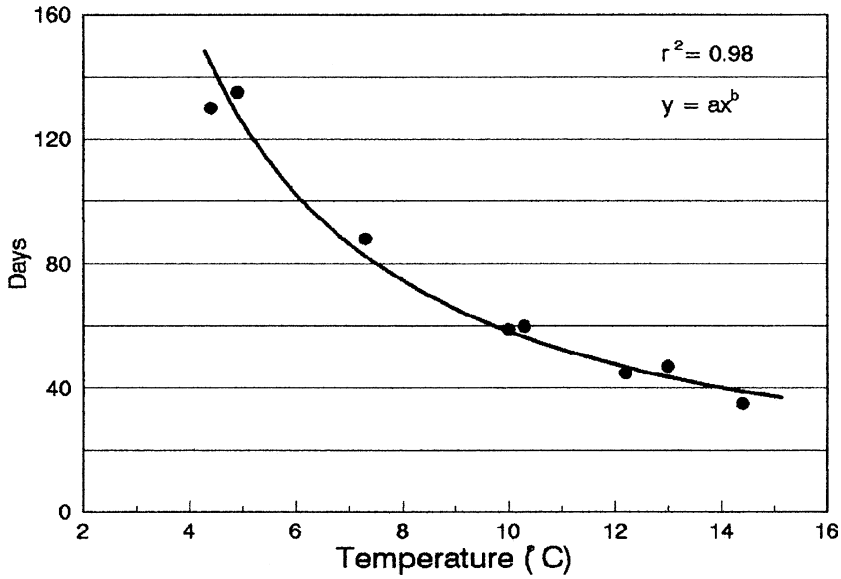


Figure 29. Relationship between mean incubation temperature and length of the incubation period in days to complete yolk absorption for steelhead trout (IDFG, USFWS, Brannon, 1987).

The evolution that occurred in *O. mykiss* to accommodate temporal changes in spawning and incubation is another interesting account of differences between steelhead and salmon. As discussed earlier, chinook and most other salmonids deposit their eggs on the descending temperature cycle of the fall, and as temperatures decrease into winter, the metabolic rate of the embryo compensates by requiring proportionally fewer temperature units to complete yolk absorption, as was shown for chinook salmon embryos in Figure 9. Spring spawning steelhead, however, deposit their eggs on the ascending portion of the temperature cycle, and incubating steelhead embryos require fewer temperature units to reach yolk absorption as temperatures rise (Figure 30).

Therefore, although high temperatures in the fall would appear to signal a late winter for incubating salmon embryos, and hence the need to slow development to synchronize spring emergence, high temperatures for incubating steelhead embryos would signal an early spring, and thus the need to speed development to synchronize emergence with the onset of earlier food availability. Thus, chinook and steelhead embryos demonstrate the opposite response in rate of development to changes in temperature. These patterns are consistent with the species ecology and underscore the role of temperature in the evolution of life history.

Spawn timing as a mechanism in life history strategy for steelhead, however, needs to be qualified compared with that of chinook salmon. Mullan et al. (1992) reported that steelhead fry emerged from their redds in mainstem environments of major streams in the mid-Columbia before spawning was completed in the tributaries of those streams. Emergence in some of the coldest tributaries didn't occur until the fall. Given that summer-run steelhead may spawn later than the winter-run, it is clear from these observations that the role of emergence on feedback for adult spawning time is muted compared to chinook. Summer-run includes some populations where timing appears to be a compromise between suitability for incubation and optimum emergence. Getting the jump on increased size

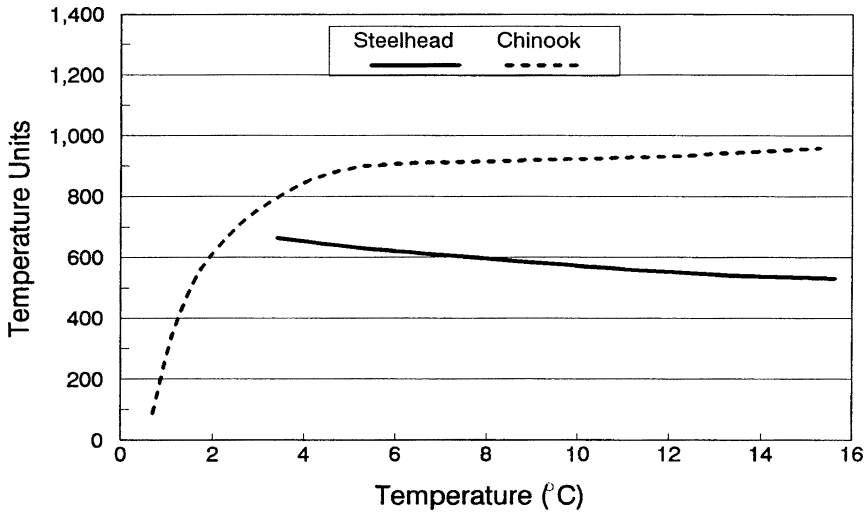


Figure 30. Relationship between temperature and the number of temperature units (degree-days) required for steelhead trout embryos to reach complete yolk absorption compared with chinook salmon (data converted from Figures 5 and 29).

during the first summer of residence by early emergence doesn't appear as critical as for salmon. In cold environments, spawning most likely occurs no sooner than is practical because incubation at low temperatures (<2°C) can prove lethal to embryos (Stonecypher et al., 1994). Under these circumstances, emergence may be delayed later than optimum, and although still the best strategic option under those circumstances, survival may initially suffer. It is apparent, therefore, that in some cases fitness of steelhead progeny may suffer because of the conditions in headwater streams.

d. Influence of the environmental template on life history forms. Upon emergence, steelhead fry appear to form small accumulations that shortly disperse downstream for cover and feeding. Steelhead fry (<50 mm) are reported to occupy stream margins in riffle areas over sand and gravel in early summer and change with the declining hydrograph to cobble and larger rock by late summer and at depths <60 cm and velocities <10 cm/s (Hillman et al., 1989a; Hillman and Chapman, 1989b; Mullan et al., 1992). At night, fry move to shallower water and lower velocities. During summer, dispersal appears to be limited (Hillman and Chapman, 1989a). However, with the onset of cooler fall temperatures, movement occurs in search of overwintering habitat, the extent of which correlates with cover (Hartman, 1965; Bjornn, 1971; Hillman et al., 1987).

Juvenile steelhead often station solitarily, but have been observed in small clusters of 3 to 5 fish. Juvenile ranging in length from 50 and 100 mm occupy areas with cover at water depths <140 cm, but change to shallower and lower velocities at night. Fingerlings (>100 mm) use the fastest and deepest water with stations behind boulders in high gradient riffles and cascades in water depths from 40–200 cm and velocities from 2–35 cm/s. As temperatures drop below 10°C, they have been observed to remain concealed in the substrate (Hillman and Chapman, 1989b).

The preponderance of the evidence indicates that steelhead occupy streams in relatively low numbers. Steelhead parr density in the mid-Columbia is generally low, with numbers in the range of 0.01 to 0.11 fish/m^2 most often reported (Chapman et al., 1994b), and in "average" habitat around 0.04 fish/m^2 (Mullan et al., 1992). These densities are similar

to coastal steelhead parr densities (0.01 to 0.04 fish/m^2) reported by Johnson (1984) and appear to be characteristic of natural carrying capacities of Pacific Northwest streams in general.

Ultimately, carrying capacity determines the upper end of egg to smolt survival rates within the various streams. Egg to smolt survivals have been estimated at 1.7% in the Wenatchee River (WDF et al., 1990), 0.4% in the mid-Columbia Basin (Peven, 1992), 0.16–3.61% in the Lemhi River, Idaho (Bjornn, 1978), 0.28–1.30% in the Keogh River, B. C. (Ward and Slaney, 1993), and 1.6% in Snow Creek, Washington (Bley and Moring, 1988). These levels of survival represent a wide range in potential adult return numbers, from less than replacement to increases of 10-fold over the brood year spawners. Mid-Columbia production appears relatively low, which may be the reason that the sex ratio of mid-Columbia steelhead favors females, and fecundities are much higher than average (Mullan et al., 1992).

With the exception of the Spokane River, Mullan et al. (1992) concluded relatively little productive habitat was available for summer-run steelhead in the predeveloped mid-Columbia region. Most tributary streams were considered to have experienced little change in potential habitat over the years because of their general inaccessibility for development. They estimated optimum escapement to the region of only around 5,000 steelhead based on estimated smolt production. Leider et al. (1986) considered survival of summer steelhead may depend largely on the availability of suitable rearing habitat in downstream areas, which Chapman et al. (1994b) suggested was one reason why natural production of steelhead in the Okanogan Basin was limited. The partial barrier of Celilo Falls would have had little influence on production potential of the mid-Columbia if productive habitat was the limiting factor.

The point is that with limited productivity the number of steelhead that can be produced per unit of rearing area is constrained, and population sizes may be smaller than one would anticipate simply from the surface area available. This applies in the Columbia River with steelhead abundance related to density (Ward and Slaney, 1993). Density-independent factors set an upper limit of abundance, but density-dependent factors ultimately determine the number and condition of fish produced (Poff and Ward, 1989). Therefore, numbers of smolts will depend not only on limitations of stream carrying capacity, but also from competition with other species. If production from tributaries limited in carrying capacity depends on the availability of suitable rearing habitat in downstream areas as suggested by Leider et al. (1986), then the large number of exotic species that now exist in mainstem habitat would place further significant caps on production potential of summer-run steelhead.

Winter-run steelhead on the other hand do not appear to be obliged to spawn in systems as temporally marginal as some populations of summer steelhead may use. Winter steelhead in the lower Columbia and along the coastal streams spawn at temperatures that provide fry greater temporal synchrony with their feeding habitat, where selective pressures are placed on optimum conditions for emerging fry survival. Coho are one of the major competitors with winter steelhead (Hartman, 1965) and inhabit some of the same areas as steelhead. Steelhead emerge later and segregate to riffles and remain in higher gradient reaches where they achieve a measure of security. Competition for habitat during the first year, however, is an important element in steelhead success and represents the major influence that coho have had on steelhead productivity when in sympatry (Hartman, 1965; Allee, 1982; Miller and Brannon, 1982). As they grow into yearlings, they have the size advantage in competition, and then potentially become predators on the next brood year's coho and steelhead fry, which could be a major selective advantage beginning in their second year.

Limitations of rearing habitat is a controlling factor on winter steelhead productivity, the same as it is with steelhead at higher elevations. Studies in the Alsea and Nestucca basins in Oregon (Solazzi et al., 2001) demonstrated the effect that expanding winter habitat had on increasing abundance of migrating steelhead the following spring, underscoring the decisive role of habitat on population abundance. The combination of limited rearing capacity in the habitat sought by winter steelhead and having to share resources with other aggressive competitors, denotes the influence of factors other than temperature in steelhead life history strategy. However, temperature is still a defining element of their habitat that influences when spawning occurs, emergence and residence patterns, juvenile growth, stream productivity, and, ultimately, what life history forms evolve.

Because emigration among steelhead generally occurs no sooner than age-2, they have the option of extending in residence until their migratory size/age relationship is met. Most Columbia River steelhead emigrate at age-2, but some juveniles have been reported to remain as long as seven years before smolting (Peven, 1990; Mullan et al., 1992). The length of residence depends on growth and physiological readiness to emigrate. Chapman et al. (1994b) concluded that steelhead in the coldest streams may be thermally fated to a resident life history pattern, regardless of having anadromous parents. Circumstances that determine which life history form (winter-run, summer-run, or resident) occurs, therefore, are temperature related.

The Temperature Model and the Evolution of Steelhead Life History Forms. The role of temperature in the development of steelhead life history forms appears clear and is different from that of chinook salmon. We attempt to demonstrate those differences in the proposed life history model for steelhead (Figure 31).

Steelhead are generally inclined to inhabit the cooler tributary environments, and thus have a more temporally focused anadromous life history strategy. The return migration also follows a temporal cline. Summer-run fish return earlier than winter-run fish, but age is not markedly different, except within the summer-run subpopulations, designated as A- and B-type fish. The A-type summer-run steelhead return and spawn in streams that will be slightly warmer than the B-type summer-run steelhead streams. The winter-run segment of the steelhead return cline is the latest, but spawning is associated with the warmest incubation temperatures. In contrast to chinook, steelhead target late winter and spring for spawning and, therefore, experience the coldest temperatures at the first of incubation, followed by a progressively increasing temperature regime over the remainder. Opposite to chinook, the earliest spawning occurs in the warmer habitats, and the cline thereafter is associated with a warming habitat progressively later in the spring. This results in early spawning by winter-run fish, and later by summer-run fish that have sought areas associated with higher elevations and thus cooler habitat. Temporal differences in spawning are not as distinct as with chinook, except where cold temperatures persist late into the spring.

As demonstrated in the model, the period of freshwater residence plays the dominant role in the determination of life history strategy. Spring spawning allows use of headwater reaches, and at a time when spawning salmon aren't present. After incubation, and emerging smaller and later than salmon fry, juvenile steelhead appear to have access to habitat either unavailable to or vacated by salmon. Size attained before marine entry is largely determined by rearing temperature and associated productivity, and thus the temperature of their freshwater rearing experience is a major factor in age at smoltification. Warmer rearing habitats encourage higher growth and earlier marine entry. Although food availability may influence distribution, it doesn't appear to be as limiting as temperature. Winter-run steelhead smolt primarily at age-2. A-type summer-run also smolt primarily at age-2, while B-type

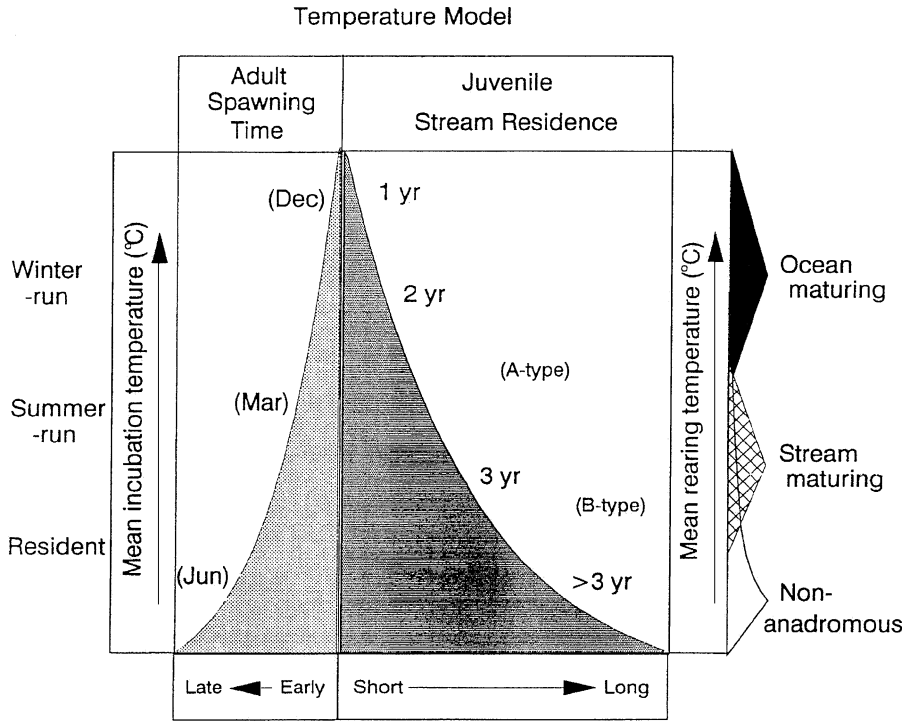


Figure 31. The model for steelhead life history in which mean incubation temperature determines early (winter) to late (spring) spawning times, and mean rearing temperatures determine age at marine entry, with nonanadromy as an option among both winter-run and summer-run steelhead, but most strongly associated with cold temperatures.

summer-run demonstrate a greater percentage of age-3 migrants. Moreover, unlike salmon, steelhead have the option of continuing as freshwater residents. Some of these may occur as genetic variants predisposed to continued residence, and others will remain as residents because of low environmental temperatures that discourage smoltification (Mullan et al., 1992; Chapman et al., 1994b).

Steelhead life history strategy, therefore, has evolved under different constraints than those confronting salmon. To succeed in their habitat and accommodate their needs as spring spawning, cooler water salmonids, steelhead have undergone significant changes from the life history strategy demonstrated by chinook. Under the constraints of competition in rivers occupied by other successful and more numerous oncorhynchids, steelhead strategy seems to have selectively segregated from salmon where environmental conditions made it possible.

Application of the Temperature Model on Steelhead from California to Alaska. Similar to the relationship of chinook life history patterns across their range, the origin of summer- and winter-run steelhead appears strongly associated with temperature, more specifically rearing temperatures, and related to latitude and elevation of the respective habitats. In the geographic distribution of steelhead, winter-run (ocean-maturing) life history forms predominate in Southern California and the Sacramento River, and a proportionally increasing number of summer-run (stream-maturing) steelhead are represented as one proceeds north

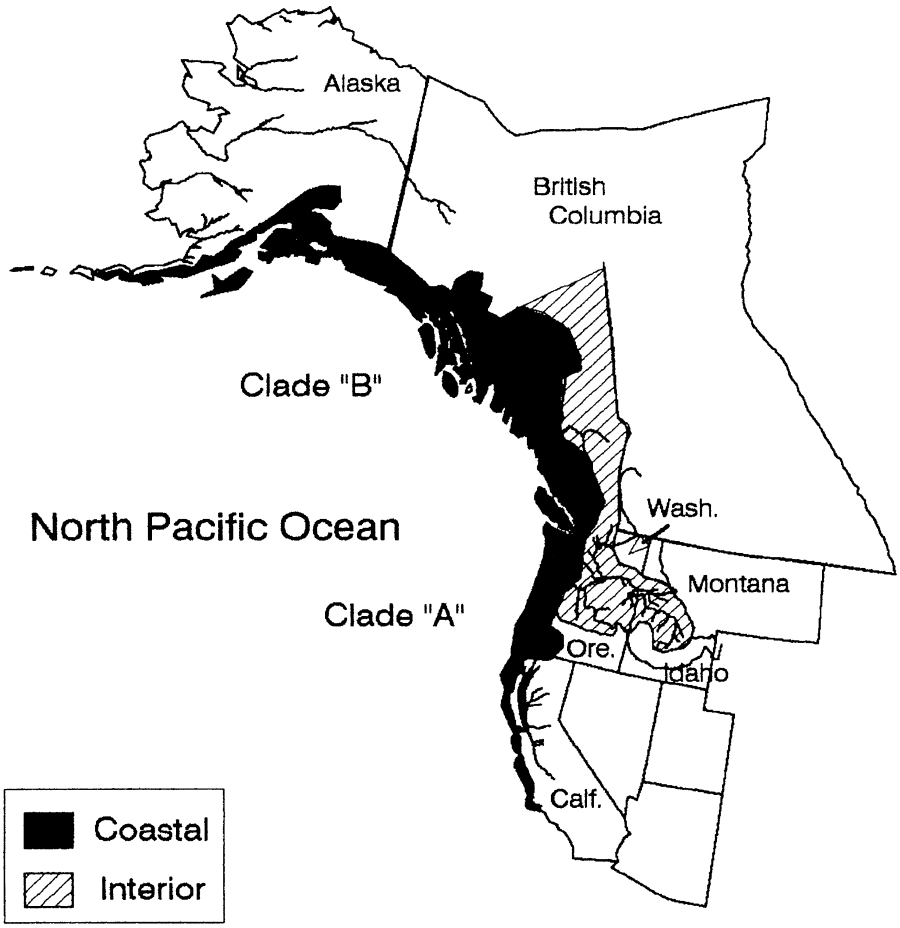


Figure 32. Distribution of coastal and interior life history forms of steelhead in their Northeastern Pacific range. Clade "A" is associated with streams of Oregon and Washington and Clade "B" is associated with areas no further south than Puget Sound.

along the Pacific Coast to Alaska (Busby et al., 1996) and into the Columbia Basin. The coastal (rainbow) and interior (redband) forms of *O. mykiss* in the Basin separate along the Cascade Crest (Figure 32). However, the picture is not as definitive as with chinook salmon, and we suggest that the major differences are the late winter/spring-time spawning patterns that evolved in these fish, and the fact that the rearing period is more of an inclusive influence on their life history form. Steelhead life history forms in Anchor River, Karluk River on Kodiak Island, and Situk River are locally referred to as the fall-run steelhead because many enter freshwater during the fall months and spawn the following late winter or spring (Van Hulle, 1989), almost intermediate between the winter-and summer-run life history forms in the Columbia. There are also spring- and summer-run fish in Southeastern Alaska, which with fall-runs are grouped together under the present nomenclature as summer-run or stream-maturing life history forms. Stream-maturing fish appear to return to larger river systems extending beyond the short-run coastal streams or to streams having colder origins. With their tendency to cease migration as temperatures drop below 3°C, these fish return

before winter low temperatures set in and reach holding areas in proximity of their spawning grounds until March or April when temperatures warm enough for spawning.

Steelhead also return to Alaskan streams that are warm enough to accommodate what is considered ocean-maturing steelhead. Short-run streams originating largely from low elevations (i.e., lower Situk and Karta rivers) generate what might be considered ocean-maturing life history forms even though the juveniles reside in these streams a year longer than in most other locations further south and migrate as age^{3+} smolts. The spawning reaches are close enough to marine waters that steelhead can get there without having to hold in distant freshwater areas before spawning.

There are no documented steelhead runs on the Alaskan mainland north of Susitna River and west of Cold Bay on the Aleutians. Anadromy terminates at that point and only resident rainbow extend further north into the Bering Sea. Rainbow trout are well represented in Bristol Bay streams and those immediately north. Similar to conditions described by Mullan et al. (1992) in headwater reaches of the mid-Columbia, temperatures appear to be too low to sustain anadromous populations of *O. mykiss* in streams entering the Bering Sea.

Population Genetics of Columbia River Chinook and Steelhead

The genetics of chinook salmon and steelhead have been extensively studied over recent years, and the genetic structure of populations has been described for chinook over their range from California to Alaska (Utter et al., 1989) and in the Columbia Basin (Utter et al., 1995; Bartley et al., 1992; Waples et al., 1991; Winans, 1989). Steelhead genetic structure has also been assessed over their range and in the Basin (Leider et al., 1994; Nielsen, 1994; Phelps et al., 1994; Berg and Gall, 1988; Hershberger and Dole, 1987; Schreck et al., 1986). Extensive reviews of population genetics have been conducted for chinook (Myers et al., 1998) and steelhead (Busby et al., 1996) in the Columbia River for consideration under the Endangered Species Act . These works have been comprehensive and provide the foundation on the genetic structure of these species in the Basin.

The objectives of our genetic analyses were to examine mitochondrial DNA diversity among chinook salmon to compare with allozyme data and to reexamine available allozyme data on steelhead populations in the interior Columbia Basin and assess how well the genetic results integrate with the conclusions derived from the life history and environmental evidence. An exhaustive reassessment of all genetic data was not possible under the scope of the present study. However, certain populations were selected for analysis that were anticipated to provide insight on relatedness and diversity between and within population segments.

In using genetic variation to establish relatedness among populations created by strong selective forces, the question resurfaces whether such variation in these life history forms is the result of only random events. The premise in population genetics is that the alleles used to characterize genetic structure are neutral, and thus over evolutionary time represent the effects of mutation, drift, and migration, but not natural selection. The polymorphic loci, therefore, are considered to represent changes that are associated with time and relatedness.

