

[U.S. Dept Commerce/NOAA/NMFS/NWFSC/Publications](#)

NOAA-NMFS-NWFSC TM-35: Chinook Status Review

[Go back to previous section](#)

Chinook Salmon Life History and Ecology

Juvenile Life History

The most significant process in the juvenile life history of chinook salmon is smoltification, the physiological and morphological transition from a freshwater to marine existence. The emigration from river to ocean is thought to have evolved as a consequence of differences in food resources and survival probabilities in the two environments (Gross 1987). Salmon juvenile life-history patterns are usually deduced by examining the developmental pattern of circuli on juvenile and adult fish scales (Gilbert 1912, Rich 1920a, Koo and Isarnkura 1967). Within the ocean-type (subyearling) and stream-type (yearling) migrant designations, several subtypes have been described (Gilbert 1912, Reimers 1973, Schluchter and Lichatowich 1977, Fraser et al. 1982). Ocean-type juveniles enter saltwater during one of three distinct phases. "Immediate" fry migrate to the ocean soon after yolk resorption at 30-45 mm in length (Lister et al. 1971, Healey 1991). In most river systems, however, fry migrants, which migrate at 60-150 days post-hatching, and fingerling migrants, which migrate in the late summer or autumn of their first year, represent the majority of ocean-type emigrants. When environmental conditions are not conducive to subyearling emigration, ocean-type chinook salmon may remain in freshwater for their entire first year. Stream-type chinook salmon migrate during their second or, more rarely, their third spring. Under natural conditions stream-type chinook salmon appear to be unable to smolt as subyearlings. The underlying biological bases for differences in juvenile life history appear to be both environmental and genetic (Randall et al. 1987). Distance of migration to the marine environment, stream stability, stream flow and temperature regimes, stream and estuary productivity, and general weather regimes have been implicated in the evolution and expression of specific emigration timing.

The success of different juvenile life-history strategies is linked to the coordinated expression of other traits. Gilbert (1912) noted that ocean-type fish exhibited a faster growth rate relative to stream-type fish. The growth difference between ocean- and stream-type juveniles has also been observed by other researchers (Carl and Healey 1984, Cheng et al. 1987, Taylor 1990a). Some of this difference may be related to differences in rearing environment, although under standardized conditions there was still a significant growth difference between ocean- and stream-type juveniles (Taylor 1990b). Clarke et al. (1992) demonstrated that the growth of stream-type juveniles was strongly associated with photoperiod, while ocean-type juvenile growth appeared to be independent of photoperiod. Juvenile life history appears to be a heritable trait. Hybridization experiments indicated that the stream-type smoltification and growth pattern are recessive relative to the ocean-type pattern (Clarke et al. 1992). Juvenile stream-type chinook salmon have also been shown to be more aggressive than ocean types. This may be a territorial defense mechanism for resource limited freshwater systems (Taylor and Larkin 1986, Taylor 1988, Taylor 1990b). Morphometric differences, such as larger and more colorful fins, observed in some stream-type populations may be related to social displays that maintain territories (Carl and Healey 1984, Taylor and Larkin 1986). Thus, the timing of parr-smolt transition appears to be associated with the expression of a number of other traits in order to maximize individual survival.

Juvenile stream- and ocean-type chinook salmon have adapted to different ecological niches. Ocean-type chinook salmon tend to utilize estuaries and coastal areas more extensively for juvenile rearing. In general, the younger (smaller) juveniles are at the time of emigrating to the estuary, the longer they

reside there (Kjelson et al. 1982, Levy and Northcote 1982, Healey 1991). There is also an apparent positive relationship between rivers with large estuary systems and the number of fry migrants (Fraser et al. 1982). Brackish water areas in estuaries also moderate physiological stress during parr-smolt transition. The development of the ocean-type life-history strategy may have been a response to the limited carrying capacity of smaller stream systems and glacially scoured, unproductive watersheds, or a means of avoiding the impact of seasonal floods in the lower portion of many watersheds (Miller and Brannon 1982). In the Sacramento River and coastal California rivers, subyearling emigration is related to the avoidance of high summer water temperatures (Calkins et al. 1940, Gard 1995). Ocean-type chinook salmon may also use seasonal flood cycles as a cue to volitionally begin downstream emigration (Healey 1991). Migratory behavior in ocean-type chinook salmon juveniles is also positively correlated with water flow (Taylor 1990a).