Although the allelic frequencies observed in a population might be viewed as a largely random event (Utter et al., 1980), the genetic characteristics responsible for survival success in that system are not. The founding population carries the genetic structure on which adaptive evolution hones the genotype in synchrony with the system. It is reasonable that some of the allelic variation, therefore, is selective or at least linked to fitness factors such as demonstrated by Chilcote et al. (1986). However, until there is greater understanding of salmonid genomics, these functional relationships will remain unresolved. Consequently,

in this study, we use the observed variation in the traditional manner as a framework on which to differentiate populations and estimate gene flow, but with the qualification that selection could alter the assessment of relatedness among populations and the estimated timeframe of change.

Chinook Salmon

Adult chinook salmon tissue samples were collected from 13 locations and different year classes (Table 4). Samples were stored separately in 70% ethanol or lysis buffer (50 mM

Table 4
Samples of adult chinook salmon collected from 13 locations in the upper Columbia and Snake rivers. Samples from the Hoko and Sooes river on the Olympic Peninsula of Washington were included as outgroups.

Evolutionary significant unit sample location	n	Sample date
Upper Columbia Summer/Fall (Ocean-type)		
Wells Hatchery	27	1999
Snake River Fall (Ocean-type)		
Priest Rapids Hatchery	55	1998
Lyons Ferry Hatchery	28	1998
Deschutes River Fall (Ocean-type)		
Deschutes River(lower)	51	1999
Sherars Falls (Deschutes)	57	1999
Deschutes River(upper)	46	1999
Snake River Spring/Summer (Stream-type)		
Imnaha River	24	1998
Johnson Creek	123	1997
Johnson Creek	98	1998
Lookingglass Hatchery	47	1998
Lookingglass Hatchery	82	1999
Rapid River Hatchery	54	1998
Rapid River Hatchery	66	1999
S.F. Salmon River	39	1998
S.F. Salmon River	84	1999
Upper Salmon River	16	1998
Upper Salmon River	19	1999
Sawtooth Hatchery	21	1998
Sawtooth Hatchery	31	1999
Olympic Peninsula		
Hoko River	28	1998
Sooes River	23	1998
Total	1019	

Tris-HCl, pH 8.0, 200 mM NaCl, 50 mM EDTA, 1% Sodium dodecyl sulfate, 0.2% Dithiothreitol) until DNA was extracted using methods modified from Sambrook et al. (1989) and Dowling et al. (1996). The polymerase chain reaction (PCR) was used to amplify sequences from each DNA sample using nucleotide primers specific for the mitochondrial NADH dehydrogenase subunit 1, and 5/6 gene regions (LGL Ecological Genetics). Amplified mtDNA gene regions were digested using six Type II restriction endonucleases to search for polymorphisms. The resulting mtDNA fragments were separated by electrophoresis using agarose or polyacrylamide gels. Gels were stained with ethidium bromide and restriction fragment patterns visualized using UV light. Photographs of each gel were converted into computer image files using a computer scanner. Restriction fragment length polymorphisms (RFLPs) observed among samples were measured using SigmaScan Pro 2.0 (Jandel Scientific, 1995), then given alphabetical designations as simple haplotypes. Fragment sizes of each RFLP from each gene region were estimated by comparison to a size standard, pUC-19 marker (Bio-Synthesis). Alphabetical designations from RFLPs of each mitochondrial gene region were combined into composite haplotypes for all samples (Table 5).

An estimate of the number of nucleotide substitutions per site (p) for each RFLP was calculated via the Nei (1987) method using the Restriction Enzyme Analysis Package (REAP 4.0) then used to generate a matrix comparing *p* values (distance) between all pairs of identified composite haplotypes (McElroy et al., 1991). Differences in haplotype frequencies among samples was also compared using the chord genetic distance measure of Cavalli-Sforza and Edwards (1967). Nucleotide diversity and diversity among populations were estimated using methods from Nei and Tajima (1981) and Nei (1987) and also in REAP (McElroy et al., 1991). The KITSCH program in PHYLIP 3.53 (Felsenstein, 1993), which assumes independence and equal rates of divergence, was used to generate a distance dendrogram from *p* values via the least-squares method of Fitch and Margoliash (1967) in

Table 5
Designations of composite mitochondrial haplotype patterns derived from combinations of observed simple patterns.

Composite haplotype designation	Simple haplotype patterns					
	ND 1				ND 5/6	
	Ase I	Dde I	Hae III	Rsa I	BstU I	Dpn II
Ot-1	A	A	A	A	A	A
Ot-2	A	A	A	A	A	B
Ot-3	A	A	A	A	B	A
Ot-4	A	A	A	B	B	A
Ot-5	A	A	B	A	A	B
Ot-6	A	B	A	A	A	A
Ot-7	A	A	D	A	B	A
Ot-8	A	A	E	A	B	A
Ot-9	A	C	A	B	B	A
Ot-10	B	A	A	A	B	A
Ot-11	A	A	C	A	A	A
Ot-12	B	A	A	A	A	A
Ot-13	A	D	A	A	B	A

PHYLIP 3.53 (Felsenstein, 1993). This illustrates the estimated evolutionary relationships and distance among the identified composite haplotypes. Additionally, a Neighbor-Joining (Saitou and Nei, 1987) dendrogram was generated from the Cavalli-Sforza and Edwards (1967) chord genetic distances and used to compare against the least-squares dendrogram of populations.

Cavalli-Sforza and Edwards (1967) chord genetic distance was also used as input for Principle Coordinate (PC) analysis to provide a graphic, ordination representation of genetic distance among chinook populations in two dimensions (Gower, 1966; Everitt, 1978). In this analysis, eigenvector components were scaled such that sums of squares equaled the corresponding eigenvalue (i.e., variance associated with PC axis). Geographic heterogeneity among haplotype distributions was tested for significance using a Monte Carlo simulation described by Roff and Bentzen (1989) for which the MONTE program in REAP 4.0 (McElroy et al., 1991) was used.

Analytical Results. A total of 13 composite mitochondrial haplotypes were observed among the 19 location/yr sampled for chinook salmon (Table 6). Overall frequencies ranged from 40.6% for *Ot*-1, the most commonly observed haplotype, to 0.1% for haplotype *Ot*-12. Haplotypes *Ot*-1 and *Ot*-2 were observed in samples from all locations and together with *Ot*-3, and *Ot*-4 accounted for 95.3% of the overall mitochondrial diversity observed. Thus, haplotypes *Ot*-1 through *Ot*-4 are considered here as major haplotypes. Figure 33 shows combined haplotype frequencies for a comparison between Snake River Fall and Snake River Spring/Summer ESUs. Although *Ot*-1 through *Ot*-4 are shared among spring and fall chinook populations, the distribution of haplotype frequencies differ significantly between the two ESUs when compared using a Monte Carlo type X^2 analysis in REAP 4.0 (McElroy et al., 1991).

Haplotype *Ot*-1 is the predominant haplotype in the Spring/Summer ESU at 50.6% while *Ot*-3 is the predominant haplotype in the Fall ESU at 46.8%. The Snake River Fall

Evolutionary Significant Unit	n	Composite Mitochondrial Haplotypes									
		Ot-1	*Ot*-2	*Ot*-3	*Ot*-4	*Ot*-5	*Ot*-6	*Ot*-7	*Ot*-8	*Ot*-9	*Ot*-10
Snake and Deschutes R., Fall Run	182	0.132	0.209	0.484	0.126	-	0.005	0.005	0.011	0.011	0.016
Snake River, Spring/Summer Run	704	0.506	0.371	0.045	0.040	0.016	0.023	-	-	-	-

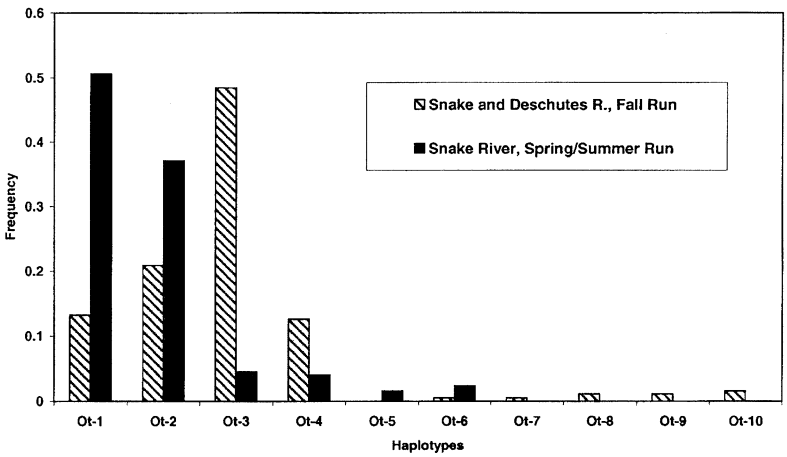


Figure 33. Distribution of composite mitochondrial haplotype frequencies between samples from Snake River and Deschutes River fall, and Snake River spring/summer chinook ESUs.

Table 6

Frequency distribution of composite mitochondrial haplotype patterns observed in chinook salmon from 19 locations in the Columbia Basin and two out-of-basin groups.

Number	Location	Year	n	*Ot*-1	*Ot*-2	*Ot*-3	*Ot*-4	*Ot*-5	*Ot*-6	*Ot*-7	*Ot*-8	*Ot*-9	*Ot*-10	*Ot*-11	*Ot*-12	*Ot*-13	*Ot*-14	*Ot*-15	*Ot*-16
Upper Columbia, Summer/Fall Run ESU (Ocean-Type)																			
1	Wells Hatchery	1999	27	0.148	0.296	0.259	0.111	—	—	0.111	—	—	—	—	—	0.074	—	—	—
2	Priest Rapids Hatchery	1998	55	0.145	0.145	0.400	0.200	—	0.018	0.036	—	—	—	0.036	0.018	—	—	—	—
Snake River, Fall Run ESU (Ocean-Type)																			
3	Lyons Feny Hatchery	1998	28	0.143	0.179	0.357	0.250	—	—	—	—	0.071	—	—	—	—	—	—	—
Deschutes River, Fall Run ESU (Ocean-Type)																			
4	Deschutes River (lower)	1999	51	0.059	0.118	0.588	0.157	-	0.020	0.020	0.039	—	—	—	—	—	—	—	—
5	Sherars Falls	1999	57	0.088	0.211	0.544	0.123	—	—	—	—	—	0.035	—	—	—	—	—	—
6	Deschutes River (upper)	1999	46	0.273	0.341	0.386	0.023	—	—	—	—	—	0.023	—	—	—	—	—	—
Snake River, Spring/Summer Run ESU (Stream-Type)																			
7	Imnaha River	1998	24	0.417	0.458	0.083	—	0.042	—	—	—	—	—	—	—	—	—	—	—
8	Lookingglass Hatchery	1998	47	0.638	0.106	0.149	0.106	—	—	—	—	—	—	—	—	—	—	—	—
9	Lookingglass Hatchery	1999	82	0.610	0.159	0.098	0.085	0.049	—	—	—	—	—	—	—	—	—	—	—
10	Rapid River	1998	54	0.500	0.278	0.093	0.111	0.019	—	—	—	—	—	—	—	—	—	—	—
11	Rapid River	1999	66	0.561	0.258	0.030	0.106	0.045	—	—	—	—	—	—	—	—	—	—	—
12	S. F. Salmon River	1998	39	0.462	0.462	—	0.051	0.026	—	—	—	—	—	—	—	—	—	—	—
13	S. F. Salmon River	1999	84	0.393	0.548	0.048	0.012	—	—	—	—	—	—	—	—	—	—	—	—
14	Johnson Creek	1998	98	0.398	0.480	—	—	—	0.122	—	—	—	—	—	—	—	—	—	—
15	Johnson Creek	1997	123	0.366	0.569	0.024	—	0.008	0.033	—	—	—	—	—	—	—	—	—	—
16	Salmon River	1998	16	0.813	0.188	—	—	—	—	—	—	—	—	—	—	—	—	—	—
17	Salmon River	1999	19	0.684	0.263	0.053	—	—	—	—	—	—	—	—	—	—	—	—	—
18	Sawtooth Hatchery	1998	21	0.714	0.286	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19	Sawtooth Hatchery	1999	31	0.839	0.161	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Olympic Peninsula (outgroups)																			
20	Hoko River	1998	28	0.036	0.071	0.357	—	—	—	—	—	—	—	—	—	—	0.536	—	—
21	Sooes River	1998	23	0.130	0.043	0.565	—	—	—	—	—	—	—	0.043	—	—	0.130	0.043	0.043

Run ESU also contained a larger diversity of haplotypes (9) than did the Spring/Summer ESU (6) though most of the haplotypes were in low frequency. Moreover, all haplotypes observed in the Spring/Summer ESU were also observed in the Fall ESU with the exception of *Ot*-5, which was only observed in the Spring/Summer ESU. Estimates were made of percent nucleotide divergence between all pairs of observed haplotypes (Table 7). Divergence between haplotype *Ot*-1 and *Ot*-3 is the result of a single polymorphism in the PCR amplified ND 5/6 gene region when digested with *Bst*U I, and resulted in an estimate of nucleotide divergence of 0.53% between the two haplotypes. The distance dendrogram using the Fitch and Margoliash (1967) least-squares clustering algorithm diagrams the percent sequence divergence between haplotypes, which ranged from 0.53% to 3.28%. Moreover, the range of divergence among haplotypes within each ESU were similar. Divergence between haplotypes within the Snake River Fall ESU as a group ranged from 0.53% to 3.28% as compared to divergence within the Snake River Spring/Summer ESU as a group, which ranged from 0.53% to 2.82%.

Chinook salmon have been extensively surveyed for genetic variation and population distinctness using protein electrophoresis (NMFS, 1998; Utter et al., 1989, 1992; Waples et al., 1991). Assuming neutrality, allele frequency distributions among populations can be used to explain related estimates of gene flow (or lack thereof) within the context of geographic distance or other factors that affect level of isolation (Slatkin, 1987; Neigel et al., 1991). These data are also typically analyzed by generating estimates of Wright's F statistics and related parameters to measure diversity and the correlation among alleles observed between populations (Wright, 1951, 1965; Weir and Cockerham, 1984). Additionally, examination of rare alleles may also be used to estimate the rate at which genes are exchanged between populations and thus indicate some level of divergence (Slatkin, 1981, 1985).

Mitochondrial DNA also has been used in numerous fish population studies (Wilson et al., 1987; Bentzen et al., 1989; Paragamian et al., 1999). Although the mitochondrial data set was much smaller than the large amount of allozyme genetic data available, mtDNA data still serves as a good estimator of genetic diversity and distance among populations (Birky et al., 1983). The observed mitochondrial variation within and among populations and the estimates of divergence between haplotypes in this study are consistent with conclusions drawn by Utter et al. (1989), Utter (1993) and Matthews and Waples (1991), using allozyme data. Primary differences between spring/summer and fall chinook populations appear to be quantitative in allele or haplotype frequencies and not due to the presence or fixation of unique alleles or haplotypes at high frequencies. Based upon an evolutionary clock (Brown, 1983), the largest estimate of sequence divergence between haplotypes, 3.2%, is comparable with a divergence among mitochondrial lineages, which would have taken place in the late Pliocene. This level of divergence would indicate the maternal lineages within chinook are phyletically quite old. However, levels of estimated nucleotide divergence are similar both within and between Snake River Fall and Spring/Summer Run ESUs, and both ESUs share the most common haplotypes observed. This suggests, along with allozyme data, the evolution of fall and spring/summer chinook occurred more recently. The dendrogram generated in Figure 34 shows spring/summer populations within the Snake River clustering together apart from fall populations, and Wells hatchery fall chinook from the upper mid-Columbia and the upper Deschutes chinook are separated from the fall run cluster in the Neighbor-Joining tree.

The dendrogram generated in Figure 35 also shows spring/summer populations separated from the fall-run fish. However, the key to this model is the comparisons with the "outgroups." Mitochondrial data from two out-of-basin fall-run populations, Sooes River

Table 7

Distance matrix (Nei, 1987) for observed mitochondrial haplotypes in 19 sample populations of chinook salmon in the Snake and Columbia rivers. (Values in the matrix must be multiplied by 100 for percent sequence divergence estimates).

	Ot-1	*Ot*-2	*Ot*-3	*Ot*-4	*Ot*-5	*Ot*-6	*Ot*-7	*Ot*-8	*Ot*-9	*Ot*-10	*Ot*-11	*Ot*-12	*Ot*-13
Ot-1	0.0000												
Ot-2	0.0053	0.0000											
Ot-3	0.0053	0.0110	0.0000										
Ot-4	0.0105	0.0164	0.0053	0.0000									
Ot-5	0.0164	0.0110	0.0227	0.0282	0.0000								
Ot-6	0.0052	0.0104	0.0104	0.0154	0.0212	0.0000							
Ot-7	0.0110	0.0171	0.0055	0.0110	0.0296	0.0161	0.0000						
Ot-8	0.0053	0.0110	0.0055	0.0053	0.0227	0.0104	0.0055	0.0000					
Ot-9	0.0154	0.0212	0.0104	0.0052	0.0328	0.0205	0.0161	0.0104	0.0000				
Ot-10	0.0110	0.0171	0.0055	0.0110	0.0296	0.0161	0.0115	0.0055	0.0161	0.0000			
Ot-11	0.0164	0.0227	0.0227	0.0282	0.0227	0.0212	0.0296	0.0227	0.0328	0.0296	0.0000		
Ot-12	0.0053	0.0110	0.0110	0.0164	0.0227	0.0104	0.0171	0.0110	0.0212	0.0055	0.0227	0.0000	
Ot-13	0.0110	0.0170	0.0057	0.0110	0.0291	0.0167	0.0115	0.0057	0.0167	0.0115	0.0291	0.0170	0.0000

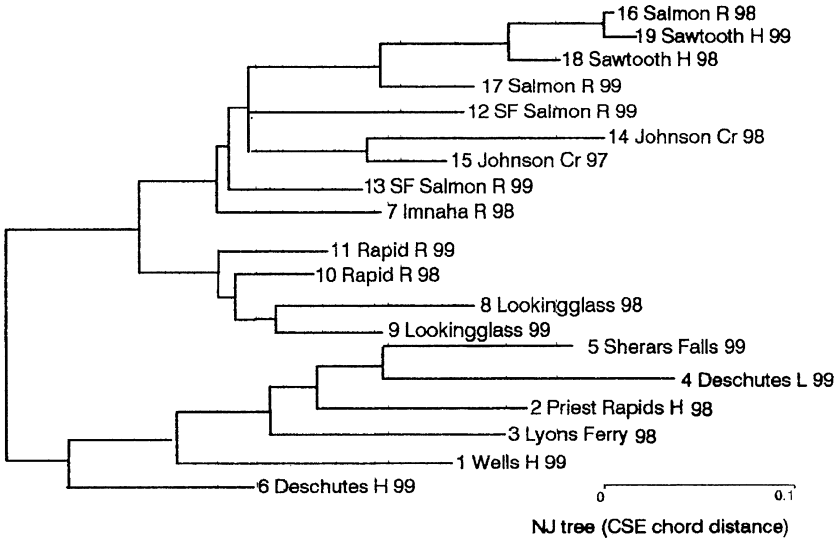


Figure 34. Neighbor-joining tree of certain Columbia Basin chinook salmon populations based on chord distance of Cavalli-Sforza and Edwards (1967).

and Hoko River on the upper coast of Washington, were included in the analysis. It is apparent in this dendrogram that the relationships between the spring/summer populations are closer to the in-basin fall-run than with the out-of-basin populations included in the dendrogram. It is interesting that the upper Deschutes population shows some association with the spring/summer cluster even though the fall-run cluster includes the lower Deschutes population. The difference in the spawning times of the upper and lower Deschutes populations are not markedly different, but the upper river population is a little earlier and thus closer to the summer run populations of the Snake River.

Lookingglass spring chinook salmon collected from the hatchery in 1998 and 1999 are closely associated with the spring/summer chinook cluster, having originated in part from

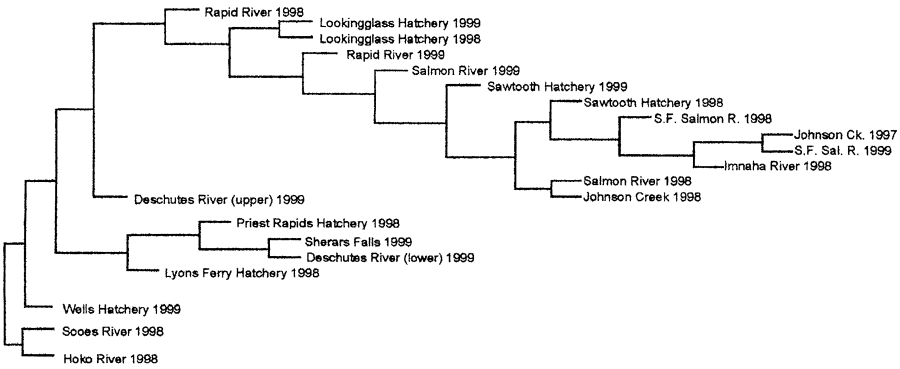


Figure 35. Dendrogram of chinook salmon populations constructed using the Fitch and Margoliash (1967) least squares method and a nucleotide substitution matrix (d values) generated using Nei and Tajima (1981). Mitochondrial data from two out-of-basin populations, Sooes (n = 28) and Hoko (n = 23) rivers were used as "outgroups."

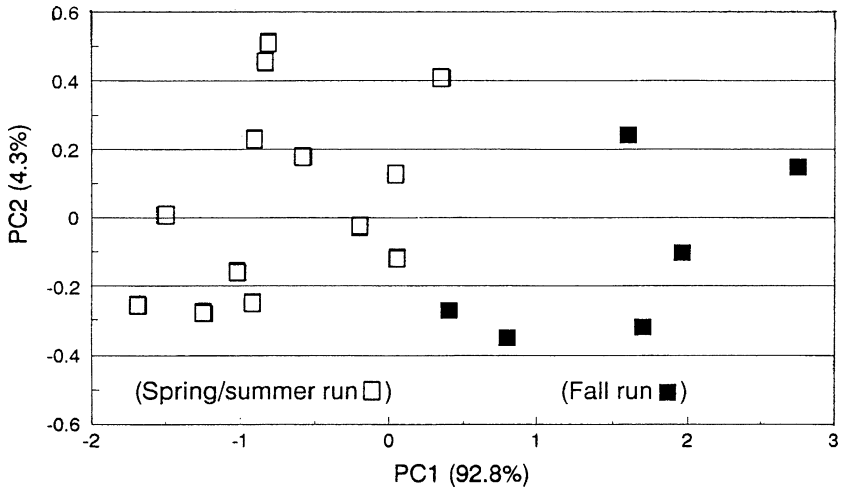


Figure 36. Principal coordinates biplot (PC axes 1 and 2) based on mean percent sequence divergence (×100) between individuals in different populations (eq. 10.21 of Nei, 1987). Fall-run and spring/summer-run populations are indicated by solid and open squares, respectively. The first two principal coordinate axes accounted for 97.1% of the total variation in genetic distances among populations.

Rapid River and Imnha stocks (Crateau, 1997). However, it is important to point out that genetic differences separating spring/summer and fall chinook populations are often not very great. Their genetic divergence notwithstanding, genetic and life history data suggest Snake River spring/summer chinook are more similar than fall chinook from the same watershed, but more closely associated with Snake River fall chinook than with Wells chinook from the upper mid-Columbia, and even more different than the outgroups from Hoko and Sooes rivers.