Stream-type juveniles are much more dependent on freshwater stream ecosystems because of their extended residence in these areas. A stream-type life history may be adapted to those watersheds, or parts of watersheds, that are more consistently productive and less susceptible to dramatic changes in water flow, or which have environmental conditions that would severely limit the success of subyearling smolts (Miller and Brannon 1982, Healey 1991). Stream-type chinook salmon juveniles exhibit downstream dispersal and utilize a variety of habitats during their freshwater residence. This dispersal appears to be related to resource allocation and migration to overwintering habitat and is not associated with saltwater osmoregulatory competence (Hillman et al. 1987, Levings and Lauzier 1989, Taylor 1990a, Healey 1991). For example, the migration of subyearling juvenile spring-run chinook salmon in the Wenatchee River (a stream-type population) may be due to competition with hatchery releases or the interspecific interaction between steelhead and chinook salmon juveniles (Hillman and Chapman 1989). There was a tendency for juveniles to move into deeper water, farther from the bank shelter, as they grew older. If suitable overwintering habitat, such as large cobble, is not available then the fish will tend to migrate downstream (Bjornn 1971, Bustard and Narver 1975, Hillman et al. 1987). At the time of saltwater entry, stream-type (yearling) smolts are much larger, averaging 73-134 mm depending on the river system, than their ocean-type (subyearling) counterparts and are therefore able to move offshore relatively quickly (Healey 1991).

The variability in the time of emigration to the marine environment among stocks of chinook salmon, combined with geographic and yearly differences in freshwater productivity, make comparisons of the sizes of smolts among different stocks difficult. Size data may be confounded by the presence within a watershed of multiple native stocks that exhibit different life-history strategies. The possible inclusion of hatchery-reared fish in smolt samples is a further confounding factor. Smolt size, therefore, was not emphasized among the life-history traits used to determine ESU boundaries.

Ocean- and stream-type chinook salmon populations exhibit a geographical distribution that further underscores the ecological adaptation of these two races. Chinook salmon stocks in Asia, Alaska, and Canada north of the 55th parallel, and in the headwaters (upper elevations) of the Fraser River and the Columbia River Basins, exhibit a stream-type life history: emigrating to sea in their second or third spring and generally entering freshwater several months prior to spawning (Healey 1991). A notable exception to this trend includes populations in the Situk River and several Yakutat foreland River Basins in Alaska, which emigrate primarily as subyearlings (Johnson et al 1992a, ADFG 1997). Ocean-type chinook salmon are predominant in coastal regions south of 55N, in Puget Sound, in the lower reaches of the Fraser and Columbia Rivers, and in California's Central Valley (Gilbert 1912, Rich 1920a, Healey 1983, Taylor 1990b). One analysis of principal components influencing life-history type (distance to the sea, daylight hours during the growing season and air temperature) accounted for 96% of the total observed variation in age at smoltification (Taylor 1990a). However, the abrupt change between stream- and ocean-type life histories at 55N occurs in the absence of a similarly abrupt change in environmental conditions (Healey 1983) and may be related to patterns of colonization following deglaciation (Taylor

1990b).

Stream-type life histories are most commonly associated with early timed runs of fish (Rich 1920a, Healey 1983). This is partially because the headwater regions south of 55N are only accessible during peak spring stream flows, additionally, temperatures in more northerly streams and headwater areas are much colder than in other areas and require early deposition of eggs to allow for proper developmental timing. Overall, juvenile smoltification strategies are one expression of a more complicated, genetically based life-history adaptation to ecological conditions (Taylor 1990a, Clarke et al. 1992). Differences in juvenile life-history strategies among chinook salmon stocks were a useful component in helping to determine boundaries between ESUs.

Ocean Distribution

Coastwide, chinook salmon remain at sea from 1 to 6 years (more commonly 2 to 4 years), with the exception of a small proportion of yearling males which mature in freshwater or return after 2 or 3 months in salt water (Rutter 1904, Gilbert 1912, Rich 1920a, Mullan et al. 1992). Differences in the ocean distribution of specific stocks may be indicative of resource partitioning and may be important to the success of the species as a whole. Current migratory patterns may have evolved as a balance between the relative benefits of accessing specific feeding grounds and the energy expenditure necessary to reach them. If the migratory pattern for each population is, in part, genetically based, then the efficiency with which subsequent generations reach and return from their traditional feeding grounds will be increased.

The vast majority of CWT-marked chinook salmon come from hatchery populations; therefore, the migratory routes of many wild fish stocks must be inferred from their corresponding hatchery populations. Furthermore, CWT ocean recoveries are obtained through commercial and sport fishery samples; therefore, the relative intensity of each fishery can bias the interpretation of the oceanic distribution of each stock. Comparisons of oceanic distributions across years can also be influenced by changes in fishing regulations and ocean conditions (such as during an El Niño). Confounding effects were considered in the interpretation of CWT recoveries, and small differences in CWT ocean recoveries between stocks were not considered as a distinguishing factor.

The genetic basis for ocean distribution has been supported by a number of different studies involving the monitoring of CWT-marked fish caught in the ocean fisheries. The relative influence of genetic vs. environmental factors on migratory pattern can be deduced from transplantation studies. Transplanted Elwha River chinook salmon continued to follow their traditional migratory pattern after being reared and released at a site 150 km to the east, except that the actual route had also been shifted 150 km eastward (Brannon and Hershberger 1984). Additionally, hybrids between the Elwha River and Green River (University of Washington) stocks exhibited an intermediate ocean migration pattern. Transplantation studies with coastal stocks in Oregon have yielded similar results (Nicholas and Hankin 1988). Chinook salmon whose natal stream lies south of Cape Blanco tend to migrate to the south, while those to the north of Cape Blanco tend to migrate in a northerly direction. Transplants of south migrating stocks to release sites north of Cape Blanco do not alter the basic southerly direction of ocean migration (Nicholas and Hankin 1988). Recoveries of CWT-marked fish from ocean fisheries indicate that fish stocks follow predictable ocean migration patterns, and that these are based on "ancestral" feeding routes (Brannon and Setter 1987).

Ocean- and stream-type chinook salmon are recovered differentially in coastal and mid-ocean fisheries, indicating divergent migratory routes (Healey 1983, 1991). Ocean-type chinook salmon tend to migrate along the coast, while stream-type chinook salmon are found far from the coast in the central North Pacific (Healey 1983, 1991; Myers et al. 1984). Studies of CWT-marked prerecruit (<71 cm) fish in the

marine fisheries off of Southeastern Alaska indicated that differences in migration speed, timing, and growth were related to the life history, age, and general geographic origin of the stocks (Orsi and Jaenicke 1996). The causal basis for this difference in migration pattern is unknown, but may be related to poor coastal feeding conditions during past glacial events for the more northerly (stream-type) populations.

The freshwater component of the adult returning migratory process is also under a significant genetic influence. In one experiment, "upriver bright" chinook salmon were captured, spawned, and the subsequent progeny reared and released from a downriver site (McIsaac and Quinn 1988). A significant fraction of the returning adults from the "upriver bright" progeny group bypassed their rearing site and returned to their "traditional" spawning ground 370 km further upriver. The high degree of fidelity with which chinook salmon return to their natal stream has been shown in a number of studies (Rich and Holmes 1928, Quinn and Fresh 1984, McIsaac and Quinn 1988). Returning to the "home stream" provides a mechanism for local adaptation and reproductive isolation.

Ocean migration patterns represent an important form of resource partitioning and are important to the evolutionary success of the species; therefore, differences in ocean migratory pattern were an important consideration in the determination of ESU boundaries.

Size and Age at Maturation

The age at which chinook salmon begin sexual maturation and undertake their homeward migration is dependent on a number of different factors. Age, body size and composition, and fecundity traits in salmonids have all been shown to be partially under genetic control (Ricker 1972) and genetically and phenotypically correlated (Gall 1975). Because of genetic correlations between these traits, natural selection on one or more of these traits may affect the expression of other traits. The confounding effects of correlated traits make it difficult to identify specific selective (ecologically important) criteria that influence size and age at maturity.

Adult body size in chinook salmon does not appear to be strongly correlated to latitude; however, there appears to be a slight negative correlation between adult body size and length of migration (Roni and Quinn 1995). The relationship between size and length of migration may also reflect the earlier timing of river entry and the cessation of feeding for chinook salmon stocks that migrate to the upper reaches of river systems. Juvenile life history has an apparent influence on the size of returning spawners. Ocean-type fish that have been at sea from 1 to 2 years are generally larger than their respective stream-type counterparts (Roni and Quinn 1995). This may reflect the more productive feeding conditions that exist in the marine environment and/or the additional 3 to 5 months that ocean-type fish remain in the marine environment before beginning their spawning migration.

Body size, which is correlated with age, may be an important factor in migration and redd construction success. Beacham and Murray (1987) reported a correlation between body size and large (< 100 km² watershed area) and small river size in chum salmon (*O. keta*). Roni and Quinn (1995) reported that under high density conditions on the spawning ground, natural selection may produce stocks with exceptionally large-sized returning adults. Spawning aggregations may select for large body size in males due to competition between males for females and the "attractiveness" of large males to females (Foote 1990). Large body size may be advantageous for females because of the success of larger fish in establishing, digging, and protecting their redds (Healey and Heard 1984). Competition for redd sites, stream flow, and gravel conditions are also thought to influence adult size in coho salmon (Holtby and Healey 1986).