In Figure 36, the Principal Coordinates Analysis (PCA) also separates spring/summer chinook populations from fall chinook populations. These data are consistent with results from previous analysis of allozyme loci (Myers et al., 1998), where it was interpreted that spring chinook (stream-type) and fall chinook (ocean-type) comprise distinct lineages. Data presented here lack the power to discern whether stream-type and ocean-type life history forms constitute separate monophyletic lineages, which subsequently radiated independently throughout the Columbia Basin following glacial recession, or whether the appearance of these chinook ecotypes have largely developed over time through environmental selection working on local populations. Allozyme data reported in the comprehensive review by Myers et al. (1998) indicate fall chinook ecotypes are more closely related between Fraser and Columbia river drainages than they are to the spring/summer runs in the same watershed (Figure 36). However, this evidence does not indicate that ecotypes between river systems always originate from a common source nor does it preclude the adaptation of ancestral chinook populations into spring, summer, or fall ecotypes on a watershed by watershed basis, as suggested by spring and fall chinook relationships within and between the Klamath and Sacramento rivers (Banks and Bartron, 1999; Banks et al., 2000).

In the same review by Myers et al. (1998), clustering of coastal populations of chinook from Oregon, Washington, and British Columbia do not show the same dramatic distinction between ecotypes. In their review, they stated:

> Strong genetic differences exist between populations of spring-run and fall-run fish in the upper Columbia and Snake rivers. In the lower Columbia River, however, spring-run fish are genetically more closely allied with nearby fall-run fish of the lower Columbia River than with spring-run fish in the Snake and upper Columbia rivers.

Thus, there is supporting evidence for local differentiation of life history types from common ancestry in the Basin, as well as colonization by life history types from outside the Basin. From the conservation perspective, genetic similarities within river basins suggest a common lineage among life history types, while genetic similarities between major river basins indicate that life history types may share a common lineage between river basins. Thus, the interpretation most consistent with both the allozyme and mtDNA data is that multiple colonization events likely occurred and included contributions from a variety of sources. Although these maternal lineages have the ability to distribute geographically into new systems to occupy equivalent habitats, they also have the ability to evolve temporally and thus contribute to new life history forms within the same river basin.

It is important when considering the broader picture that care also be given to what constitutes stream- and ocean-type life history types. Regardless of spawning times, lower Columbia chinook experience temperature conditions that encourage higher growth during the summer, and thus demonstrate a high level of ocean-type migratory behavior. In the interior of the Basin, at elevations where rearing temperatures are cooler, the opposite occurs with a high percentage of stream-type behavior. However, where temperatures are warm enough in the interior Basin, such as mid-Columbia streams and the Hanford Reach in the mainstem, the summer/fall populations are a mixture of stream- and ocean-type, migrating at age-0 and age-1 (Chapman et al., 1994a). How these data apply to the more academic question about the origin of the ancestral types during the Pleistocene and phylogeographic dispersal is not being debated here. The important point is that regardless of their origins, selection has a major role in chinook life history strategy and in how temperature shapes life history types and dispersal.

Steelhead Trout

McCusker et al. (2000) used mitochondrial DNA variation to test biogeographical hypotheses in rainbow trout throughout the Pacific Northwest (every major watershed in B.C., Athabasca River in Alberta, Puget Sound, Lower Columbia River, Snake River, Alsea River in Oregon and several watersheds in Alaska). They sequenced parts of the ND1 and D-Loop for phylogenetic analyses. Analysis of Molecular Variance (AMOVA) and nested clade analyses were conducted to distinguish between mechanisms that may have resulted in the observed genetic and geographic association between populations, namely range expansions, allopatric fragmentation and restricted gene flow. From these analyses, McCusker et al. (2000) found some support for the subspecies groupings of Behnke (1992), but that model did not explain variation among regions as well as the Refugia Hypothesis.[2] Although resolution at the scale of the Columbia will require further analysis, McCusker et al.

[2]The Refugia Hypothesis were grouped into (1) Southwestern B.C. rivers such as the Tahuya, Vancouver and Queen Charlotte Islands; (2) Central, which included the Skeena, Kitimat, Nass and Dean Rivers, North Coast (incl. Alaska) and Yukon, Upper Fraser, Peace/Williston Rivers, Athabasca River; (3) Inland group, which included the Columbia and Snake. The Behnke hypothesis is from Behnke (1992).

(2000) broke down *O. mykiss* in two clades, labeled "A" and "B" (not to be confused with A- and B-type summer-run in the Columbia) that appear to have diverged well before the last glaciation. Only clade "A" was found in Oregon and the Columbia River Basin, but some clade "B" were found as far south as Puget Sound (Figure 32). A high level of diversity was found among closely related haplotypes, indicating that the Columbia River may have been and continues to be a source of population or refugia for the species. From this study, the most detailed to date addressing phylogenetic relationships, we conclude that *O. mykiss* in the Columbia River Basin is from a single ancestral lineage that subsequently subdivided into inland and coastal forms.

We made a hierarchical analysis of genetic variance on allozyme data to test the hypothesis that inland and coastal steelhead belonged to two major phylogenetic groups. We used Genetic Data Analysis (GDA) (Lewis and Zaykin, 2000) based on Weir (1996) and Weir and Cockerham (1984). Allozyme data from 94 samples (77 populations) were used in the analysis (Table 8) involving only "Class A" loci (Waples et al., 1993).

A number of alleles are found only in the inland and coastal populations. The presence of rare alleles is generally accepted as indicating that the populations have been isolated for a certain period. The rare alleles are listed in Table 9 (Busby et al., 1996).

Distribution of the genetic diversity of *O. mykiss* samples examined with the hierarchical analysis of Nei (1987) showed several patterns in the resulting dendrogram (Figure 37). The magnitude of the genetic distances between different geographical areas is important, particularly among coastal/Willamette and inland samples. Based on average F_{st} estimated among all samples, these differences are largely due to variation in loci *GPI-B1, NTP, LDH-B2,* and *sSOD-1* (individual $F_{st} > 0.15$), in decreasing order of importance.

The GDA was used on Nei's 1978 distance and identity matrices. The PCA was done with NTSY Spc V2.0, using the matrices as input and the pooled streams and years (Figure 38). The analysis shows a change from coastal genotypes to the inland genotypes.

Also, the analysis supports the conclusion that resident *O. mykiss* are not a separate or divergent group from the anadromous form when from the same geographic area. In systems where numerous, interconnected anadromous and resident populations exist, a correlation between geographic distance and genetic relationships have been described (Currens et al., 1990; Hindar et al., 1991; Northcote, 1992). In these cases, genetic differences between remote populations of the same life history were greater than the genetic difference between anadromous and nonanadromous forms living in the same tributary (Currens and Shreck, 1993), which suggested that if not of a common ancestry, they are at least interbreeding to some degree when sympatric within a sub-basin. Our analysis, therefore, is consistent with the conclusions of Shapovalov and Taft (1954), Currens et al. (1990), Hindar et al. (1991), and Northcote (1992). These results are particularly relevant to the issue of steelhead listings under the ESA, and the part that the resident form should play in their classification as species at risk, their role in recovery of listed species, and whether attempting to address the anadromous form (steelhead) apart from the resident form (rainbow) is justified. The analysis is also supported by work of Williams et al. (2000) that shows the several life history forms of *O. mykiss* are genetically similar over the entire Kamchatka Peninsula, suggesting a monophyletic lineage and gene exchange between anadromous and resident forms.

Variance components were estimated for the population subdivision described in Table 10, with results obtained with bootstrapping 1000 times over the 42 loci selected. All variance components are significant, including the inland/coastal groupings (θ_p). The results support the separation of inland and coastal groups based on allozyme data.

Table 8
Location and year of steelhead divided into four geographic groups.

Coastal	Year	Inland	Year
Lower Columbia/Willamette		Mid-Columbia	
Calapooia River	97	John Day, Beech Cr (2)	96
Clatskanie, Alder Grove	96	Umatilla (3)	96
Clatskanie, Conyers	96	Warm Springs River	96
Clatskanie, Swedetown	96	Snake	
Clatskanie, Wilark	96	Bedrock Cr	95, 96
Luckiamute River	97	Big Canyon Cr	89, 90, 94–6
McKenzie, Upper, Deer Cr	98	Boulder Cr	94, 97
Mollala, North Fork	96	Cedar Cr	94
Rickreal Canyon Cr	97	Chesnimnus Cr	89, 90
Santiam, North, Rock Cr	97	Clear Cr, Idaho	96
Santiam, North Mad Cr	96	Clearwater, Lapwai Cr	94
Santiam, South, Wiley Cr	97	Clearwater North Fork	96
Willamette, Middle Fork	98	Cottonwood Cr	94, 95
Yamhill, Willamina Cr	97	Hat Cr, Lower	94
Oregon Coast		Hazard Cr	97
Chetco River, Eel Cr	92	Imnaha, Camp Cr	90-2
Coquille, China Cr	97	Imnaha, Cow Cr	97
Coquille, South Fork	97	Imnaha, Grouse Cr	90
Coquille, Steel Cr	97	Imnaha, Lick Cr	80, 90–2
Elk River	92	Imnaha, Little Sheep Cr	80, 90–2
Illinois River, Briggs Cr	92	Imnaha, Upper Lick Cr	91
Illinois River, Grayback Cr	92	Indian Cr	94
Illinois River, Indigo	92	Iron Cr	97
Illinois River, Lawson Cr	92	Johns Cr	97
Nehalem River	92	Little Canyon Cr	96
Rogue River, Little Butte Cr	92	Little Salmon River	97
Rogue River, Lobster Cr	92	Lochsa River, Upper	92
Umpqua, North, Summer	94	Lochsa, Fish Cr	89, 90–1
Winchuk River	92	Lochsa, Old Man Cr	89
Yaquina River	92	Mission Cr	95
		Morgan Cr	97
		Owl Cr	94
		Salmon River, Upper	90
		Selway River	90, 96
		Selway, Gedney Cr	91–2
		Selway, Moose Cr	89
		Tucannon River	95
		Tucannon River, Lower	89, 90
		Tucannon River, Upper	89, 90
		Whitebird Cr	94

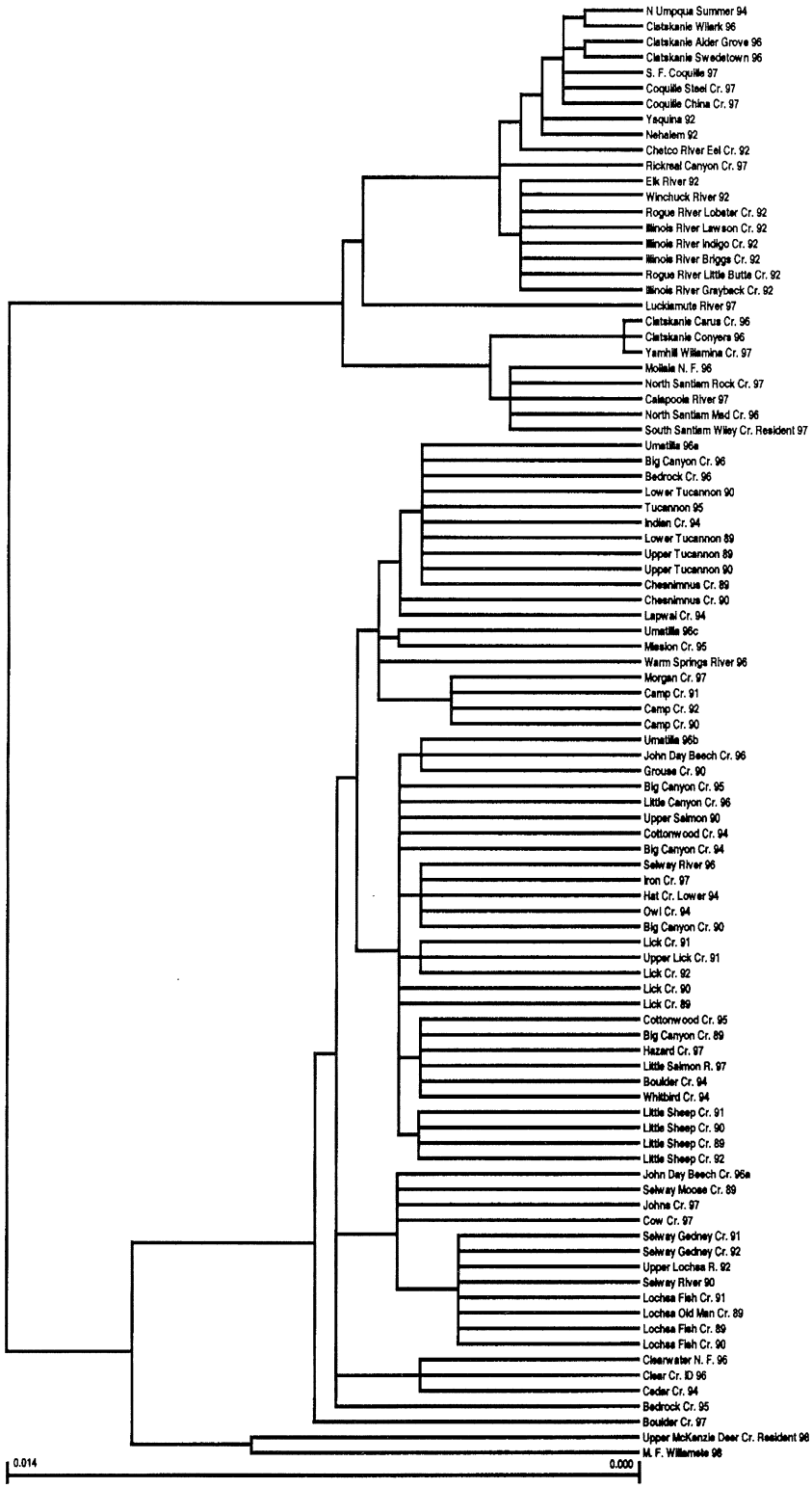


Figure 37. Dendrogram of *O. mykiss* populations constructed from spawning sites and years using hierarchical analysis of Nei (1987) data from Waples et al. (1993) and NMFS Coastwide Database.

Table 9
Rare alleles in Northwest Coast *O. mykiss*.

Locus	Allele	Frequency	Located
ADA-2	4	0.000544	Coastal
FH	4	0.000545	Coastal
G3PDH-1	4	0.006482	Coastal
GPI-BI	6	0.000542	Coastal
LDH-C	3	0.002709	Coastal
MPI	4	0.000542	Coastal
PGM-2	3	0.001083	Coastal
PGM-2	5	0.002167	Coastal
sIDHP-2	7	0.001101	Coastal
sMEP-1	5	0.002714	Coastal
CK-A1	2	0.001240	Inland
FDHG	3	0.003135	Inland
GAPDH-3	2	0.044915	Inland
GAPDH-3	3	0.000371	Inland
GAPDH-3	4	0.000124	Inland
LDH-B1	2	0.003688	Inland
LDH-B2	3	0.001729	Inland
LDH-C	2	0.000766	Inland
mAH-33	3	0.000389	Inland
MPI	5	0.000124	Inland
NTP	4	0.005537	Inland
PEPA	3	0.004658	Inland
PEPA	5	0.001839	Inland
PEPA-1	7	0.001593	Inland
PEPA-1	8	0.000133	Inland
PEPA-1	4	0.000627	Inland
PGK-2	5	0.000125	Inland
PGM-12	2	0.000241	Inland
PGM-15	5	0.000125	Inland
sAAT-3	2	0.003966	Inland
sAAT-3	3	0.002047	Inland
sIDHP-1	4	0.000868	Inland
sIDHP-2	6	0.000383	Inland
TPI-4	3	0.000124	Inland
TPI-4	5	0.001239	Inland

Interpretation of allozyme data is limited in distinguishing between the two major hypotheses on the origin of inland and coastal life history forms. The first hypothesis is that *O. mykiss* distribution is the result of two distinct phylogeographic lineages (Behnke, 1992). The inland form would have reinvaded glaciated areas in the interior basins, whereas the coastal populations would have reinvaded or continued to inhabit coastal rivers and streams. The second alternative hypothesis is that the observed genetic variation between inland and coastal *O. mykiss* is the result of geographic isolation and genetic drift (McCusker

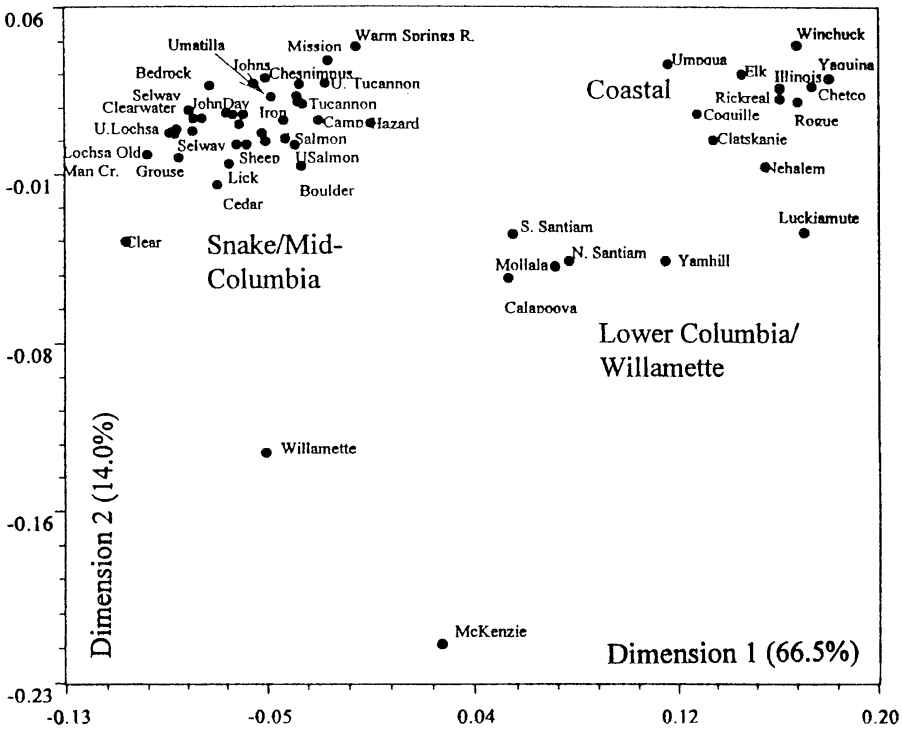


Figure 38. A multidimensional scaling plot of the 58 steelhead populations.

et al., 2000). The results of the present work are consistent with both hypotheses. Because allozyme frequency data will not permit resolution, a more detailed genetic analysis using sequenced segments of mitochondrial or nuclear DNA and analysis of base pair substitution would be required to resolve the competing hypotheses.

Evolution of Chinook and Steelhead Population Structure

Oncorhynchid evolution established the separate genotypic framework of the species: *O. shawytscha* as totally anadromous and semelparous, and *O. mykiss* as optionally anadromousand iteroparous. As poikilotherms, distribution of these species over their range is characterized by ecological types synchronized temporally with environmental temperatures

Table 10

Variance components among samples and groups described in Table 9 above. θ_P is F_{st} among inland/coastal groups. θ_s is F_{st} among population groups within the inland/coastal groupings, and θ_{ss} is F_{st} among populations within the θ_s groups.

Bound	F_{is}	F_{it}	θ_p	θ_s	θ_{ss}
Median	−0.019133	0.1714985	0.121724	0.153405	0.186216
Upper 95%	0.000508	0.277238	0.201621	0.249147	0.279377
Lower 95%	−0.038773	0.065759	0.041827	0.057714	0.093055

associated with changes in latitude and elevation. Key environmental elements affecting timing patterns, growth responsiveness, and dominance relationships have had decisive roles in the evolution of life history strategies of each species, and these strategies taken collectively are the foundation of population structure. The complexity of chinook and steelhead population structure rests with the diversity of opportunities that exist among the respective environments. As directional environmental changes are elaborated, exploitation of those opportunities by new life history forms occurs through selection that elicits the specificity required for optimum fitness. Population structure, therefore, is the reflection of the genetic composition of the founding sources within the respective region, shaped by the environment that defines life history configurations. The population structure of Columbia Basin chinook and steelhead presented here is an assimilation of the life history forms that represent functional traits, along with the general relatedness of populations based on allele frequencies that are assumed to show differences that have no selective significance.

Columbia River Chinook Salmon Population Structure

The previous view on population structure of chinook salmon was based on the racial theory where present chinook populations originated from two life history types that evolved as subspecies in isolation during Pleistocene glaciation (McPhail and Lindsey, 1970; Healey, 1983). Upon glacial recession, they repopulated the northeastern Pacific Coast independently, each allegedly having a geographic distribution consistent with the habitats related to those founding genotypes. Thus, within the Columbia Basin their population structure was previously considered as two separate monophyletic lineages divided along ocean-type and stream-type life history lines.

Our present understanding of population structure contrasts with the view that "racial" types, defined as subspecies, account for the life history forms observed today. From ecological, life history, and genetic analyses of chinook populations we conclude that population structure in the Columbia Basin, as well as elsewhere, is a reflection of diversity in life history forms expressed by ongoing adaptive evolution in diverse environments. The genetics of the population units are the result of both multiple colonization events and dispersal into new habitats through temporal adaptation. We have presented evidence of temperature as a dominant factor in the environment that defines what life history options are available to chinook salmon. Whether the founding sources evolved within the Columbia Basin or came as distinct life history forms from adjacent river systems that colonized different regions of the basin is not the issue, but we argue that ocean- and stream-type life history types are not linked to subspecies. The point is that while chinook are separated into several life history forms over a temporal framework, each has the potential of establishing other life history options when given such opportunities, as demonstrated in the Great Lakes (Kwain and Thomas, 1984) and New Zealand (Quinn et al., 2000; Unwin et al., 2000), and gene exchange should be expected to occur whenever population units overlap temporally regardless of their origin.

In an area as large as the Columbia Basin, population structure exemplifies a multiplicity of the life history patterns that when presented together form a cline representing the temporal sequence in mean incubation and rearing temperatures of natal stream reaches throughout the basin. Whether spawning occurs early or late, or emigration to marine waters occurs before winter (ocean-type) or after winter (steam-type), we argue that temperature is the primary influence for temporal differentiation. We suggest that diversity in population structure, therefore, is characterized by life history forms that occur as genotypes that evolved in synchrony with the various environmental templates of the Basin.

The dynamic nature of chinook life history is encouraged by the options that exist through different environments. Under this model, distribution by dispersal from founding sources would be a natural phenomenon within the major river basins. As temporal environmental changes are elaborated, directional selection allows exploitation of those opportunities by the adaptive evolution of new life history forms, which are then shaped by other environmental influences to establish discrete population specificity.

There is little doubt that more than one colonization event from external sources would have occurred in the Columbia, and from which different genotypes are expressed. In fact, it is assumed that migration of new genetic material from outside the system is a continuing event, and these fish can contribute to populations throughout the system. Therefore, it should not be surprising that genetically discrete forms are found distributed temporally within the same sub-basin, such as has been described in the mid-Columbia and the Snake rivers, when such different environments are present. Temporally specific life history forms that stray into the sub-basin from adjacent areas or other river systems will not succeed simply by randomly distributing around the sub-basin. Because of temporal predisposition, they will be most successful when by choice or by happenstance they are associated with the environmental template most similar to that from which they came.

Subsequent incremental changes in spawning time can occur from the inherent genomic variability of those fish as they adapt directionally to the new or dynamic environmental template. However, unless the environmental stepladders provide sufficiently small increments of change to accommodate the genetic variability present, colonization into temporally disparate environments by dispersal from these founding sources will not readily occur, and if the founding source is sufficiently isolated, it will remain distinct from other conspecifics in the sub-basin.