An alternative strategy for chinook salmon is for males to mature at an early age. "Mini-jack" or "jack" chinook salmon males mature in their first or second ocean years, respectively. Early maturation among male chinook salmon was first described by Rutter (1904). Early maturation offers a reduced risk of mortality, but younger (smaller) males may be at a competitive disadvantage in securing a mate (Gross 1987). The incidence of jack males has underlying genetic determinants and appears to be, in part, a response to favorable growing conditions. A variant of this life-history strategy is maturation without emigrating to the ocean. Rich (1920a) estimated that 10-12% of the juvenile males on the McCloud River were maturing without leaving the river. Mullan et al. (1992) found that early maturing resident males were common in both hatchery and wild populations in the Wenatchee River. Non-migrating mature males have also been observed in the Snake River Basin (Gebhards 1960, Burck 1967, Sankovich and Keefe 1996), Methow and Yakima Rivers (Hubble⁵), and the Deschutes River. Resident males have been observed among some stream- and ocean-type chinook salmon stocks in the Fraser River above Hell's Gate, which would have historically been a potential barrier to small migrating early maturing males, but not among lower river or coastal populations (Taylor 1989, Foote et al. 1991). The location and physical characteristics of each river may determine the expression of this life-history trait. It is unlikely that small jack males would be physically able to undertake the arduous return migration to many upriver areas (Mullan et al. 1992) or that sufficient time exists for the completion of the smolt emigration and return migration. Nonmigrating early maturing males may have a good chance of mating success, especially during poor return years when there may be a shortage of large males on the spawning grounds. The modification of smoltification, a major physiological process, to produce early maturing males in a population is indicative of the importance of this life-history trait to the reproductive success of specific populations.

The heritability of body size and age has been more extensively studied in chinook salmon than have other traits. Crosses between different aged parents have demonstrated that the ages of maturity for parents and progeny were strongly correlated (Ellis and Noble 1961, Donaldson and Bonham 1970, Hershberger and Iwamoto 1984, Withler et al. 1987, Hankin et al. 1993). The expression of early maturation in chinook salmon was found to have a significant genetic component; moreover, different stocks exhibited different levels of early maturation in response to environmental changes (Heath et al. 1994). The positive response of chinook salmon to selective breeding experiments is indicative of a significant genetic component to body size (Donaldson and Menasveta 1961). Chinook salmon stocks exhibit considerable variability in size and age of maturation, and at least some portion of this variation is genetically determined.

From an evolutionary standpoint, the potential increases in size, fecundity, and egg size gained from remaining on the marine feeding grounds an additional year must be weighed against the chances of mortality during that year (Healey and Heard 1984, Healey 1986). The specific conditions that exist in each river must also influence, in part, the expression of these characteristics. The size and age of spawning chinook salmon in any given population may have a significant impact on their survival, and trends in size and age were utilized in determining ESU boundaries. However, the large environmental influence (on a regional and annual basis) on chinook salmon size and age, as well as possible biases resulting from different fishery harvest techniques and the inclusion of hatchery reared fish, would suggest that available size and age data be used with caution.

Run Timing

Early researchers recorded the existence of different temporal "runs" or modes in the migration of chinook salmon from the ocean to freshwater. Two major influxes of chinook salmon were observed returning to the Sacramento-San Joaquin River system, although "...there is no definite distinction between spring and fall runs; there is no time during the summer when there are no salmon

running" (Rutter 1904, p. 122). It was also reported that spring-run fish tended to migrate to the upriver portions of the Sacramento River and spawn earlier than the fall run, which spawned in the lower regions of tributaries and in mainstem river areas. A similar distinction was made between spring, summer, and fall or "snow" salmon runs in the Klamath River (Snyder 1931). The underlying genetic influence on run timing was initially demonstrated by Rich and Holmes (1928), when spring-run chinook salmon from the MacKenzie River were reared, marked, and released from a predominantly fall-run watershed. The transplanted chinook salmon displayed no apparent alteration in their normal time of return or spawning, although there was an increase in straying. Subsequent stock transplantations have further substantiated the heritable nature of run timing. Heritability estimates for return timing among early- and late-returning pink salmon (*Oncorhynchus gorbuscha*) runs in Alaska were 0.4 and 0.2 for females and males, respectively (Gharrett and Smoker 1993).