To portray the species in this ecological dimension, chinook salmon population structure is presented within the context of what is referred to in the ecological literature as a metapopulation (Lande and Barrowclough, 1987), or an assemblage of closely related populations within a geographical identity (Williams et al., 2000). We represent metapopulations in this paper as first-, second-, and third-order categories beginning with the most closely related populations in a common geographic area. Over the length of the river continuum and its conjunctive streams, a founding population will initially become established at a location where the temperature regime provides the greatest synchrony with its genotype. Subsequent expansion from the founding unit will occur first in similar environmental conditions within the range of variability present in the founding genome, representing a first-order metapopulation cluster, and later into second- and third-order categories as mutation and selection move new colonizing units further from the spatial/temporal mode of the founders. Thus, a first-order metapopulation refers to genetically similar populations spatially segregated around a given temporal profile within distinct geographical areas, such as the upper Yakima River or upper Salmon River. Classification as second- and third-order categories refers to differences in the degree of relatedness among first-order units. Therefore, second-order categories represent situations where clusters are considered similar to one another, but divergent enough to exclude their combination, for example, the Middle Fork and mid-Salmon River. Third-order categories represent those situations where clusters are most distantly related, such as comparative metapopulations of the Salmon and Deschutes rivers. Using percent nucleotide divergence to distinguish among the first-, second-, and third-order metapopulations, we suggest first-order units are those where divergence among populations is estimated at $<0.8\%$, second-order approximates divergence estimated between 0.8% and 1.8%, and third-order is when divergence between clusters is above 1.8%.

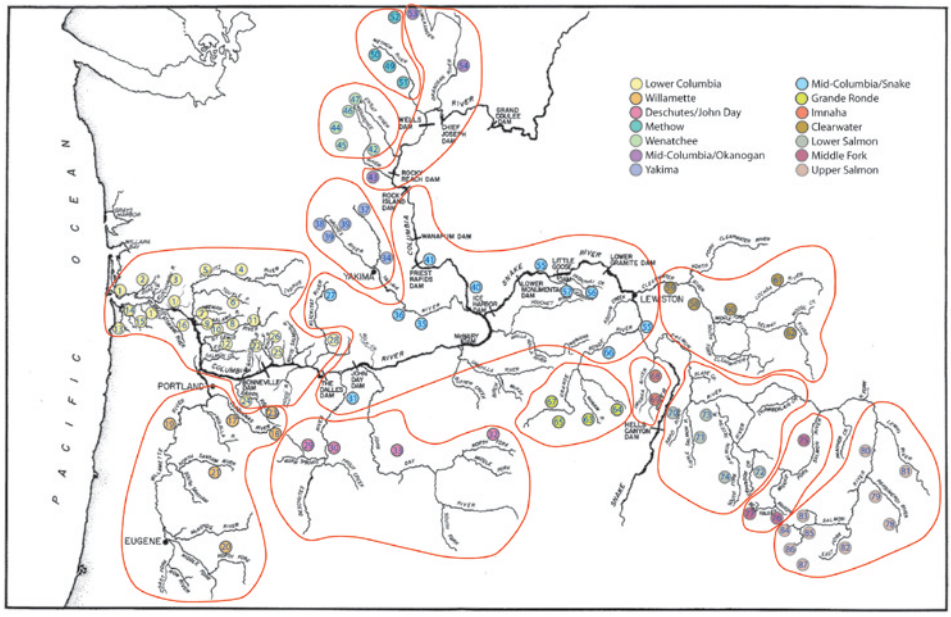


Figure 39. Chinook salmon population structure in the Columbia Basin shown in clusters as 14 first-order metapopulations. Member populations in the clusters are color coded and outlined in red to represent metapopulation geographic boundaries.

Therefore, based on ecological and genetic criteria, Columbia Basin chinook population structure is portrayed as clusters within a mega-metapopulation (all metapopulation units in the Basin). The clusters represent population entities most closely linked in origin and identified as first-order metapopulations by the geographic boundaries circled in red on Figure 39.

In this archetype, 14 first-order metapopulations are identified based on genetic data and temperature profiles. Generally, those in closest proximity, such as the Salmon River Basin clusters, are considered more closely related (second-order) than with those in the Willamette or upper mid-Columbia (third-order). Genetic identities and suggested relationships may change as phylogenies are resolved and genetic technology improves, but as a starting point, the identities of 87 chinook populations (Table 11) are assigned to one of 14 first-order metapopulations constituting the Columbia Basin chinook salmon mega-metapopulation. The premise is that population units within first-order metapopulations originated from within those respective clusters, and that degree of relatedness is consistent with proximity, except where founding sources originated through different colonizing events, as discussed later.

Columbia River Steelhead Trout Population Structure

In the same line of reasoning with regard to redistribution following continental glaciation, steelhead are believed to have survived only in the Pacific refuge, but segregated along coastal and interior genotypic lines nearly 15,000 years ago as the origin of the interior and coastal forms (Allendorf and Utter, 1979; Hershberger, 1992). One form is presently represented up and down the coast and separate from the other genotype that is associated

Table 11
Columbia Basin chinook salmon runs recognized as 87 separate populations and assigned to one of 14 first-order metapopulations indentified below as spring—(s), summer—(Su), and fall-run (F) fish.

Lower Columbia	Methow	Grande Ronde
1. Lower Columbia streams-F	49. Twisp River	63. Minam River
2. Grays River-F	50. Methow River	64. Lostine River
3. Elochoman River	51. Methow River	65. Catherine Creek
4. Cowlitz River-S	52. Chewack River	67. Upper Grande Ronde River
5. Cowlitz River-Su	Wenatchee River	Imnaha
6. Toutle River	42. Wenatchee River	68. Imnaha River
7. Coweman River	44. Little Wenatchee River	69. Imnaha River
8. Kalama River NF	45. Nason River	Clearwater
9. Kalama River EF	46. White River	58. South Fork Clearwater R.
10. North Fork Lewis River	47. Chiwawa River	59. Clearwater River
11. Upper N. Fork Lewis River	Mid-Columbia/Okanogan	60. Middle Fork Clearwater R.
12. East Fork Lewis River	43. Lower Wenatchee River	61. Lochsa River
13. Lewis and Clark River	53. Similkameen River	62. Selway River
14. Youngs River	54. Okanogan River	Lower Salmon
15. Klaskanine River	Yakima	70. Rapid River
16. Clatskanie River	34. Yakima River	71. Little Salmon River
22. Washougal River	37. Cle Elum River	72. Johnson Creek
24. Sandy River	38. American River	73. Secesh River
25. White Salmon River	39. Naches, Little Naches & Bumping rivers	74. South Fork Salmoon River
26. Wind River	Mid-Columbia/Snake	Middle Fork
28. Klickitat River	27. Klickitat River	75. Middle Fork Salmon River
Willamette	31. Deschutes River	76. Marsh Creek
17. Clackamas River	35. Marion Drain	77. Bear Valley Creek
18. North Fork Clackamas R.	36. Yakima River	Upper Salmon
19. Willamette River	40. Hanford Reach	78. Pahsimeroi River
20. McKenzie River	41. Priest Rapids	79. Pahsimeroi River
21. Santiam River	55. Snake River	80. Salmon River
23. Sandy River	56. Tucannon River	81. Lemhi River
Deschutes/John Day	57. Touchet River	82. East Fork Salmon River
29. Warm Springs	66. Grande Ronde River	83. Yankee Fork River
30. Deschutes River		84. Valley Creek
32. North Fork John Day River		85. Upper Salmon River
33. John Day River		86. Blaine Bridge
		87. Frenchman Creek

east of the Cascade Crest. Distribution of the former is argued to have been facilitated by emerging coastal habitat that paralleled glacial recession, and the latter motivated by the southern flow of water between the Cordilleran and Laurentide ice sheets, connecting at least parts of the Peace, Fraser, and Columbia rivers (McPhail and Lindsey, 1970). Early in the creation of this inland corridor, isolation of the resident form of *O. mykiss* may have occurred which permitted the evolution and persistence of the inland genotype that later reintroduced anadromy. Of course, the markedly different environments between the coastal and high desert regions west and east of the Cascade Crest are sufficient in themselves to have encouraged the evolution of different genotypes through natural selection. Leider et al. (1995) put the boundary of the inland and coastal groups somewhere

between Wind and the Big White Salmon River on the Columbia in proximity to the Klickitat River.

Attempts to resolve the question of origin of different genotypes has been complicated by the introgression of stocked *O. mykiss* throughout the Columbia Basin. Rainbow introductions in Idaho, Oregon and Washington states numbered over 12 million from 1933 to 1994, and steelhead have also been spread extensively (Lee et al., 1997). Beginning primarily in the 1960s, but regularly from the early 1980s, a total of over 35 million steelhead have been released in mid-Columbia streams. Most of these fish were either nonnative or from mainstem interceptions of unknown origin. Skamania steelhead, for example, have been released in the mid-Columbia, the Wenatchee, and Entiat rivers (Chapman et al., 1994b). The extensive translocations have introgressed genotypes and appear to have created an artificial homogeneity in *O. mykiss* within the interior. Phelps et al. (1994), Currens et al. (1997), Currens and Schreck (1993), and Campton and Johnston (1985) all report evidence of imported rainbow and steelhead having integrated genetically with local stocks. However, what is apparent as introgression also needs to be carefully examined. Chapman et al. (1994b) suggested that intermediate allozyme frequencies in Yakima River rainbow, for example, may represent ancestral forms in that system, rather than integration of hatchery rainbow.

Steelhead population structure appears to have been strongly influenced by the risk inherent in their habitat choices, influenced at least in part by avoiding negative interaction with salmon. It is argued that iteroparity and the totally freshwater resident option among steelhead function to serve as security against extinction. Iteroparity it-self may involve "bet hedging" to accommodate limited food resources or uncertain breeding conditions in ephemeral freshwater environments (Miller and Brannon, 1982), but the resident option seems to be related closely with extended freshwater residence undertaken by the anadromous form.

With some level of gene flow maintained between steelhead and rainbow, and the cooler habitat that *O. mykiss* is associated with, extended rearing and the option of total freshwater residence appear to be variations of the same strategy. However, gene flow between anadromous and resident forms also helps maintain site specific characteristics within a population, and thus the appropriate genetic reservoir if anadromous members of the subpopulation were at risk. Given that such gene flow occurs as part of *O. mykiss* life history strategy, divergence of phenotypes would be inhibited, and it appears that although traits may favor only one or the other life history form, they are still maintained in the general genotype.

Steelhead life history strategy is markedly different from that of chinook salmon, but the basis of their population structure follows the same archetype in distribution as metapopulations. At least 65 populations of steelhead exist in the Basin, which we have clustered in 10 different suggested first-order metapopulations (Figure 40), based on genotypic relatedness and temperature profiles. Nucleotide divergence in first-order units is estimated $<1.0\%$, second-order clusters when divergence is between 1.0% and 1.5%, and third-order above 1.5%. Distinctness, inclusive of both wild and hatchery populations that are viewed as self-sustaining units, is thus identified at the stream level, involving panmictic spawning population segments, but clustered together based on their hypothetical relationship. Among the 65 recognized steelhead populations (Table 12), there are A- and B-run summer steelhead that are placed within the same first-order metapopulation units. The environmental template associated with the A-run steelhead permits more rapid freshwater growth and thus younger smolts, which, in turn, encourages an earlier return age. The B-run summer steelhead remain in freshwater longer because of cooler temperatures and return generally

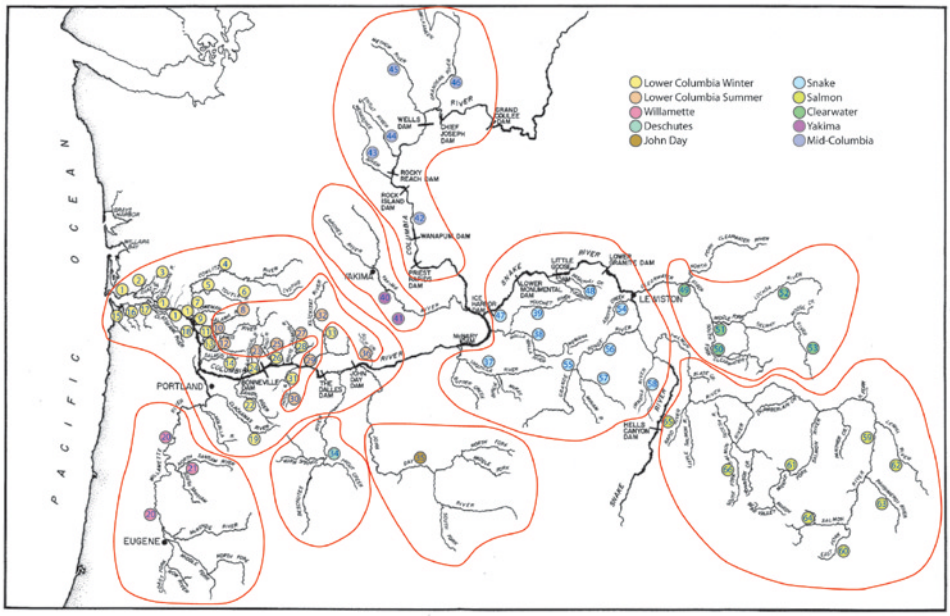


Figure 40. Steelhead population structure in the Columbia Basin shown in clusters as 10 first-order metapopulations. Membership in clusters are color coded and outlined in red to represent metapopulation geographic boundaries.

at least a year older than the A-run fish. Consequently, based on what appears as only a phenotypic difference, the A- and B-run summer steelhead have not been placed in separate metapopulations.

We conclude, therefore, that chinook and steelhead population structure, demonstrated as a system of first-order metapopulations, has been developed as a perspective where stock biology and environmental criteria are elevated to the forefront, at least equal to information based on population genetics. Regardless of the importance of population genetics, the characteristics critical to the ability of runs to sustain themselves are clearly evident by unique stock-specific behavioral patterns that place the fish in synchrony with their respective environmental templates. Those traits are not discernible by tools presently employed in population genetics. Figures 39 and 40, therefore, can be viewed as the basic archetype of the population structure in the Basin on which to base new recovery and management paradigms for these species. First-order metapopulations provide the resources from which to introduce seed stock to streams extirpated of anadromous forms or for introductions into rehabilitated habitat in the geographic area. Where such populations are absent, the closest second-order cluster is the next prospective donor source for consideration. Functional units at the recovery level, therefore, are not determined only by genetic relatedness but, more specifically, based first on the identity of life history forms and their spatial/temporal distributions.

Population Relatedness Within the Columbia Basin

Interspecific relatedness among the constitute populations is basic to population structure of both chinook and steelhead in the Columbia Basin. The model that appears most applicable

Table 12
Columbia Basin steelhead runs recognized as 65 separate populations and assigned to one of 10 first-order metapopulations listed below as summer (S) and winter (Su) steelhead.

Lower Columbia River Winter
1. Lower Columbia Streams
2. Grays River
3. Elochoman River
4. Cowlitz River
5. Toutle River MS
6. Toutle River NF
7. Coweman River
9. Kalama River
11. North Fork Lewis River
13. East Fork Lewis River
14. Salmon Creek
15. Lewis and Clark River
16. Youngs River
17. Klaskanine River
18. Clatskanie River
19. Clackamas River
22. Sandy River
24. Washougal River
26. Wind River
28. White Salmon River
31. Hood River
33. Klickitat River

Lower Columbia R. Summer
8. Kalama River
10. North Fork Lewis River
12. East Fork Lewis River
23. Washougal River
25. Wind River
27. White Salmon River
29. Major Creek
30. Hood River
32. Klickitat River
36. Rock Creek

Willamette
20. Willamette River
21. Santiam River

Deschutes
34. Deschutes River

John Day
35. John Day River

Snake
37. Umatilla River
38. Walla Walla River
39. Touchet River
47. Lower Snake River
48. Tucannon River
54. Asotin Creek
55. Upper Grande Ronde R.
56. Lower Grande Ronde R.
57. Wallowa River
58. Imnaha River

Salmon
59. Salmon River
60. East Fork Salmon River
61. Middle Fork Salmon River
62. Lemhi River
63. Pahsimeroi River
64. Yankee Fork
65. Rapid River
66. South Fork Salmon River

Clearwater
49. Clearwater River
50. South Fork Clearwater River
51. Middle Fork Clearwater R.
52. Lochsa River
53. Selway River

Yakima
40. Toppenish River
41. Satus River

Mid-Columbia River
42. Mid-Columbia River
43. Wenatchee River
44. Entiat River
45. Methow River
46. Okanogan River

to relatedness within the respective species is the Neighborhood Model (isolation by distance, Wright, 1943) of populations. Under the model, geographically close populations have similar genetic profiles (in terms of allele frequencies), and they gradually but increasingly differ with distance. Gene flow to a population, therefore, comes principally from proximate populations and as a decreasing function of distance. Because most migrants are

expected to come from proximal populations with similar gene frequencies, the differences among populations is hierarchical in nature, which is true also among metapopulations.

The clinal pattern in chinook timing is the best demonstration of the environmental conditions that facilitate the Neighborhood Model of populations. In general, with the gradual changes that occur in temperature as one advances from the lower reaches to the headwaters of the basin, neighboring populations are going to be the logical source from which to colonize new habitat, thereby increasing their range. Protein electrophoretic frequencies, in many cases, show greater similarity between spring, summer and fall chinook, or summer and winter steelhead, from a particular area than with their counterparts from different streams (Banks et al., 2000; Utter et al., 1995; Shreck et al., 1986; Utter and Allendorf, 1977). When viewed from the basin-wide perspective, the sub-basin environments and their component population networks, therefore, are the sanctuaries of variability from which recolonization and extension take place.

However, major discontinuities exist in the temperature profile of some river systems from the influence of ground water and lakes, as pointed out in the Methow and Wenatchee rivers. Understandably, these conditions can promote the adaptive evolution of new stocks from adjacent populations, but they also offer unique situations for strays from similar habitats to reestablish themselves in suitable locations well displaced from their parental system. Therefore, although the Neighborhood Model may provide the most appropriate theoretical concept describing population relatedness for chinook salmon and steelhead, it isn't an entirely representative model of the relationship within these species in the Basin. As poikilotherms, the overriding influence of temperature in habitat isolation among salmonids presents a feature that can create abruptly different environments within the same geographic area (Adams et al., 1994; Mullan et al., 1992; Burger et al., 1985; Brannon, 1987). As demonstrated in the mid-Columbia (Utter et al., 1995) and in the Kenai and Kasilof rivers (Adams et al., 1994), genetically similar early runs can be different from and seemingly unrelated to other genetically similar late runs in the same geographical area. The Neighborhood Model, therefore, in some cases, must be adapted to represent overlapping distributions of distinct genotypes that are temporally isolated, but within close proximity. In essence, in large river basins such as the Columbia more than one metapopulation may occupy portions of the same geographic area when separated temporally by markedly different temperature regimes. The proximal metapopulations in such a case could have originated from different sources, perhaps from strays of other river systems.

The role of strays in limiting genetic drift and inbreeding and contributing new genetic material to chinook salmon and steelhead populations is fundamental to the maintenance of diversity. However, although nominal strays may be an important source of genetic material, they may not be the primary mechanism establishing new founder populations. In looking at Fraser River sockeye, for example, over the last century major events in the Fraser Basin have resulted in large displacements of populations returning to their historic spawning grounds. Abnormally low or high flows through Hell's Gate Canyon prior to the 1940s (Thompson, 1945), the Chilcotin River land slide in 1963 (IPSFC, 1964), and high water temperatures in 1997 and 1999, all resulted in extensive redistribution of segments of the Fraser sockeye run. Displaced adults entered different tributary systems in large numbers and even spawned in other river systems. Although occurring at rare frequency in the real-time perspective, in evolutionary time such displacement would be considered a common occurrence and would provide opportunities for substantive numerical introductions to take place.

However, other factors have also altered gene flow that subsequently affected the diversity in Columbia River species. Hatchery management and fish distribution from a variety

of origins have altered chinook and steelhead species diversity throughout the Columbia, which makes the original genetic relationships difficult to ascertain. The Grand Coulee Fish Maintenance Project from 1939 to 1943, for example, was a major influence on the general homogeneity of species diversity above Rock Island Dam following the construction of the Grand Coulee (Mullan et al., 1992; Utter et al., 1995). Fish were intercepted at Rock Island and distributed to the remaining upriver habitat with no consideration of stock structure or origin. Similarly, the Bonneville hatchery intercepted fish of unknown destination, and they were propagated and distributed in the lower Columbia without regard for their origin. Steelhead may have been especially affected by management programs for rainbow trout sportfisheries (Campton and Johnston, 1985) because of the gene flow that occurs between rainbow and steelhead.

Consequently, it is difficult to determine "natural" gene flow levels from man-induced changes that have affected population structure. The difficulty stems from our inability to construct a natural baseline against which current stock structure is tested. This issue is important because it is the basic element in determining the size of conservation units (Lande, 1999) and in the development of recovery strategies.

The basic relatedness of populations, therefore, is subject to a level of happenstance regarding what founding source or sources have colonized a particular river basin, and what temperature profiles were present that defined the temporal diversity of the evolving metapopulation. The genetic identity of the inhabiting populations will be subject to the founding sources and will remain open to some level of genetic alteration depending on the degree of gene flow into the system. Not withstanding the importance of other population characteristics, we argue that the nature of the environmental temperature profile within the basin is the baseline on which stock structure has developed, and most often genomic patterns will be neighborhood related.

Plasticity of Chinook and Steelhead Life History Forms

Although the emphasis in this document has been the critical importance of stock structure and the synchrony between the phenotype and the environmental template for survival success, the evidence should not imply that chinook and steelhead do not also demonstrate a high level of plasticity in response to the circumstances confronting them. The fact that chinook are semelparous is evidence of their plasticity. Semelparity is a characteristic of r-selected species (Miller and Brannon, 1982) that typically exhibit rapid development and a high innate capacity for increase. Semelparous species are opportunistic species that almost always inhabit unstable or highly variable environments, and thus must demonstrate the ability to accommodate uncertainty.

Plasticity of steelhead has taken a different route through mechanisms that provide a level of security against loss in highly variable habitats. Repetitive spawning, the ability to maintain some level of gene flow with their freshwater resident form, altered sex ratios, and the option of extended rearing provides an extensive level of plasticity that is expressed when faced with uncertain conditions. Also, the tetraploid ancestry of chinook salmon and steelhead (Allendorf and Thorgaard, 1984) suggests that in addition to helping offset inbreeding depression and genetic drift, duplicate loci within the genome of these species may enhance phenotypic plasticity (Allendorf and Waples, 1996).

Although these species home to their natal stream, which permits them to acquire adaptive traits specific to their transit and local needs, their ability to accommodate the dynamic environments exemplifies plasticity. Chinook and steelhead demonstrate temporal return patterns that respond to variability in the temperature regimes of their transit routes by

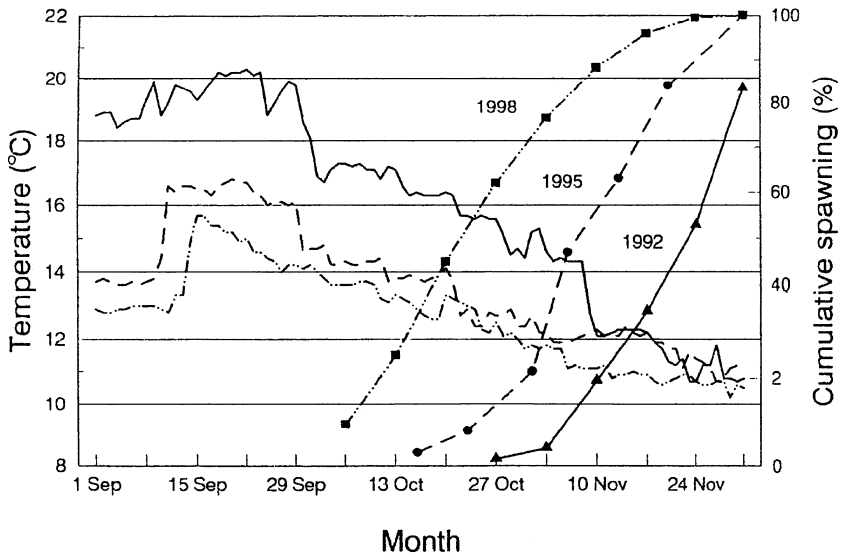


Figure 41. Flexibility in spawning times of Yuba River fall chinook in response to annual variability in river temperature (YCWA, 1999). Compared to 1998, spawning in 1992 and 1995 was delayed until temperatures fell below 14°C, and the early cumulative percentage of spawning was further extended into the year by the persistence of higher temperatures. Approximately 70% of the spawning occurred in temperatures below 12° to 13°C.

delaying or accelerating return patterns based on the temperatures they confront (McCullough, 1999). Variability is also demonstrated on the geographic scale with spring chinook in the Columbia returning months before spawning, although spring chinook in the Kenai system may spawn within a couple of weeks of entering freshwater, similar to fall chinook to the south.

Both species have the ability to adjust spawning times based on the temperature conditions they find upon returning to their home streams. This is most demonstrative by the variable annual temperatures that chinook experience on their spawning grounds below Daguerre Point Dam on Yuba River, tributary to the Sacramento (Figure 41) (Yuba County Water Agency, 1999). River temperatures cooled late in 1992, intermediate in 1995, and early in 1998. Consequently, in 1992 spawning was delayed until after October 27. However, in 1995 spawning commenced about October 18, and in 1998 it started prior to October 8. In all three cases, the Yuba fall chinook compensated for the conditions they were experiencing by adjusting their behavior accordingly and waiting until temperatures fell within the desirable range to start spawning.

As discussed previously, alteration in the development rate of embryos during incubation also provides considerable plasticity in responding to temperature variability that occurs in the stream during the post-spawning period. However, in addition, the temporal range in the timing curve of emerging fry (Figure 6) is also evidence of plasticity in response to the dynamics of spring conditions. When an early or late spring occurs, a temporal segment of the emerging fry population will correspond to the altered optimum in emergence time on that particular year, providing a degree of plasticity in synchronizing with altered conditions.

Also, as suggested in the discussion of fry distribution following emergence, the variability in the pattern of distribution provides a great deal of plasticity to adjust to variable

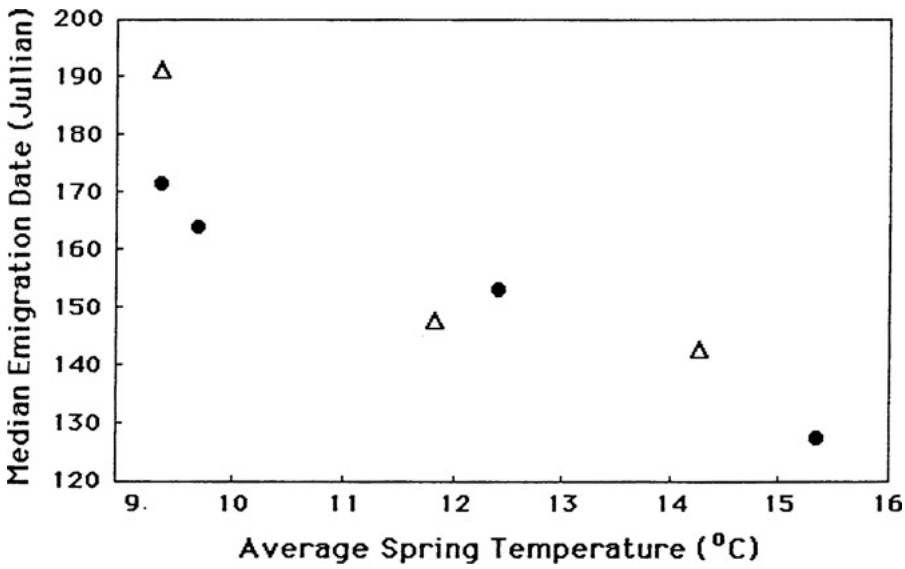


Figure 42. Altered chinook smolt median emigration date and average stream temperature on the Umpqua River (●) and Jackson Creek (Δ) (Roper and Scarnecchia, 1999).

feeding opportunities to improve growth. The ability of chinook and steelhead fingerlings to alter the length of the freshwater rearing phase to accommodate the time necessary to reach migratory size or other suitable conditions (Reimers and Loeffel, 1967; Bjornn, 1971; Congleton et al., 1982; Roper and Scarnecchia, 1999) is a demonstration of a significant level of plasticity in the life history strategy of these salmonids. Altered smolt migratory timing of emigrating South Umpqua and Jackson Creek chinook in response to temperature (Roper and Scarnecchia, 1999) shows their ability to alter their behavior based on river conditions (Figure 42).

Although the temporal distribution of returning and spawning adult salmon and steelhead is predominantly determined by temperature, juvenile stream residence behavior is an adaptive response to a much more complex assemblage of conditions associated with interactions between temperature, growth, competition, and predation. These characteristics are evidence of the ability of chinook salmon and steelhead to accommodate environmental variation by the level of plasticity demonstrated over their life history. Temporal synchrony is paramount in their life history strategy, but they show a high degree of plasticity in achieving their temporal and spatial goals to meet the critical time and size relationships that optimize fitness under the influence of a dynamic environment. Although each breeding population has a distinct niche that includes high specificity for temporal integrity in their life history, the initiation of different life history forms is within the inherent variability of a population.

Management Implications Under the Present River System

In looking at chinook and steelhead population structure in the Columbia Basin from the historical perspective, it is important to recognize that in spite of the concern being raised about the decline of natural populations and the public alarm that such information evokes, the federal plan for the developed river never had any intention of supporting natural production.

This becomes obvious when one looks at the measures taken to address the anticipated losses of wild salmon from river development. The first effects of development in the Basin were the severe reduction of salmon and steelhead populations from the commercial fishery (NRC, 1996; Lichatowich, 1999). Overexploitation prior to the 20th century was so severe that spring chinook were fished nearly to extinction in the Columbia River before 1890 (Brannon, 2000). As runs of summer and fall chinook followed similar pathways, attention was turned to steelhead, which were also overfished and plummeted in abundance. The remedy to the decline was the initiation of hatcheries to sustain the fishery (Stone, 1879), and they were used to produce salmon solely for harvest purposes.

The second major effect of development was the loss of salmon habitat. Early in the 20th century, water diversion dams were initiated in sub-basins of the Columbia Basin under the Bureau of Reclamation to usher in an era of irrigated agriculture to the parched lands of Idaho, Oregon, and Washington. Apart from unscreened diversion ditches, the major impact was construction that created barriers to salmon migration. Grand Coulee Dam, built in 1936, was the unparalleled example with the exclusion of over 191,660 square kilometers of upper Columbia to anadromous fish (Fish and Hanavan, 1948), an area that previously supported sockeye, chinook, and steelhead runs. In anticipation of the loss of wild runs, the remedy again was to mitigate through hatchery programs. The Leavenworth, Entiat, and Methow hatcheries were built to replace the loss of production above the Grand Coulee (Chapman et al., 1994a). From 1939, the Grand Coulee Fish Maintenance Project (GCFMP) intercepted wild fish headed above the barrier dam and redistributed them to other rivers in the region, terminating in 1943 with the last returning fish to the upper Columbia. Fish were redistributed with little pretense of rebuilding natural populations.

Another major effect was the introduction of exotic fish species during the 20th century. Bass, crappie, perch, walleye, shad, carp, and brook trout were some of the major species introduced to the Columbia. The introductions of these fish were intentional, and came west first by railroad under a program of the US Department of Fish and Wildlife Service, and later by state management agencies, with the objective to provide greater sport fishing diversity in the Pacific Northwest, and later to offset losses of the anadromous fishery from river development. Exotic species were successful and changed the Columbia ecosystem permanently, which is a point often overlooked by those wanting to mimic the historic ecosystem. Predation and competition from exotic species did not receive sufficient concern because hatcheries released large salmonid fingerlings that could better elude exotic predators.

Hatchery production of other species as substitutes for anadromous species was also part of the mitigation (NPPC, 1994). The Indian and sport fisheries that had depended on anadromous salmon and steelhead no longer had access to those fish in the areas above barrier dams. As mitigation for those losses, nonanadromous hatchery fish were often used as replacements. The problem was that in most cases nonlocal stocks were used (Busack et al., 1979). Introductions were numerous and local stock structure was altered by interbreeding of introduced and endemic strains (Chapman et al., 1994b).

Another component of federal development of the river was hydropower (see Whitney et al., 1997 for comprehensive review). It started in 1933 with Rock Island Dam and continued through the 1970s with over 22 dams constructed just on the mainstem Columbia and Snake rivers. Hells Canyon Dam on the Snake blocked another 189,070 square kilometers of river drainage that had been used by large populations of steelhead and salmon (Brannon, 2000). In total, 60% of the Columbia Basin watershed has been made inaccessible to anadromous species, and over 64% of the remaining mainstem rivers were changed into reservoirs, altering the migratory success of adults and juveniles in the nearly continuous

series of mammoth pools above Bonneville. Mitigation for these losses was to build hatcheries and increase artificial production. This was an intentional change from the historic river condition, and the increase in hatchery production was part of the federal plan to address the loss of wild fish.

A generally unrecognized potential impact on chinook salmon in the Hanford Reach, one of the last free-flowing sections of the river, was the nuclear reactor activities from 1943 to 1987. Much of the early concern was about the threat to fish of radioactive waste that might be carried to the river in the cooling water from the reactors. Those concerns proved to be unfounded (Becker, 1990), but attention wasn't given to the implications of the temperature changes that occurred below the discharge points of the cooling effluent. Winter flows in the Hanford Reach ranged around 30,000 to 60,000 cfs at temperatures that dropped well below 5°C. Approximately 2000 cfs was discharged from the cooling towers at temperatures above 80°C in the 1940s. This effectively increased temperatures estimated by as much as 5°C over ambient background river temperatures immediately below the mixing zones, and 2.5°C measured over 90 km downstream (Becker, 1990; Jaske and Synoground, 1970). Mixing that quantity of hot water with the ambient river temperatures during December, January and February, would have accelerated emergence by over a month, and represented a major change from the historic synchrony of the fall-run chinook in the Hanford Reach. Incubating eggs and alevins could have been affected in 9 of the 10 spawning reaches that have been identified by Dauble and Watson (1997) along that section of the river.

Finally, there have been negative impacts on natural production of Columbia River salmon and steelhead through the fisheries management process itself. In the past, management attempted to minimize escapement to increase the harvestable portion of the runs. Mixed stock fisheries and the disparity between the needs of wild and hatchery fish escapements resulted in fewer wild fish returning to maintain natural production. Even if one could assume equitable distribution of spawners, minimizing escapement with the aim of only sustaining reproduction (short-term yield) overlooked the biological requirements necessary to maintain fitness and even the contribution of salmon carcasses (Cederholm et al., 2000; Stockner, 2002) to the health of the ecosystem. These problems were further exasperated by hatchery management (Brannon, 1993). Timing, behavior, health, size and condition of hatchery fish can be very different from that of the wild counterpart (Maynard et al., 1998), with the ultimate effect of reduced survival. With the lower abundance of wild fish (Lichatowich, 1999) and the routine transfer of hatchery fish between watersheds (Peven, 1992), the natural processes accentuating stock structure were disrupted (Utter et al., 1995). Although fisheries managers have been aware of these problems for many years, the concern for wild populations was never sufficient to alter management practices until late in the 20th century. However, with management still viewing Columbia River chinook as three separate segments (spring, summer, and fall), the natural continuity of run timing in the system will remain under the artificial influence of the harvest fishery, unrelated to natural forces affecting population structure.

The federal development of the Columbia was to help build the Pacific Northwest economy. That was done with anticipated losses of wild salmon and steelhead that were mitigated for by increased hatchery production. Consequently, wild salmon and steelhead production in the Basin has been decreased to a fraction of its historic level (Anderson, 1993; Brannon et al., 1999; Lichatowich, 1999) because of the reduction in natural habitat from river development. Given those realities, and regardless of the emphasis now on natural production, recovery goals need to be put into the perspective of present river conditions. Sustained natural production is an achievable goal. Sustaining major fisheries with natural production is a different matter, and if the non-Indian commercial fishery, treaty Indian

fishery, and recreational fisheries are to have any level of sustainability, enhanced production through artificial means must be viewed as part of the recovery program.

Therefore, it is necessary to carefully inventory what recovery potential may exist in the Columbia Basin. One should not discount that nearly 90% of the chinook and steelhead habitat originally available in the Columbia Basin has been lost or changed. It must also be remembered that by 1886 an estimated catch of only 1.7 million spring chinook salmon at the mouth of the Columbia caused the spring chinook populations in the Basin to crash (Brannon, 2000), which suggests that average runs of chinook salmon in the Basin may not have exceeded 4 or 5 million fish at their height of abundance. Major fluctuations in that abundance also occurred before the non-Indian commercial fishery resulted in the precipitous declines of salmon and steelhead runs, and on occasion they were so low to have threatened starvation among the dependent Indian communities along the river (Chance, 1970). The point is that rather inflated estimates of carrying capacity and natural run sizes have appeared in various reports and for various reasons, most of which were not based on objective assessment of the habitat's carrying capacity. Estimates of juvenile fish/100 m^2 are generally in single digits (Chapman et al., 1994b, 1995), and the present production capacities of some mid-Columbia and Snake River streams are considered near their maximum (Mullan et al., 1992; Bjornn, 1971), which leaves the prospects of increased natural production in some streams equivocal in many instances. Therefore, it is particularly important that realistic expectations are developed on what is possible based on the scientific evidence accumulated over the years. It is also important that the implications of the projected increase in the human population growth be considered in the equation. Lackey (2000) suggests that by 2050 the population in the Pacific Northwest will at least double, proportionally increasing requirements for energy, water, and space. If recovery of Columbia Basin chinook and steelhead is to be effective for the future, it is particularly important that we first concentrate on the biological needs of those resources.

Approach to Recovery

Based on species life history and population structure, rebuilding salmon and steelhead runs in the Columbia will require that work proceed under the biological constraints of the species, which are the natural forces around which life history strategies have been established within the system. The biological constraints have been largely overlooked, and that problem is at the root of failed recovery attempts of the past. The smallest unit in which population structure is represented within the Basin is the metapopulation or the assemblage of closely related population segments.[3] In large rivers such as the Columbia, more than one first-order metapopulation will exist, and recovery must be directed within those structures and concentrated on individual population segments at risk. In areas extirpated of populations, the metapopulation becomes the source of related genes from which new populations can be initiated. The approach is similar to the concept of a Genetic Conservation Management Unit (GCMU), proposed by Leider et al. (1994) and reviewed by Chapman et al. (1994b). The GCMU includes the stocks that would provide the recovery base within the

[3] A population segment is not analogous with the Evolutionary Significant Unit (ESU) of Waples 1991 and should not be confused with the ESU concept. The ESU designation was adopted by the National Marine Fisheries Service to represent "distinct population segments" under the Endangered Species Act, and technically serves a different purpose. Utter et al. (1995) state the "definition of an ESU by no means implies a single panmictic unit." The population segment referred to here is a single panmictic unit, and represents the focus of recovery recommendations.

larger geographic area or major catchments, and we suggest these geographic areas should represent the boundaries of first-order metapopulations. The primary difference between the GCMU and first-order metapopulations is that genetic similarities are not the only focus under the latter, but the temporal patterns and life history have to take priority.

First-order metapopulations as the focus of recovery, and ultimately management, also contrast with the ESU concept of a management unit by the level of specificity addressed. ESUs, as applied by NMFS's interpretation of the ESA, can include multiple nonpanmictic populations within a large geographic area, such as the Puget Sound chinook salmon ESU of over 20 populations. The focus again is the genetic similarity, and thus can include populations that represent very different temporal specificity, such as spring and fall chinook within the same ESU. However, if recovery programs are to be effective based on ESU designations, the unit must be broken down to workable subunits that recognize specificity of the member populations. Even here, there is the risk of oversight from the assumptions associated with ESU rationale. To base segregating criteria principally on frequency patterns of neutral alleles, for example, assumes only isolation and drift from the donor genotype, and overlooks the high likelihood that founding members of new populations may have represented only a portion of donor stock diversity in the first place. Placing significant reliance on behavior for donor stock in new habitat, with temporal similarity high on the list of criteria, involves functional genetic traits that have been of selective importance to the donor population. We suggest that such a refinement in segregating criteria is accommodated in the definition of first-order metapopulations, and differs from the ESU concept in both degree of specificity and the ranking of characteristics associated closely with fitness traits.

The target of recovery under the temperature model, therefore, is the smallest population segment for which such measures can be applied, defined as a panmictic unit. Recovery at this level develops genotype synchrony with the environmental template. Notwithstanding the major problems that harvest rate and fish passage have on population success, we suggest that recovery of individual population units within the context of first-order metapopulations must involve three critical steps. The first step is to apply what we understand about life history strategy and population structure as the biological template for recovery. The second is to address environmental needs of wild stocks through habitat improvement in areas utilized by chinook and steelhead. The third is how to employ hatcheries.

1. Application of Life History Strategy and Population Structure in Recovery. The first step of applying what we have learned about life history strategy and population structure is in defining the approach. The Columbia Basin chinook and steelhead populations still demonstrate considerable remaining genetic diversity, which needs to be preserved as an important resource for recovery and stability. Over the long-term under natural conditions, extirpation of populations around the geographic parameter of a metapopulation would be expected when such subunits are small, isolated, and prone to inbreeding. Loss and reestablishment of such populations may have been the normal course of events in the history of chinook and steelhead in the Columbia. Attempting to preserve every population segment through captive broodstock programs is not a practical strategy in recovery, but taking measures to prevent such losses needs to be given highest priority. It would appear easier to strengthen existing runs that already have genetic specificity than to establish new runs.

Frankel (1983) stated "*Wild species must have a pool of genetic diversity if they are to survive environmental pressures exceeding the limit of developmental plasticity.*" In the evolution of chinook salmon, life history and patterns of behavior have resulted because of the advantages they endow to fitness. These processes are dynamic and genotypes are

constantly under selective pressures to conform to the environmental changes confronting population components. As major changes occur in that relationship, the genotype is challenged with the increased cost to fitness, and the pool of genetic variation may determine whether or not extinction of a population can be avoided.

This, in essence, is the emphasis in conservation genetics. Alleviating the risk of extinction is to enhance genetic diversity and to avoid the conditions that hinder the process. Among the forces that limit population diversity, genetic drift and inbreeding understandably are the effects most pronounced in small isolated populations. Consequently, the size of the breeding population (*Ne*) is of major importance. Fifty was suggested by Frankel (1983) as the minimum effective number necessary to preserve fitness and 500 to maintain genetic variance for subsequent adaptation. Small populations, however, are not rare. Liu and Godt (1983) discussed the differentiation of populations at the microgeographical scale, and in their examples, differentiation often occurred without physical barriers to gene flow, effectively isolating populations at the microscale. Genetic drift and inbreeding depression, the precursors to extinction, therefore, are taken for granted in small isolated populations, especially those that have been initiated with very few breeding pairs.

Herein lies the dilemma for anadromous salmonids and, most certainly, a major influence in the conservation geneticist's view of their long-term viability. Salmonid populations overwhelmingly experience the equivalence of microgeographic isolation. Many are presently small, isolated units in space or time. Some streams are small and do not provide the habitat for large numbers of fish. Yet in most cases, these systems require high degrees of specificity in genetic traits of the organism, not the least of which is conformity to the temperature regime available. Consequently, with regard to that single parameter, temporal isolation from adjacent populations can be nearly complete if mean incubation temperature differences amount to just 1°C. Trunk stream spawners that may stray into such a tributary would be too far out of synchrony to successfully interbreed with the tributary population at higher elevations. Genetic contribution, therefore, would have to come via strays from other areas that are similarly timed or from components of the trunk stream population that have adapted, stepwise, in transition. The number of generations to conclude such a distinct temporal shift is not trivial.

Moreover, behavioral traits such as homing evolved to assure a high degree of specificity within the population. The whole process of adaptive evolution of chinook salmon in synchrony with their native habitat would be impossible without the population being able to precisely return to the separate environments responsible for their uniqueness. However, homing restricts gene sharing between populations and thus serves to essentially contain diversity within population units. Then to further complicate the effects of limited population size, assortative mating occurs among salmonids, which limits random distribution of genes and contributes to assortative diversity within the population. Even further, male hierarchies are universal among salmonids and dominance of primary males tends to decrease contributions of other males.

These characteristics of salmon populations are not entirely compatible with evolutionary genetics theory, and yet it appears that chinook populations thrived before the advent of restrictive fisheries and habitat loss. It must be reiterated that populations of stream dwelling salmonids such as chinook are founded by members of other populations and probably by small numbers of viable breeding pairs not necessarily reinforced at frequent intervals. Many of the founding populations would have obviously experienced a loss of genetic variation in the course of the population bottleneck that characterized their inception, and inbreeding would have been the matter of fact, but they flourished nonetheless. Even in the

present decline of wild chinook populations in the Columbia Basin, one cannot help but be impressed at their perseverance in the face of adversity.

Adaptive specificity, in spite of the disadvantages that loss of diversity may have on the ability to respond to change, establishes a high degree of fitness. The negative influence of asynchronous timing on spawning and emergence success alone exemplifies the high priority of adaptive specificity at the sacrifice of diversity. It could be argued that inbreeding and genetic drift are time controls limiting the duration on such highly adapted populations, because the number of effective breeding migrants exchanged between salmonid populations can be very low in isolated tributaries, distant both spatially and temporally from adjacent populations. As discussed by Franklin (1980) in closed populations, variance through drift is lost at $1/2\,Ne$ per generation, the same as the inbreeding coefficient, and at that rate with a population size of $Ne = 50$, only 36% of the original variance present would be remaining after 100 generations. However, with chinook and steelhead that would represent a period of at least 400 years. Even isolated populations of chinook and steelhead are not closed populations, and the amount of additive variance derived through gene flow (m) would be very substantial over that length of time, especially when even rare events disrupting distribution can randomly divert large numbers of fish throughout river systems in 400 years. Furthermore, because several year classes often return from a given brood year, interyear crosses are going to ensure the distribution of additive variance among year classes and further counteract the loss of diversity. We should not underestimate the influence that natural selection and even the influence that relatively low rates of gene flow (m) have on reducing the extinction risk of small, relatively isolated populations of highly specialized salmonids susceptible to inbreeding and genetic drift.

Metapopulations may be the primary source from which gene exchange originates, as suggested by Williams et al. (2000). In a simulation model, Allendorf (1983) showed that in the absence of natural selection, genetic drift can be abated by a low amount of migrant exchange (m) between populations that maintain a qualitative similarity but doesn't inhibit the ability of the population to respond to selective pressures. Because divergence is a function of migrant number (mN), the same amount of allele frequency divergence will occur with a given mN regardless of population size (Allendorf, 1983). An average exchange of only one reproductively successful stray ($mN = 1$) containing a particular allele per generation, therefore, is sufficient to maintain the representation of that allele between populations, and thus counteract the effects of drift.

Therefore, in approaching recovery to afford the optimum conditions for reproduction of the remaining chinook and steelhead in the Basin, there are two strategies that can make substantial progress in rebuilding and maintaining population structure: (1) increasing effective population size (Ne) and (2) genetic intervention (m). These strategies do not require substantial changes in the management programs, but they will require commitments to follow through with the changes and monitoring such actions require.

1. Increasing effective population size. Escapement based on maximum (MSY) and optimum (OSY) sustained yield are old concepts associated with harvest. The new approach should be to emphasize the biological health of the species, best referred to as the biological sustained yield (BSY). Increasing the size of the breeding population will help maintain the diversity present in the population, and it will help attract other potential breeders. Increased escapement will also help reestablish the competitive rigor under which chinook and steelhead population structure evolved. As pointed out by Peterman (1980) and Miller and Brannon (1982), the finely tuned patterns in niche definition and behavior were affidavits of forces that are no longer evident. In terms of the biological health of the species, escapement in excess of replacement needs is not a negative situation. Population structure

evolved historically under conditions that are now referred to as "over-escapement" or "surplus" and through that crucible of competitive interaction and exclusion evolved the array of life history strategies that characterize the species today. Abundance is necessary to maintain the competitive performance of these species and to respond to adaptive evolutionary forces. Excess escapement is the force that propagates rapid response to environmental opportunities, maintains diversity, and reinforces fitness. The existence of unique strategies, such as the Puntledge early and late returning chinook segments, but both having similar October spawn timing, are examples of behavior that may not have occurred without an abundance that encouraged expansion of habitat utilized.

2. *Genetic intervention*. Strays may be the mechanism that has allowed small chinook populations to succeed without experiencing inbreeding depression and the negative effects of drift. A measured amount of genetic intervention through introduction of migrants (m) of the appropriate predisposition to prevent the loss of diversity would not be a difficult task. The need for such intervention would be determined by monitoring genetic variance of the stock, but based on population theory (Allendorf, 1983), the level of intervention necessary to mitigate for loss of diversity is low and should not be expected to interfere with the adaptive fitness of stocks.

Genetic intervention can occur through the transfer of males to population units of concern or it can occur through artificial spawning and planting eggs in prepared redds. Intervention in the latter case would be by the use of milt transferred from the donor population to fertilize eggs from selected females and planting the fresh or water-hardened eggs in the stream gravel. When populations may be declining in abundance, it is critical to preserve genetic variation and the specificity they represent by the use of gene banks. Having such genetic resources available for reintroduction to a stock or compatible founding population when recovery is progressing is one of the prudent actions that can be taken to help rebuild viable chinook and steelhead resources. Gene banks, at very little cost, will prevent the loss that generations of adaptive selection have created, but we emphasize that although their use can advance recovery programs immeasurably, genetic intervention must be judiciously applied.

Through increased effective population size and genetic intervention, the first step in recovery will have been taken by reinforcing the present numbers or mix of life history strategies of chinook and steelhead in the Basin that characterize the population structure of these species in the region. The next step in recovery is to determine sites or streams where populations can be reestablished. This should first include areas where populations were known to have existed in the past and then areas that appear available as acceptable sites. Superficially, this seems to offer no challenge when one looks at the extensive stream reaches unused for spawning in the Basin, but unused areas can be deceiving. Generally, populations of chinook will be found spawning in a given section of stream, distant from other populations. This leaves proximal areas that might be viewed as suitable spawning habitat unused for incubation. We suggest that the biological basis for such situations is at least twofold. First, carrying capacity has to be considered a limiting factor. Fry will distribute to utilize stream areas very much larger than that used for spawning, and spawning sites used will be those consistently most productive.

Another component is the temperature gradient. Just as Mayr (1966) debated sympatric speciation, the same arguments apply to founding populations and dispersal. Although subunits within a population can diverge, they won't become genetically distinct unless or until they are effectively isolated. We believe absence of spawning populations in certain reaches of river adjacent to areas supporting spawners is because maximum fitness is associated with rather specific temporal identities. If spawners randomly distribute over a steep temperature

gradient of a stream, gene sharing would tend to make the population continuum homogeneous, with loss of specificity to temporal patterns associated with narrow temperature definitions, and fitness would suffer. Where subunits originate from a single population, as suggested for the John Day River (Lindsay et al., 1986), and where sympatric subunits exist within discrete spawning areas (Brannon, 1987), some level of spatial or temporal isolation has to exist. If gene exchange is too high, synchrony would not occur among subunits, and adaptive specificity would be discouraged. Therefore, in recovery efforts where a temperature gradient characterizes an extensive length of stream, reestablishment of the spawners may occur only in certain reaches, and efforts to artificially expand local spawnable areas with the same stock may not always prove fruitful. In these cases, the better strategy is to allow the existing population to determine the extent and nature of population growth.

The point is that the criteria used in site selection for restoration is critical. As demonstrated in life history strategies, temperature and migratory distance are two criteria that need to be included in population characteristics sought for rehabilitation of new sites. In many cases associated with larger rivers, flows may continue many kilometers before a noticeable change in temperature occurs. For instance, the lower 75 km of the Cowlitz River in the 1950s showed nearly the same mean September temperatures and chinook spawned at the same time over that length of river (Chambers et al., 1954), indicating that continuous distribution of spawners can occur when the temperature gradient is minimal. Therefore, mean incubation and rearing temperatures need to be worked out in detail to define the spatial parameters and the brood match for the site plan. Determinations of rearing capacity supporting the site, including downstream and distant reaches, should also be included in the inventories. As demonstrated by Brannon (1972), Quinn (1982), Taylor (1990b), Linley (2001) and others, population specificity exists in every detail that we have the ability to measure. The more that is known about the fish considered for use in restoration, the better.

When replacing extirpated populations, in most instances the genotype of the donor stock will not be a perfect match for the new site. This can occur whether the sources of fish are strays that venture into new habitats or methodical care is taken in attempting to match stock source with the introduction site. The approach in these circumstances is to utilize natural variability around the characteristics sought for the stream reach being seeded. The fish should be artificially spawned and eggs manually planted at low densities/nest to make sure high egg to fry survival and imprinting on the site are facilitated. Transferring fish for natural spawning is not recommended because they have no identity with the new site, maturation schedules can differ, and it limits flexibility. When introduction is justified, it should involve a substantial number of eggs for a given project, and, in some cases, interstock hybridization of at least a proportion of the gametes may be used to increase the genetic base on which selection can work. This is not to be confused with supplementation programs where stock hybridization should be discouraged in routine production, or with genetic intervention where maintenance of diversity is the objective. Interstock hybridization breaks down coadapted gene complexes and releases genetic variability on which selection can work to develop specificity for the new environmental template, but there is also a high cost. Introduced stock should be used only until return spawners are forthcoming, and enhancement using returning fish should not terminate until sufficient numbers of natural spawners have become established.

2. Application of Habitat Improvement in Recovery. The second step in approaching recovery is to address environmental needs of wild stocks through habitat improvement in areas presently utilized by chinook and steelhead. In general, steelhead rearing densities range from 1 to 10 parr/100 m^2 in the Basin (Johnson, 1984; Mullan et al., 1992; Griffith

and Hillman, 1986; Bjornn and Reiser, 1991; Rich and Petrosky, 1994). Chinook salmon as smaller residents are found from the same to higher densities, reported as high as 90 fish/100 m^2 (Andrews, 1988) in some areas of the upper Salmon River. Reported densities in some unimpaired streams are often near the carrying capacity and may not be able to accommodate increased production. Mullan et al. (1992) suggested steelhead in the mid-Columbia tributaries in undeveloped areas were near to their production capacity, and because steelhead appear to utilize the mainstem of the Columbia only for migration (Chapman et al., 1995), greater numbers of fingerlings in the system may not result in increased adult return. With the exception of the Salmon River and sections of the Clearwater in Idaho, remaining habitat in undeveloped streams for spring chinook may also be close to carrying capacity and not benefit markedly from increased production. However, although the number of such streams is believed very limited, much of the habitat originally available to spring chinook is no longer accessible. In the lower Snake and mainstem Columbia, fall chinook river habitat has been reduced by the hydropower reservoirs, leaving less high-quality habitat available for spawning and rearing.

In working under the assumption that habitat lost due to river development will not become available for the long-term, the only recourse is to improve the habitat that is remaining and to create new habitat. It is suggested, therefore, that to improve production in the Basin, considerable effort needs to be expended on a habitat program. As indicated in the discussion of population expansion, working to increase productivity around the present population structure is considered the most effective approach in assisting recovery in the Basin. Established populations have overcome the problems facing colonization and expanding their numbers involves fewer unknowns. Work in the upper Salmon River on instream habitat improvement for chinook salmon and steelhead (Andrews, 1988), for example, was estimated to increase rearing habitat by 10%. Similarly, habitat recovery in Oregon on the John Day River (Claire, 1995) has demonstrated the benefits of habitat restoration.

Programs to create entirely new habitat are other elements that can be employed in habitat expansion. The goal is to recover habitat previously disconnected from river channels and to create additional natural-type habitat through engineered systems to meet the biological requirements of salmon and steelhead. Habitat disconnected by flood containment dykes, agriculture and highways can be made accessible in many cases through collaborative programs with state and private landowners without compromising the other uses of such lands. Thousands of additional acres of highly productive habitat associated with present river systems can be added through such mechanisms.

One such habitat project has been developed on the Dungeness River, for coho salmon (Figure 43). An engineered stream was constructed on the flood plain to represent coho-type habitat with runs, riffles, pools, and ponds, including woody debris, root wades, and cover. Natural feed and supplemental feeding were the nutrient base during the first year of study. Rearing density of 50 to 100 mm fish during late fall of 2001 was estimated at >15 fish per m^2. Survival and return success of fish produced in the managed natural habitat will be assessed with otolith marks on adult returns, but production of wild-like fish up to the fingerling stage at the end of summer had been much greater than experienced in the adjacent stream. These types of natural-like stream habitat systems can be developed as a new hatchery concept to produce hatchery fish with characteristics of wild fish, or they can be developed to reclaim habitat lost behind mainstem channel containment dykes or on isolated floodplains.

A principle component in this concept is that engineered stream systems will provide controlled and stable habitat for higher production than in stochastic systems. It is anticipated

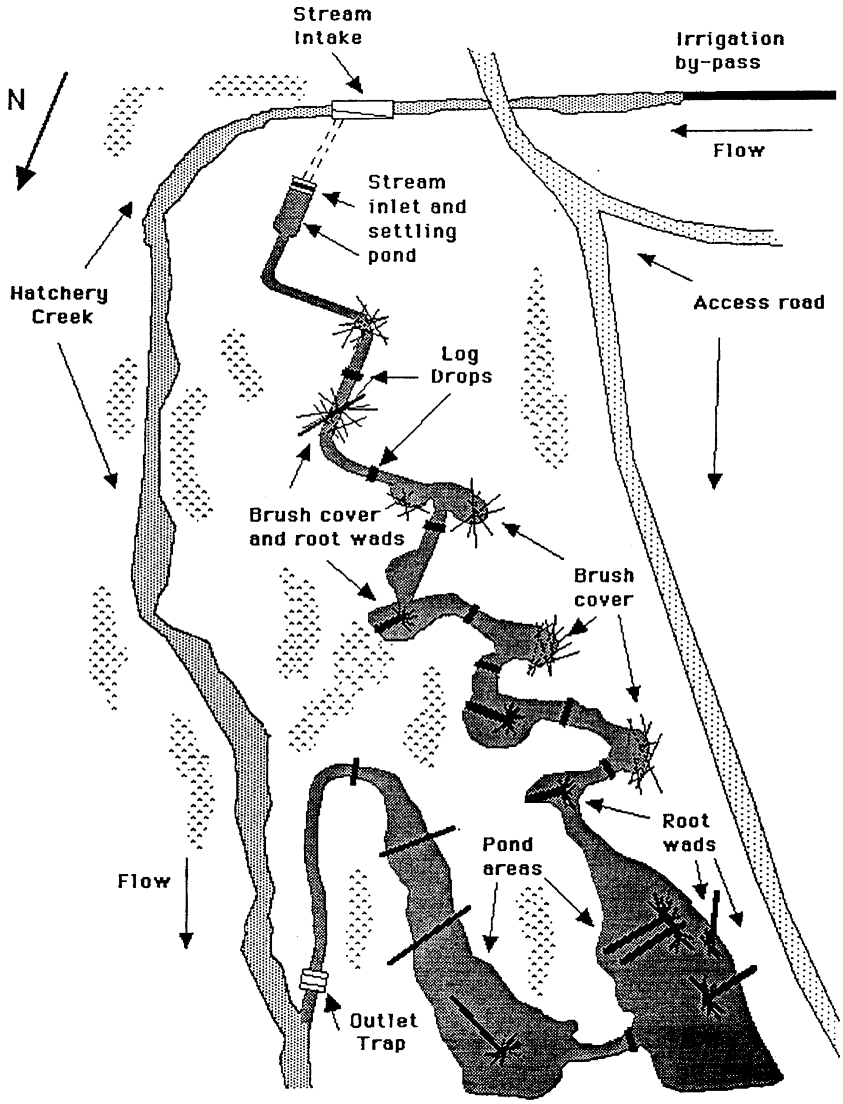


Figure 43. Engineered stream for natural-type coho production on the floodplain of the Dungeness River.

that managed flow through engineered streams that mimic the braided side channels with cover and enhanced rearing conditions can produce many times the benefit to wild-like salmon production per unit of area than what occurs in the adjacent river, based on the present analysis of data being collected from the Dungeness engineered stream project. In an era of advanced science and engineering, it would seem intuitive that technology can be applied to outperform stochastic natural systems if care is taken in the design and management of created habitat.

Another potential habitat opportunity that needs to be considered is the reservoirs (Figure 44). As mentioned above, some of the summer and fall chinook in the mid-Columbia and Snake rivers remain in the reservoirs and feed and, subsequently, leave as age-1 migrants

Figure 44. Snake River mainstem reservoir habitat presently used by chinook salmon for rearing through their first year of freshwater residence.

(Murdock and Petersen, 2000). Mullan et al. (1992) suggested that rearing habitat in the reservoirs should be given attention with the objective of perhaps improving the rearing conditions to support increased salmon and steelhead production. We agree that such opportunities need to be developed to help overcome the lost stream habitat from reservoir development. It is suggested that engineered streams can be built to provide spawning, incubation, and early rearing areas adjacent to reservoirs where fingerlings can complete rearing in reservoir environments if such habitat can be enhanced for that purpose. Chinook salmon life history flexibility has been demonstrated by their use of reservoir habitat, and by the evidence of successful residency in Lake Coeur d' Alene and Lake Chelan. Chinook life history is not segregated into fixed life history forms, but is malleable within the biological parameters of the species to take advantage of opportunities that favor otherwise uncommon phenotypes.

3. Application of Hatchery Technology. The other method of increasing the effective population size is through supplementation of natural runs with hatchery fish. As discussed above, hatcheries have constituted a major part of fisheries management on the Columbia since commercial harvests caused the precipitous decline in spring chinook at the end of the 19th century (Peven, 1992; Chapman et al., 1995; Brannon et al., 1999; Lichatowich, 1999). Although hatchery contributions are an issue of considerable debate, it is important to reiterate the fact that natural habitat in the system has been reduced to a small percentage of its original area, which means that natural production potential has also been reduced from its historic level by approximately the same extent. Recovery of significant fisheries will not occur without artificial production. The issue, therefore, is how has hatchery

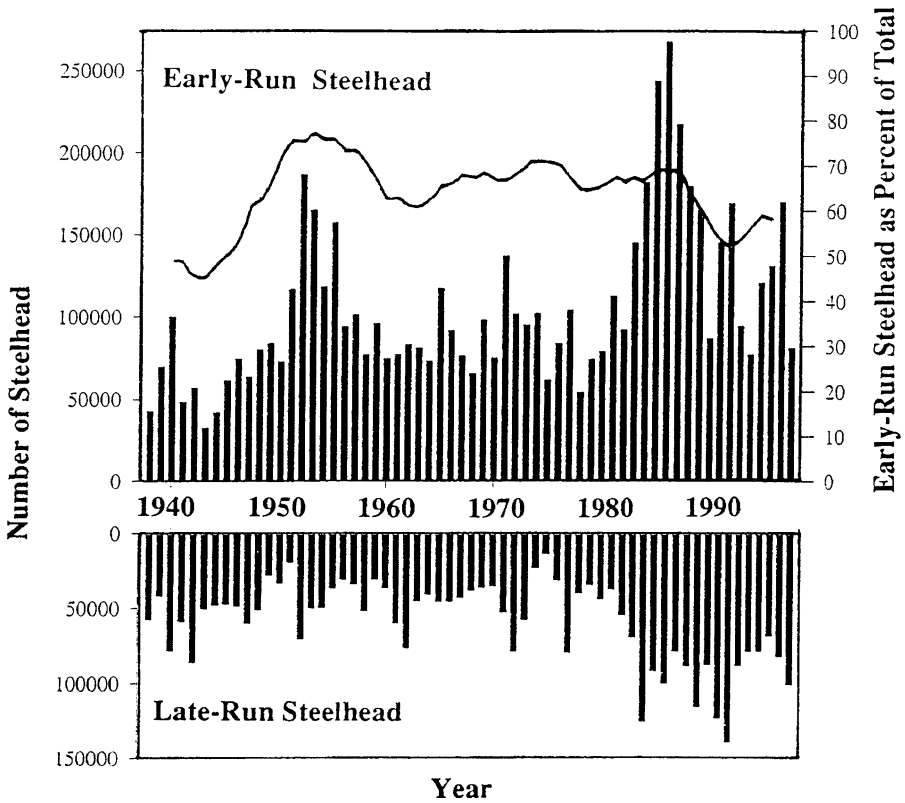


Figure 45. Abundance of early- and late-portions of the summer steelhead run passing Bonneville Dam. The irregular line is a 5-year running average of the proportion of the run that is defined as early (i.e., passing Bonneville Dam on or prior to August 26).

management altered the population structure, and if there are risks, how can hatchery practices be modified to reduce or alleviate negative effects.

Hatchery chinook comprise over 90% of total chinook returns to the Columbia (Brannon et al., 1999). Similarly, the majority of steelhead returning to the Columbia are also hatchery fish (Peven, 1992). The 2001 return of spring chinook has been the highest return since before the end of the 1800s, attributable primarily to hatchery fish. Current summer-run steelhead abundance in the Columbia Basin has also been maintained since the 1940s (Figure 45). Returning summer-run steelhead at Bonneville Dam showed an increase in the number of early-run fish during the early 1950s, but the most noticeable increase was from the late 1970s until the mid-1980s. This pattern in abundance was also observed below Bonneville Dam for unimodally-migrating summer-run steelhead on the Sandy and Clackamas Rivers. The relative proportions of the early- and late-segments of the summer run have also varied over time. At the start of the 1940s, the early run accounted for approximately 40% of the steelhead passing Bonneville Dam between 1 June and 31 October. This rapidly increased to a maximum of 86% in 1951 and subsequently declined to approximately 50% by the 21st century. However, it is important to note that abundance of steelhead passing Bonneville does not take into consideration the influence of the commercial harvest below Bonneville that terminated in the mid-1970s. In the 1940s between 59,000 and 286,000 steelhead were harvested below Bonneville annually (J. Lichatowich pers. comm.).

The proportion of wild steelhead present when enumeration first began in 1938 is unknown, but only four hatcheries existed above Bonneville Dam on the Columbia and Snake Rivers prior to 1940 (Busby et al., 1996). In contrast, since the 1970s, the mainstems and at least 19 tributaries of these rivers have been receiving steelhead from 18 different hatchery sources (Busby et al., 1996). The loss of habitat and proliferation of hatcheries have decreased wild steelhead stocks to less than a quarter of the original abundance. Tending to disregard the high level of genetic control over salmonid timing of migration and spawning discussed in this report helps explain how hatcheries have affected timing by stock redistribution, and thus altered populations structure within steelhead populations (Ayerst, 1977; Fessler, 1977).

Genetic divergence of hatchery and wild fish resulting from several generations of artificial selection and domestication is a potential issue that management of the Columbia Basin fisheries must address. Verspoor (1988) and Allendorf and Phelps (1980) reported in one case where hatchery-reared salmon had a reduced genetic diversity after as little as a single generation of artificial propagation. Such effects can have important consequences in terms of quantitative traits. Cooper (1961) showed that inbred groups of rainbow trout had markedly different weight-length curves from those of randomly bred groups. Several studies have shown divergence in allele frequencies between hatchery and wild populations (reviewed by Busby et al., 1996 and discussed previously). Fleming et al. (1994) noted morphometric differences between adult sea-ranched coho cultured for several generations and their wild counterparts, suggesting that changes accumulated over time. Swain et al. (1991) detected small genetic divergences between hatchery and wild coho in controlled studies, and Swain and Riddell (1990) showed differences in agonistic behavior between newly emerged hatchery and wild coho salmon grown in a common environment. Of these cases comparing hatchery and wild fish, however, many have little long-term relevance because observed differences may disappear among second generation hatchery fish when removed from hatchery conditioning and exposed to natural selection in the wild.

It is also important to make the distinction between single locus effects detected at the molecular level and cumulative effects on quantitative genetic characters accrued over many generations. Temporal variability in the frequencies of molecular genetic markers can simply reflect the dynamic nature of age-structured populations and should not be confused with long-term, multigeneration responses to selection regimes that result in different means and/or variances in phenotypic characters that have significant heritabilities (e.g., behavioral traits, life history traits, etc.). For example, interyear-class variation in allozyme frequency has been observed in steelhead from the Snake River (IDFG, 1991, 1993). Monitoring programs, such as the one on Snake River sockeye, also show year to year variation among mtDNA haplotypes (Powell and Faler, 2000). These intrapopulation genetic differences are most often attributed to limited sample sizes or the inability to represent the entire range of the population sampled.

a. Hatchery success. It is noteworthy that in 1931, prior to Columbia mainstem dam construction, the total annual salmon and steelhead catch was around 1.5 million fish (Brannon et al., 1999). Since that time, the average annual return to the Columbia has been maintained around 1.2 million fish (Figure 46), attributed largely to hatchery production. Although reproductive success of hatchery fish has been reported low in some studies (i.e., Chilcote et al., 1986[4]), the fact that hatchery fish have integrated in the gene pool of

[4]However, see Campton, Allendorf, Behnke, and Utter, 1991; Chilcote, Leider, and Loch, 1991 for comments and reply to the paper by Chilcote, Leider, and Loch, 1986.

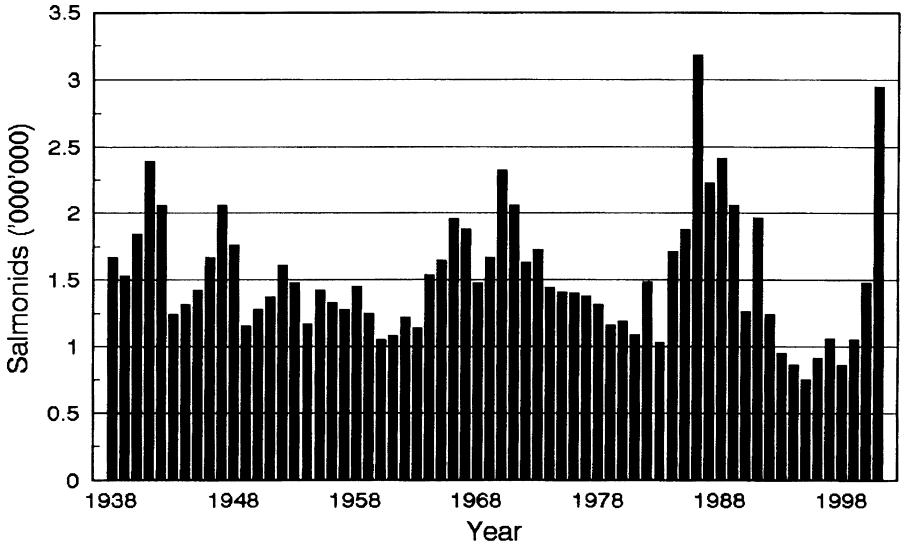


Figure 46. Total salmon and steelhead returns to the Columbia River from 1938–2001.

wild fish over the years, and thus are represented in what is considered wild populations, makes interpretation of the results difficult and provisory.

The successes of hatchery steelhead in the Basin, and the 2000 and 2001 runs of spring chinook are noteworthy because, in spite of the hatchery problems that have been enumerated, hatcheries have succeeded at maintaining fish for harvest, which historically was the principal objective for their development. The intent of turning to hatchery production in the early years of river development, as well as the more recent goal of doubling the salmon returns to the Columbia River, have been to mitigate for the loss of natural production through the use of fish culture. From that perspective, we can conclude that those objectives have been realized to a significant extent, at least since the 1930s. Moreover, hatcheries have also been instrumental in maintaining genetic diversity. In the genetic analyses performed in this study, hatchery populations tend to show greater diversity than their wild counterparts.

As our understanding of salmonid life history and population structure increases, the challenge is to develop and apply hatchery technology in a manner that conforms to the biological requirements of these species (Brannon, 2001). The ability to adapt to environmental change, whether under natural or artificial conditions, is strong evidence that these fish have evolved to be responsive to the dynamic nature of their freshwater environments. Also, by the relatively large fecundities of the anadromous forms, we are reminded that salmonids have evolved in stochastic systems and have the ability to contend with the degree of environmental variability found in natural river systems. How well we use life history information in developing technology to revive these species in a manner consistent with the salmonid ecosystem will determine the long-term viability of these species in the Columbia Basin.

b. Hatchery risks. The risks created by using hatchery fish have had a long history of controversy, and we do not want to minimize the problems that have occurred from the application of hatchery technology. It is important, however, to put these issues in perspective and not fall error to the popular misconception that hatchery fish are at the root of all problems. It is instructive, therefore, to address some of these issues and briefly discuss how their resolution must be approached.

Translocation of hatchery fish throughout the Columbia Basin has been routine over the years (Flagg et al., 1995; Peven, 1992; Busack et al., 1979) and is still part of management practices. The chinook salmon introductions to Carson hatchery from upriver destined spring chinook spawned at Bonneville, and then introduced into the Methow River, Rapid River, and the Grand Ronde River; and also the Lyons Ferry hatchery fish derived from Lower Granite and transferred into the Umatilla River, are some of the more recent distributions of hatchery chinook in the Basin. Similar translocations of steelhead (B-run) have been made from Dworshak Hatchery to the Lochsa, South Fork and North Fork of the Clearwater, and to the Pahsimeroi River, tributary of the Salmon River. Skamania hatchery eggs were also transferred to the Pahsimeroi and smolts grown in the Pahsimeroi Hatchery have been released into the East Fork of the Salmon River. The management of the A-run was even more complex. The A-run broodstock at Pahsimeroi hatchery was created from adults trapped at Hells Canyon Dam and translocated to the Salmon River, Middle Snake drainages, such as the Owyhee, Malheur, Bruneau, Boise, Payette, and Weiser Rivers, as well as the Middle Snake itself up to Shoshone Falls (Simpson and Wallace, 1982). We see, therefore, that transfers of hatchery-reared fish from one stream to another has been a continuing management practice in the Basin, and, in many cases, these fish were mixtures created by interceptions in the mainstem and hence of unknown origin. When such transfers are made without stock identity and asynchronous with the sites selected, little or no benefit in promoting natural propagation can be expected.

In other cases, mitigation measures were taken without the option of having a choice of stock to work with, or at least little appreciation of the specific biological requirements associated with the stocks utilized. There is little doubt that development of the river system and attempts to mitigate for losses of wild fish have had negative effects on the natural salmonid resources. The Grand Coulee Fish Maintenance Project tended to homogenize population diversity above Rock Island Dam (Utter et al., 1995), and each successive hydropower facility downstream has altered the mainstem habitat. The Bonneville hatchery program had similar impacts on genetic diversity by intercepting fish destined for upriver, and mixing stocks for redistribution in the lower Columbia and elsewhere. How these changes altered the population structure of chinook isn't fully known, but the mixing of stocks that occurred in the lower and mid-Columbia was bound to have eliminated some of the heterogeneity between stocks. In general, the historical genetic diversity is believed to have been reduced substantially with the reduction in abundance, translocations, and loss of subpopulations.

A major risk associated with mixing of stocks, whether by transfers of wild fish or the introduction of hatchery fish, is the concurrent loss of local genetic specificity that can occur from interbreeding, and hence the loss of fitness. Genetic control in the timing of upstream migration and spawning has been established for several salmonids (e.g., Atlantic salmon (*Salmo salar*), Hansen and Jonsson, 1991; pink salmon (*O. gorbuscha*), Gharrett and Smoker, 1993; sockeye salmon (*O. nerka*), Brannon, 1987; and rainbow trout, Siitonen and Gall, 1989). There is little doubt that genetic equilibrium of native fish with environmental conditions can be confounded by introductions (Ayerst, 1977; Leider et al., 1984). This involves more than just development of temporal synchrony with the local habitat. Other aspects of their life history will have to be altered to some extent, even their response to environmental cues, notably flow and temperature, that affect entry into freshwater and upstream migration rates (Major and Mighell, 1967; Banks, 1969; Gilhousen, 1980, 1990; Jensen et al., 1989; Smith et al., 1994; Symons, 1968a, b; Trépanier et al., 1996; Quinn et al., 1997).

Asynchrony with their habitat will be a problem regardless of the source of fish. Although hatchery fish are most often faulted for their inability to perform under natural

conditions, even wild fish are probably rarely preadapted to successfully colonize new habitat. This was evident in the diversion of Fraser River sockeye returning to Chilko Lake in 1963. A landslide blocked the Chilcotin River, and the early returning segment of the run strayed throughout the Fraser Basin when confronted with adverse conditions in their migratory path. Because of their specific timing and behavior as a lake outlet spawning population, the fry of which display positive rheotaxis to reach their upstream nursery lake (Brannon, 1972), Chilko sockeye would not be expected to perform well unless they strayed to a similar habitat. It so happened that several dozen Chilko sockeye were observed to have strayed and spawned in the outlet of Little Horsefly Lake, which appeared to be a habitat that satisfied at least some of the unique requirements of that stock. However, there was no observed success of Chilko sockeye in establishing a new population in the Little Horsefly. The point is that wild fish will be no more successful than hatchery fish in establishing new runs if the donor and receiving environments are sufficiently different to meet the biological needs of the donor phenotype. In the case of Chilko sockeye, the compass orientation of the Horsefly Lake outlet (≈260°SW) was probably not close enough to correspond to the innate compass coordinates demonstrated by emigrating Chilko sockeye smolts (≈345°N) (Groot, 1965; Quinn, 1981).

Nonnative resident rainbow trout have also been released in a very large number of streams, lakes and impoundments (Busack et al., 1979) as discussed previously, but the pattern is widespread in all Northwestern States. Such introductions have potentially important consequences for Columbia River steelhead as well as cutthroat and redband trout. Earlier it was shown that because of extensive gene flow between resident and anadromous forms of *O. mykiss*, in most cases sympatric resident and anadromous forms are more similar than either life history type among other populations (Busby et al., 1996). It appears that resident native fish function as a reservoir for the conservation of genetic diversity in *O. mykiss* among streams as suggested by Leider et al. (1994), and thus gene flow to steelhead populations that are in decline or are small demographic units. Such influx of genotypic diversity would be a buffer against the genetic and demographic problems of small population size.

Therefore, introduction of nonnative fish or progeny of inbred captive broodstock represent potential risks to any benefit that resident populations may afford their anadromous counterparts. This includes the lack of resistance to local diseases, which was demonstrated among transplants to the Deschutes River from coastal populations (Currens et al., 1997). Under such conditions, the genetic reservoir of local adaptive traits provided by resident *O. mykiss* would be compromised to some degree, and offspring from such mating with returning steelhead would be less fit.

Behavioral and morphological differences have also been observed between hatchery and wild fish because of the effect of the rearing environment (Fenderson et al., 1968; Sosiak et al., 1979; Dickson and MacCrimmon, 1982; Coughlin, 1991) and phenotypic divergence (e.g., Fleming et al., 1994). These are effects related to hatchery conditioning and are considered responsible for the poorer survival of artificially propagated fish after their release compared to their wild counterparts. However, these are acquired effects of the artificial environment on alteration of physical and behavior characteristics of the cultured fish, and most often probably represent short-term differences without a genetic basis. Among the second generation in the wild, these fish would be expected to show little evidence of any acquired characteristics from hatchery environments. It should also be pointed out that potential problems created from transfers of hatchery fish depend on the source of stock and the extent of such introductions. Continuous introduction of large numbers of fish with different heritable life history characteristics into local populations represents the greatest

risk. Infrequent introductions may pose little risk, and if spawning times are markedly different little or no introgression may occur. However, where introductions are necessary, such practices should be exercised only long enough to establish a reproducing run, and then to let selection work to develop the self-sustaining population.

A problem that is sometimes attributed to hatchery fish is an inability to spawn successfully, or perhaps the inability to know where best to spawn. Captive brood reared to the adult form and released in Idaho streams to spawn naturally have shown asynchrony in maturation between males and females (Chinook Salmon Captive Propagation Technical Oversight Committee, unpublished). However, except for such anomalies under captive programs, assumptions that hatchery-reared juveniles, even if purposefully diverged from wild populations, will not mature and successfully spawn in the wild are not supported by data. In the Kalama River, Chilcote et al. (1986) demonstrated that Skamania steelhead, a much diverged, nonlocal and putatively domesticated[5] hatchery fish, were able to spawn successfully under natural conditions. Given the importance of temporal specificity, it was remarkable that in spite of the broodstock having been purposefully advanced 3 months in spawning time over the previous 30+ years and then translocated to a different stream, these fish were still able to show a significant level of spawner to spawner reproductive success in a totally different environment.

However, it is apparent that the ability of hatchery fish to spawn and survive well in the natural environment is not that uncommon. Lofy et al. (1997) showed that nonlocal steelhead outplanted in the Lookingglass Creek had a spawner-to-spawner return rate similar to local wild stocks. Rhodes and Quinn (1999) show that hatchery-reared fish released from a conventional program grew and survived as well as their wild counterparts. Mullan et al. (1992) found no difference between wild and hatchery smolt success in the mid-Columbia. And other examples of hatchery fish success have been shown (Fuss, 1998), which demonstrate that fish raised in hatcheries can spawn successfully and do well under natural conditions.

It also follows that if they are not derived from local stocks, these transplanted fish will have some longer-term adaptation to undergo before enjoying fitness comparable to native fish. The extent to which nonnative hatchery-origin fish will potentially reduce the overall productivity of the native fish is unknown, but this presents a level of risk that needs careful evaluation, and it will vary depending on the stock, environmental template, and the ecosystem involved. However, it is also a risk that can be avoided by using fish only from local stock, or using only returning fish when working with an introduced population.

Further, salmon and steelhead hatcheries release their fish into the wild, where they spend 1–3 years under natural selection in the river and marine waters before reaching

[5]We use the term "putatively domesticated" because there are no measures of domestication nor norms for determining domesticated stocks (Doyle, 1983). Further, domestication is a process and not a state. Fish that remain in hatcheries are subject to selection in that environment as they are under any other environment, and a fish adapting to the hatchery environment would thus be considered "domesticated." Domestication in hatchery fish is believed to reflect three independent processes: (1) direct artificial selection by hatchery personnel, (2) natural selection in an artificial environment, and (3) relaxation of natural selection that occurs in the wild. Therefore, the mechanism for domestication would be principally selection on a set of traits related to fitness in the homogeneous environments, but also to inbreeding (i.e., absence of gene flow among populations, gradual loss of additive genetic variance). There are several studies that show that rainbow trout raised in hatcheries for the entire life cycle for several generations do poorly when released in the wild (Flick and Webster, 1976). It is unclear whether hatchery-reared fish that spend a large fraction of their life in the wild can become domesticated in the same sense (Campton, 1995; Purdom, 1994; Wohlfarth, 1993; Rhodes and Quinn, 1999).

maturation. These circumstances are significantly different than closed hatchery systems that control the entire life cycle of cultured fish. We would argue that fish from properly managed hatchery programs are not the mongrels suggested by some hatchery critics (*Science*, 2001), but rather the continuing legacy of the founding population. Where hatchery fish have been successful in seeding habitat, natural selection will continue to increase fitness under the respective environmental template, much the same as with wild fish expanding their range.

Finally, it is important to reemphasize the need to integrate the sustaining mechanisms of population structure in the operational plan that hatcheries develop for their respective stream systems. Management plans too often have given insufficient attention to the behavior and life history of salmon species, or have broadly employed hatchery technology in the absence of consideration given to the critical link between genetics and the environment. Well intended transplants of salmonids have been made to enhance or supplement production of dwindling natural runs without realizing that the environmental incongruity imposed upon the introduced strain by such a transition would make it incompatible with opportunities available in the new habitat. This was a major flaw in early hatchery management demonstrated at Bonneville as mentioned above, where mixed stocks were intercepted and the progeny released at Bonneville or translocated to other sites (Lichatowich, 1999). The original stock structure that existed among the intercepted subpopulations broke down because of forced out-breeding and redistribution. The assemblage of returns were sustained only because the hatchery substituted for the natural freshwater habitat requirements.

New supplementation hatcheries have to avoid the same problem in their management protocol. The Yakima hatchery, located near Cle Elum, about 288 km up the mainstem Yakima River from its confluence with the Columbia, (Figure 47) approved by the Northwest Power Planning Council to increase natural production and harvest in the Yakima River (Clune and Dauble, 1991), is a case-in-point. Four major sub-basins exist in the upper Yakima, three of which originated from lakes close to the headwaters; Keechelus Lake, Kachess Lake, and Cle Elum Lake. The forth sub-basin drains via the Teanaway River. Consequently, temperatures of the main streams flowing from the four sub-basins vary substantially because of differences in water retention and sources. In the 1997/98 season, the Teanaway River was the coldest, dropping to 0°C during January, compared to the lower Cle Elum River, mainstem Yakima, and upper Yakima that measured from 1°C to 3°C warmer at the same time of year. Based on the differences in temperature profiles among the sub-basins in the upper Yakima River, and given that emergence timing is key to subsequent survival, peak spawning times should differ by as much as 60 days between extremes of Teanaway and Cle Elum, and 33 days and 38 days between Teanaway and the upper Yakima and middle Yakima, respectively.

Present operations intercept unmarked fish as broodstock from traps over 70 kilometers below the hatchery, and their progeny are distributed to release sites irrespective of their sub-basin origin. The operation plan for the hatchery will have to take into account the temperature differences among their release sites, and thus the stock structure that should be developed to optimize fitness in the different sub-basins, or else the hatchery will function simply as another production facility.

A consistent problem is that hatchery programs are not often designed with the life history needs of the fish in mind. An example is the Umatilla hatchery located on the Columbia River below the confluence of the Umatilla with the Columbia. The water supply for incubation and thus the initial imprinting source as the ultimate homing cue of returning fish is well water drawn from the water table next to the Columbia, and not from the Umatilla River to which the chinook are expected to home. Disjunction between the early life history experiences and the release sites developed to supplement natural production

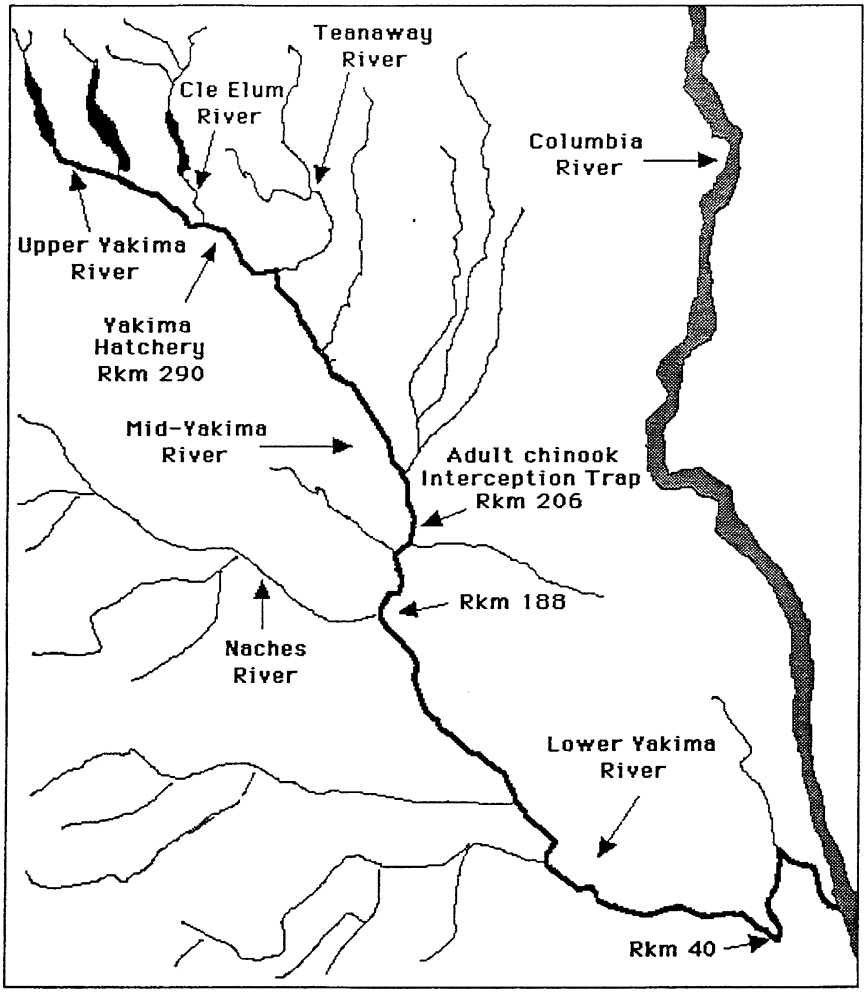


Figure 47. The Yakima River Basin showing Yakima, Naches, Teanaway, and Cle Elum rivers, with the adult return interception facilities at Rosa, and the hatchery site at Cle Elum.

probably contributed to higher stray rates past the Umatilla River, continuing further up the mainstem. Once they returned in proximity to the hatchery, their ultimate homing objective will have been recognized when confronting hatchery effluent water, and less specificity to the subsequent release sites would be an expected response in the sequence of acquired experiences (Quinn et al., 1989). These examples demonstrate that opportunities exist to make definite improvements in present hatchery operations that will help the integration and performance of hatchery fish in supplementation or recovery programs.

Another example of the need for comprehensive planning around stock structure is in the Methow River, tributary to the mid-Columbia north of the Wenatchee. Chinook salmon were eliminated from the Methow in 1915 by dam construction (Mullan et al., 1992) at the mouth of the river except possibly the late chinook spawners in the lower 4 km of river. From 1939 through 1943, redistribution of upper-Columbia spring and summer chinook was part of the Grand Coulee Fish Maintenance Project and juveniles from the GCFMP

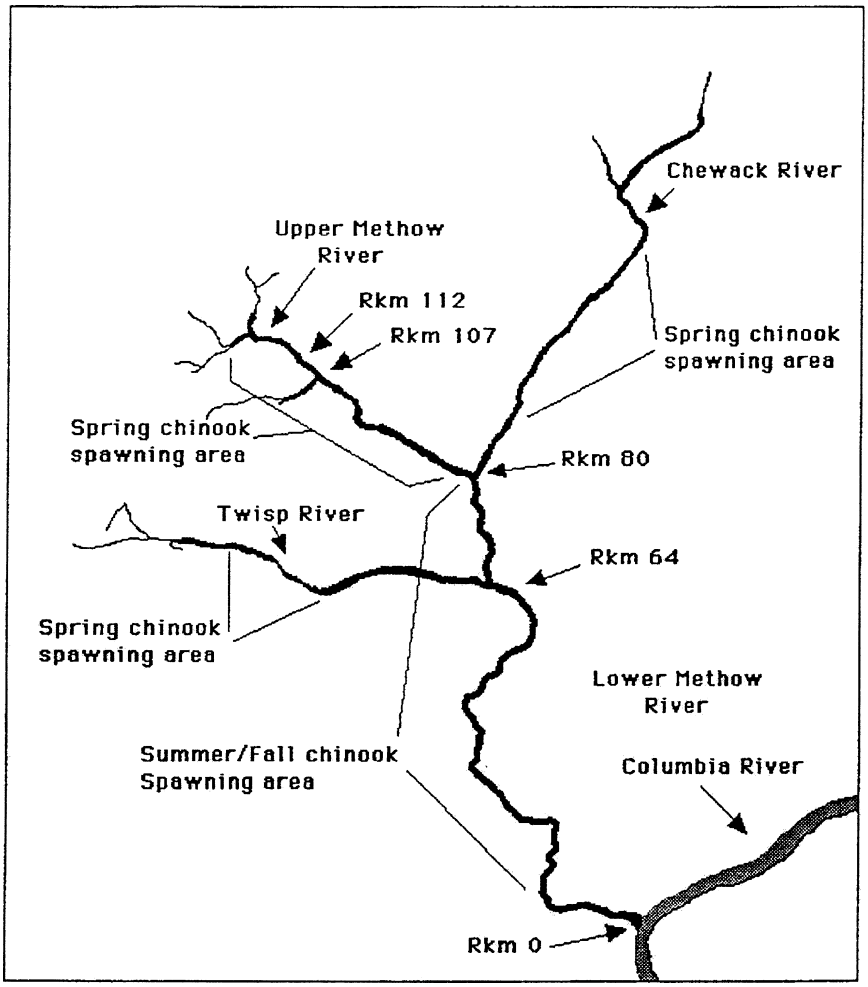


Figure 48. Methow River spawning areas of spring and summer/fall chinook.

were released in the Methow River (Utter et al., 1995; Mullan et al., 1992). The stream drains east from the high North Cascades area, and spring chinook habitat in the upper river above river-km 112 (mile 70), 830 meters elevation, extends up the West Fork and other small sub-basins (Figure 48).

Temperatures in the upper river are cold and typical of early (spring) chinook, with spawning in mid-August [Met-SA 20-1] at mean incubation temperatures around 3.7°C, and fry emerging in April. Immediately below that area at river-km 107 (mile 67) large groundwater flows enter the river and mean incubation temperatures rise to over 8°C, typical of late (fall) chinook spawning grounds. As the river flows downstream it warms through October and then cools until the next spring (Figure 49). However, spring chinook spawn below river-km 107 all the way down to river-km 80 next to the Winthrop hatchery in August at the same time they spawn above river-km 112. (French and Wahle, 1965; Scribner et al., 1993; Hubble and Sexauer, 1994). The problem is that with incubation at mean temperatures slightly above 8°C at river-km 107 down to 6.3°C at river-km 80, the spring chinook fry

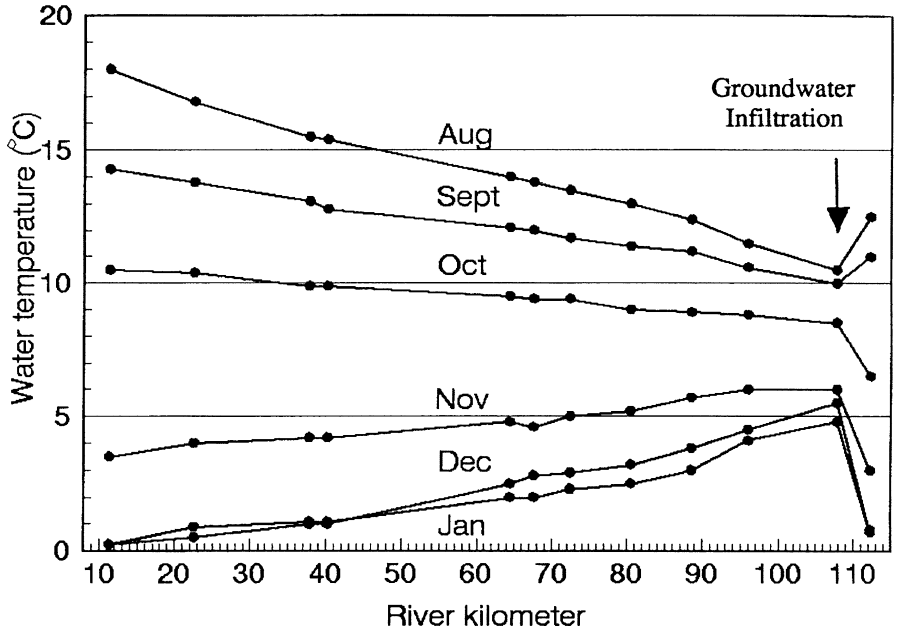


Figure 49. Mean temperatures in the Methow River from the river mouth (km 0) to river-km 112, August through January (Mullan et al., 1992).

use up yolk stores over 2 months earlier than fry incubated above river-km 112, and emerge into temperatures that remain below 5°C for 3 months before spring warming. We suggest that fitness among the spring chinook progeny below river-km 107 suffers from asynchrony in timing, and that the population is there only because of the federal and state hatchery programs. Based on these incubation and rearing temperatures, the later summer/fall-run [Met-SuO9-1] that spawns between river-km 50 to 80 is better suited for river-km 80 to 107, but even later spawners [Met- SuO25-0] would seem more appropriate for that upper reach.

The disconcerting issue in these cases is that each of the hatchery programs have undergone extensive review prior to their development, and still problems associated with the most basic life history requirements are overlooked. The point that needs to be emphasized is that these problems are not the fault of hatchery fish, but rather the fault of our hatchery programs. Hatchery programmers need to take measures to assure the compatibility of hatchery fish with their receiving environments. Such measures would include at a minimum the appropriate genetics and the temporal pattern in return and spawning that is in synchrony with the target stream.

In many cases, hatcheries are located on the warmer lower reaches of their respective rivers and intercept spawners traversing upstream. Because the progeny of these fish have the temporal pattern of the parent run, but will imprint on the hatchery water supply and the adjacent lower river upon release, they can be out of synchrony with the temperature regime of the lower river. If the excess hatchery fish home and spawn adjacent to the hatchery site, they would be spawning too early with regard to local temperatures, and emergence timing would be asynchronous. Kalama, Washougal, and Elokoman hatchery fish may demonstrate such a pattern. Based on the temperature profiles of the hatchery

streams, it appears that if they spawned relatively close to the hatchery reach, each of these summer/fall-run populations would be spawning at least a month too early to synchronize emergence timing with the local environmental template. However, if these fish ventured further upstream and spawned close to their historic incubation reach, they would be more closely synchronized with the temperature regime, and their expected performance should be measurably better.

The Methow chinook stocks experience a similar situation, except the temperature regime undergoes an abrupt change at river-km 107 from the influence of groundwater. Beer and Anderson (2001) suggested that differences in fry advancement at emergence between the early upper river [Met-SA 20-1] and later midriver [Met-SuO9-1] populations were related to the constraints faced by the midriver spawners. We agree that the lower river spawners are constrained from spawning early by the high temperatures, and temperatures fall so precipitously thereafter that the incubation environment appears unsuitable for chinook in the lower river. Midriver spawners around Rkm 50 to 80, however, have suitable temperatures for incubation with emergence at the appropriate time in the spring, even earlier than the upper river population. The problem is in the area where both the [Met-SA 20-1] and [Met-SuO9-1] populations overlap (Figure 48). Temperatures are too warm at Rkm 80 to 107 for either of the present spring or summer chinook populations because of the warm ground water, and fry from excess hatchery spawners in that reach will emerge too early for optimum survival. Hatchery supplementation of the midriver population below Rkm 80 and the upper river spawners above Rkm 107, however, will benefit natural production in those reaches.

It is apparent that hatchery fish must continue their role in replenishing salmon and steelhead in the Columbia if sustainable major fisheries are to be rebuilt. To make such programs functional within the ecosystem, it is necessary that hatchery programs are developed around the stock structure present within the sub-basins, utilizing local stocks for both production and supplementation. This will mean that in addition to their obvious role in recovery, hatcheries must also be part of the sustaining process of the population structure. If hatchery populations are not representative of their native counterparts, it will be necessary to change the program until that requirement is satisfied. To strengthen natural populations and maintain their legacy, it is imperative that hatchery fish become integrated within the native population system, and that wild and hatchery fish be managed together as composite units.

Other Measures to Assist in Recovery

Several other measures can be employed to assist in the recovery of salmon and steelhead, two of which are suggested here as examples of different actions that could help in the recovery process.

Reconditioning Steelhead Kelts to Aid in Recovery. An opportunity is presented by the steelhead kelts that pass downstream in the spring. The kelt fallback migration is important from two points of view. First, they represent fish that have successfully spawned. Kelts from natural production represent an important resource, because these fish have successfully spawned in the natural habitat for which they are most likely adapted. Therefore, their second spawning would assist in maintenance or recovery of those respective resources, and are considered worth assisting for another contribution.

The second point of view is that a larger number of hatchery fish are apparent among the kelts. These fish also have successfully gone through the spawning process, which

Table 13
Maturation status and origin of adult steelhead examined with ultrasound at Lower Granite Dam, 2000.

	Origin no. (%)					
Maturation status	Hatchery		Wild		Total	
Prespawn	28	*(2.1)*	24	*(1.8)*	52	*(3.8)*
Kelt	527	*(38.9)*	774	*(57.2)*	1,301	*(96.2)*
Total	555	*(41.0)*	798	*(59.0)*	1,353	*(100)*

provides evidence that hatchery fish spawn in the wild, because steelhead returning to hatcheries are terminated. Therefore, with the presence of kelts originating from hatcheries as juveniles and returning as wild spawners, it implies that there are many more hatchery-reared fish spawning in the wild than previously thought. The uncertainty is the value of their contribution to the long-term success of establishing or supplementing self-sustaining populations. In the process of these fish integrating with naturally produced wild stocks, they will have an influence on wild production and stock structure as discussed at some length previously.

Based on ultrasound examinations, 219 (85.6%) and 1301 (96.2%) of the specimens were classified as kelts in 1999 and 2000, respectively. From fin clips (adipose, pectoral, and/or ventral) on those 2 years, 174 (67.2%) and 527 (38.9%) were identified as hatchery in origin, while the remaining 85 (32.8%) and 774 (57.2%) kelts were considered naturally produced individuals (Table 13). The juvenile bypass collected 2400 and 4182 adult steelhead in 1999 and 2000, respectively. It is not known what fraction of the total "fallback" population is collected by the juvenile bypass, as fish alternatively may use the spillgates, turbines, locks, and fish ladders. However, from their number and apparent success in spawning, the potential contribution of these fish on gene flow and population structure needs to be given consideration, and their appropriate application given careful attention.

There is also a pronounced attrition of kelts subsequent to their passing McNary; fewer than 5% of those passing McNary Dam were observed at The Dalles Dam. Evans and Beaty (2000, pers. comm.) examined 259 adult steelhead at Little Goose Dam in 1999, and 1353 at Lower Granite Dam in 2000 using the separator at the juvenile bypass facilities. The energetic demands of reproduction are considerable, and the survival rate of steelhead kelts from upriver populations seems low (see also Withler, 1966; Busby et al., 1996). Historically, all upriver populations may well have been largely semelparous. Overall, summer steelhead repeat spawners contribute <1% of returns compared to <5% for winter (coastal) steelhead populations (ODFW/WDFW, 1995). Body weight of steelhead kelts, most of which appear to be female (USCOE, 1989; consistent with Atlantic salmon, Fleming, 1998) is reduced by up to 40% of their prespawning levels, possibly leaving many fish with insufficient reserves to make a long downstream journey, irrespective of their ability to bypass dams. It is unclear whether the present mortality rate (Figure 50) differs from predam days. The summer-steelhead life history pattern does not seem to favor iteroparity; however, comparative data on the prevalence of iteroparity among wild steelhead populations are insufficient to support general conclusions on this subject. However, the plans proposed by

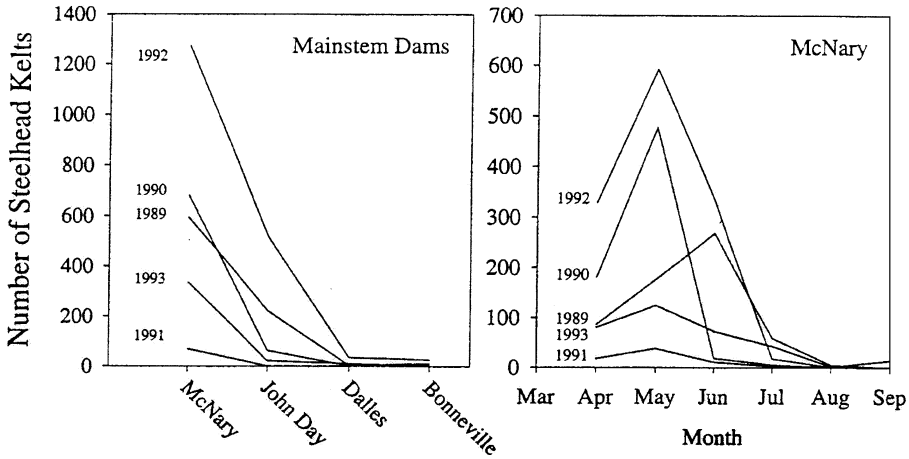


Figure 50. Counts of steelhead kelts at Columbia River dams downriver from McNary Dam (left panel), and timing at McNary Dam of greatest numbers counted (right panel).

others (CRITFC, H. Senn pers. comm.) to intercept kelts and either sustain them in culture facilities or assure their safe return to saltwater would be an option to consider. These fish have survived through reproduction and could effectively contribute again to natural production.

Undertaking a program to intercept kelts and reconditioning them for release to spawn again will require a definite program designed specifically for that purpose: to include a site where reconditioning activities can be centered. Kelts should be intercepted as high in the system as practical, and transferred to a reconditioning facility designed for such a purpose, at a geographical location suitable for such activities. This will include facilities for observation, anesthetic application, prophylactic treatments, appropriate nutritional provisions, at least 12-ft-diameter circular tanks that allow the fish to have stream-type orientation and freedom of movement during reconditioning, large earthen ponds in which the reconditioned fish can be held until release to their recapture sites, and adult transfer capability.

Fertilized and Eyed Egg Plants. There has been a revival in the interest of planting eggs to supplement or reintroduce salmon or steelhead in streams where they have been extirpated. In the early years of fish propagation, egg and fry plants were widespread but generally failed to establish new salmon runs. Although the eggs were often accelerated by incubating in warmer water before planting, and thus emerging too early, it appears that the main fault was the lack of attention given to selecting the appropriate genetic stock to match the environmental template of the receiving sites. With better knowledge about salmon and steelhead life history, genetics, and population structure, egg planting is now considered an option that provides a low-cost approach to enhancement. The requirements for such projects are to have the appropriate egg source, and in sufficient numbers, to establish a strong population base of fry seeding the stream.

In natural production, egg mortality ranges from less than 50% to over 95% of the total number spawned with an average survival to emergence around 10%. These relatively high mortalities are associated with the density of eggs in the nest, overspawning by other

fish, siltation, predation, gravel scour, dewatering, and freezing. Where care is taken in selection of the nest sites, incubation success of eggs planted in the stream gravel can be much improved over natural spawning because the nests can be placed in favorable sites in protected areas, and the eggs can be planted at lower densities than in natural redds, which will improve irrigation efficiency through the gravel.

Planting the eggs in the stream eliminates the problems associated with stream-side incubation systems where floods and freezing temperatures can limit success, and where a reliable water supply becomes a major uncertainty. Eggs planted in the natural stream gravel are irrigated with the local stream temperatures, they have a natural incubation environment free of surface ice, and water supply problems that plague stream-side incubators are totally eliminated. Eggs can be planted right after water hardening to eliminate the need for hatchery or incubation buildings, artificial incubators, auxiliary water supplies, and maintenance personnel. Planting eggs in the stream also eliminates discontinuities in the incubation odor sequence that might disrupt home stream imprinting.

The main requirement for planting eggs is to have an efficient planting device that reduces labor and the time required. Because the nest site must first be cleaned and prepared before the introduction of eggs, the hydraulic planter developed by Collins and Brannon (1999) is an effective device that prepares the site and introduces eggs with little interruption of the planting routine (Figure 51). To be most effective with the hydraulic planter, a two-person crew is best, one to operate the planter and the other to transport and volumetrically measure eggs for the nests. Densities within the nest should not exceed 200 eggs, but separation of nests within each column, and separations between ranks of columns can be as little as 30 cm, as long as sites are well marked to prevent overplanting.

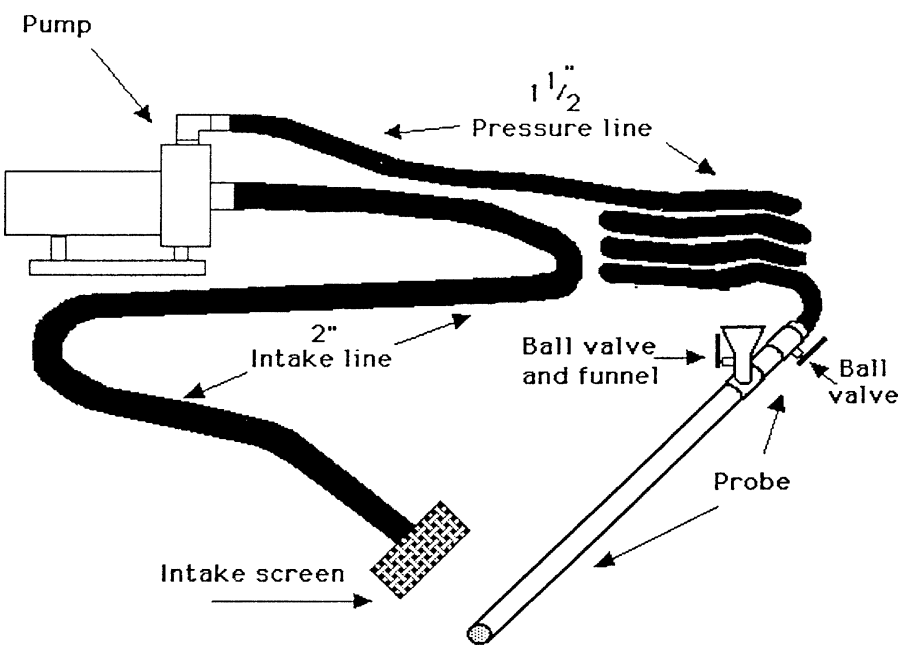


Figure 51. The Collins hydraulic egg planter showing probe and ball-valves that allow nest cleaning and egg placement as a single operation (Collins, 2000).

Conclusions and Recommendations

We view the Columbia Basin chinook salmon and steelhead trout as a complex of locally adapted populations within genetically linked assemblages referred to as metapopulations. Moreover, metapopulation structure is also hierarchical, with closer relatedness among those generally in closer proximity. Although colonization events were likely numerous and may have included many different sources from along the coast, we believe the Columbia River stocks of *O. tshawytscha* can each be managed as though from a common ancestry. Although segregated along coastal and interior genotypic lines, we believe this is true for *O. mykiss* as well. The population structure of chinook and steelhead within the Columbia Basin, therefore, can be described as segregated populations within which temperature has had a predominant influence in the determination of spring-, summer-, and fall-run spawning strategies, and in the formation of stream- and ocean-type, or stream- and ocean-maturing life history forms. Once colonization was successful, members spread through adaptive evolution into distinct temporal life history forms within geographic boundaries characterized as metapopulations, and further subdivided around a similar temporal framework as first-order metapopulations.

Consistent with evolutionary theory, life history patterns are the product of natural selection, and thus are continuously subject to the dynamic environments that characterize every fragment of their range. Rather than attempting to simply preserve the population structure that exists in the Basin, chinook and steelhead diversity must be leveraged to expand their range to new or restored habitat that can accommodate genetic adaptation. Artificial propagation can have a critical role in this process, and the emphasis must be placed on promoting the ability for anadromous salmonids to respond to change by assuring that the genetic diversity to facilitate such responses is present. Changes that can occur in fish over relatively few generations of artificial propagation underscore their ability to respond to major environmental alterations, and is evidence that these species have the ability to adapt to new conditions in natural river systems through both acquired and genetic mechanisms.

The key to recovery of Columbia Basin chinook and steelhead is to understand the processes of adaptive evolution that create different genotypes, and the dynamic equilibrium between genotypes and phenotypic expressions under environmental stochasticity/heterogeneity. The controlling variables of the environmental templates in life history strategy of anadromous salmonids must be recognized and accommodated in recovery and management programs. By using the appropriate genetic base to strengthen diminishing runs and to establish new runs, evolution can be put on a manageable timeframe to recover and expand the chinook and steelhead resources of the Columbia Basin.

The following recommendations address the critical elements in the application of population structure for the recovery, management, and expansion of chinook and steelhead in the Columbia Basin.

1. Consideration must be given to functional genetic factors and life history in addition to population genetics as components of population structure for management and recovery of salmon and steelhead.
2. It is essential that the functional genetic diversity present within the existing populations of chinook and steelhead be maintained. The genetic diversity represented in the Basin will enhance the continued evolution of existing populations, and the resource from which adaptive combinations can be formed to reinforce stocks and establish new populations.

3. Chinook and steelhead runs in the Columbia River should be managed as a continuum of returning locally adapted subunits destined for different areas with stream specific requirements, rather than simply three distinct runs of spring, summer, and fall chinook, or two runs of summer and winter steelhead.
4. Population structure within the Basin is the key for successfully managing enhancement, supplementation, and recovery programs. Management strategies for distinct population segments should match temporal and spatial migratory patterns consistent with the destination to facilitate the most effective response with those measures.
5. The important role of temperature in adaptive evolution of chinook and steelhead, and thus its foundation in life history and population structure, needs to be recognized as a critical element in the baseline around which management and recovery should take place.
6. Adaptive response to temperature profiles by chinook salmon and steelhead for incubation needs is considered under intense selection pressures that result in changes over relatively short timeframes. Consequently, because of severe losses of progeny that would take place when emerging fry are out of synchrony with the environmental template, introductions to replace extirpated populations must be within the approximate temporal range that is associated with the system. It is necessary, therefore, to acquire detailed information on temperature profiles of incubation reaches to establish the parameters required for rehabilitation programs.
7. Success of native populations of chinook and steelhead is critically linked to the synchrony of emergence with the environmental parameters defining their habitat. Therefore, supplementation and enhancement of existing populations should involve only the use of native stock to maintain the population structure supporting sustained natural production.
8. Ocean-type and stream-type chinook life history forms, and ocean-maturing and stream-maturing steelhead, reflect evolutionary responses to the environmental parameters of their respective rearing habitats. Stocks used for supplementation and reintroduction must be able to conform to the local rearing temperatures to sustain those life history forms.
9. The emphasis that must be given to enhancement, supplementation, and recovery programs is that the "unit" of conservation is the fish within its habitat, not simply the stock or the habitat. Delineating a population as being a genetically distinct population segment will only be effective in sustaining that stock if the environmental template responsible for their distinctness is also preserved or recreated.
10. Recovery of natural production and diversity in population structure will not occur without available habitat. It is necessary, therefore, to put emphasis on making better use of the habitat remaining and on creating appropriate habitat to replace that which has been lost.
11. Columbia River reservoirs should be considered as alternative habitat in which new life history strategies can evolve. If such environments can be improved for production of these species, steps should be taken to make the reservoirs more conducive as rearing systems for anadromous salmonid fingerlings before they emigrate.
12. Escapement levels of returning chinook and steelhead should be guided by a new paradigm of Biological Sustained Yield rather than attempts to maximize (MSY) or optimize (OSY) harvest. Under the BSY concept, emphasis is placed on the biological needs of the population where greater escapement is not viewed as waste, but rather a tool to encourage intraspecific competition, hone fitness, and expand the range.

13. It is important to consider higher escapements of spawners to assist nutrient recruitment and increase habitat productivity to more effectively address the needs of the ecosystem.
14. To provide appropriate seed reservoirs for reintroduction of extirpated runs, phylogenetic core populations must be identified from which genetic material can be secured to reinforce depressed populations, and from which new populations can be established.
15. Management programs need to consider genetic intervention as a basic method of maintaining stock diversity when justified. Monitoring stock diversity and introducing genetic elements to maintain appropriate genetic variability will assist in retaining long-term fitness and alleviate some of the risks of small populations from drift and inbreeding.
16. New runs can be developed in restored habitat, but it must be recognized that donor stock most likely will not be well adapted to those environments. Stock integration (hybridization) among candidate stocks for use in establishing maximum variability on which natural selection can work needs to be included in the recovery tool chest to assist in species rehabilitation. Use of such strategies needs to be carefully considered and will succeed only if natural selection is allowed to work its course without repetitious introductions of introduced broods.
17. Germ plasm repositories need to be developed to preserve genetic diversity for later application in stock strengthening and maintenance of diversity. Application of stored germ plasm will help maintain stock specificity and reinforce diversity among small populations.
18. Natural-producing chinook and steelhead will not sustain extensive sport and commercial fisheries in the Columbia River. To develop such fisheries, it will be necessary to continue and to improve artificial propagation. Such measures need to redefine appropriate technology to assure that hatchery fish are phenotypically matched with the local receiving environment.
19. It is important to establish both management units and conservation units in Columbia River salmon and steelhead recovery. Conservation units are meant to address recovery, maintenance, and the proper use of population segments that are at risk of dropping below a sustaining threshold. Conservation actions taken should focus recovery measures to facilitate natural production. Management units are meant for harvest purposes, and they can include contributions from conservation units if those populations can sustain commercial and sporting activity. Management units will include the use of production hatcheries for the purpose of harvest augmentation, but management protocols should not deviate from the population structure within the geographical area, and fish produced should conform to the appropriate genetic composition and fidelity of stocks representing the unit.
20. Hatchery programs must target local stock as the source of genes for recovery and enhancement. With this prerequisite, second generation hatchery fish originating from local stock and reproducing in the wild will be most similar to wild natural stock.
21. Hatchery fish need to be recognized for their value to help preserve the genetic diversity and population structure of Columbia Basin populations.
22. Hatcheries can have a much greater role in rehabilitation if they are operated with breeding protocols to sustain stock discreteness.
23. Hatchery fish developed from local stock and contributing to natural production in the local population should be considered a component of the local stock structure.

Hatchery contributions under such a scenario would be included in the management of the local population, and should be considered integral to the legacy of the respective populations.

24. It is important to recognize that hatchery fish have integrated with the population structure of chinook and steelhead in the Columbia River. Where natural populations are small, hatchery contributions may be the primary source of genetic diversity and thus may better represent the genetic elements of historic populations.
25. In using hatchery fish to reestablish natural-producing runs, protocols must be followed to initially maximize diversity around the appropriate life history requirements for the environmental template, and thereafter to concentrate only on returning fish for supplemental assistance to minimize interference with the natural progress of selection in establishing runs.
26. In hatchery programs, the continuous introduction of large numbers of fish with differing heritable life history characteristics must be recognized as a major problem in the use of hatchery fish to meet management objectives. Such practices prevent the maintenance of local stock structure and retard fitness.
27. Steelhead kelts need to be recognized as an important potential resource for increased natural production. These fish successfully returned and spawned, and if measures are taken to assist in recovery from post-spawning condition, they will facilitate natural production in their respective stream systems and help maintain genetic diversity within brood years.
28. Projects to promote the recovery of salmon and steelhead natural production in new habitat can use egg plants of the appropriate stock as a component in the recovery tool chest. Egg plants can reduce the cost of recovery programs, because no costs associated with hatchery operations are required. Egg plants facilitate natural selection on emergence timing, assure homestream odor imprinting as the ultimate home recognition cue, and promote more rapid development of synchrony with the environmental template.

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