Freshwater entry and spawning timing are generally thought to be related to local temperature and water flow regimes (Miller and Brannon 1982). Temperature has a direct effect on the development rate of salmonids (Alderdice and Velsen 1978). Only one run timing for chinook salmon is found in most rivers in Alaska and northern British Columbia, where summers are short and water temperatures cold (Burger et al. 1985). The Kenai River in Alaska is an exception to this trend, having mid-June and mid-July runs that ultimately spawn in areas with distinct thermal regimes (Burger et al. 1985). Asian rivers are thought to contain only one run of chinook salmon, with the possible exception of the Kamchatka and Bol'shaya Rivers (Vronskiy 1972, Smirnov 1975). Among stream-type stocks, the King Salmon River in Alaska differs from the general trend in that adults return in a relatively mature condition and spawn in the lower river, extending down to the intertidal area (Kissner 1985, ADFG 1997). The majority of multiple run rivers are found south from the Bella Coola and Fraser Rivers.

Runs are designated on the basis of adult migration timing; however, distinct runs also differ in the degree of maturation at the time of river entry, thermal regime and flow characteristics of their spawning site, and actual time of spawning. Early, spring-run chinook salmon tend to enter freshwater as immature or "bright" fish, migrate far upriver, and finally spawn in the late summer and early autumn. Late, fall-run chinook salmon enter freshwater at an advanced stage of maturity, move rapidly to their spawning areas on the mainstem or lower tributaries of the rivers, and spawn within a few days or weeks of freshwater entry (Fulton 1968, Healey 1991). Summer-run fish show intermediate characteristics of spring and fall runs, spawning in large and medium-sized tributaries, and not showing the extensive delay in maturation exhibited by spring-run chinook salmon (Fulton 1968). Winter-run chinook salmon (which presently exist only in the Sacramento River) begin their freshwater migration at an immature stage and travel to the upper portions of the watershed to spawn in the spring. All stocks, and especially those that migrate into freshwater well in advance of spawning, utilize resting pools. These pools provide an energetic refuge from river currents, a thermal refuge from high summer and autumn temperatures, and a refuge from potential predators (Berman and Quinn 1991, Hockersmith et al. 1994). Furthermore, the utilization of resting pools may maximize the success of the spawning migration through decreases in metabolic rate and the potential reduction in susceptibility to pathogens (Bouck et al. 1975, Berman and Quinn 1991). In the Stilliguamish River, there was a high correlation between the location of pools and redds, suggesting that the pool abundance may limit the amount of spawning habitat available (PSSSRG 1997).

Run timing is also, in part, a response to streamflow characteristics. Rivers such as the Klickitat or Willamette Rivers historically had waterfalls which blocked upstream migration except during high spring flows (WDF et al. 1993). Low river flows on the south Oregon coast during the summer result in barrier sandbars which block migration (Kostow 1995). The timing of migration and, ultimately, spawning must also be cued to the local thermal regime. Egg deposition must be timed to ensure that fry emerge during the following spring at a time when the river or estuary productivity is sufficient for juvenile survival and growth. The strong association between run timing and ecological conditions made

this trait useful in considering potential ESU boundaries.

Straying

The high degree of fidelity with which chinook salmon return to their natal stream has been shown in a number of studies (Rich and Holmes 1928, Quinn and Fresh 1984, McIsaac and Quinn 1988). Returning to one's natal stream may have evolved as a method of ensuring an adequate incubation and rearing habitat. It also provides a mechanism for reproductive isolation and local adaptation. Conversely, returning to a stream other than that of one's origin is important in colonizing new areas and responding to unfavorable or perturbed conditions at the natal stream (Quinn 1993). High rates of straying by returning Umatilla River fall chinook salmon (an introduced upriver bright stock) into the Snake River in 1987-89 were apparently related to poor acclimation, high water temperatures, and lack of water in the Umatilla River (Waples et al. 1991b). Straying coho salmon (*O. kisutch*) and sockeye salmon have rapidly colonized newly deglaciated habitat (Milner and Bailey 1989), and summer-run chinook salmon may have recolonized the Okanogan River following the cessation of trapping operations at Rock Island Dam, which blocked entry from 1939-43 (Waknitz et al. 1995). The degree of straying in wild populations determines the extent of reproductive isolation and the potential for the formation of ESUs.

Available information on straying rates primarily involves hatchery-reared, transplanted, or transported fish. Rich and Holmes (1928), in one of the earliest studies of homing, released marked chinook salmon juveniles from a number of hatcheries along the lower Columbia River. Of the 104 chinook salmon that were recovered in spawning areas or at hatchery racks, only 5 (4.8 %) had strayed to areas other than their release sites (Rich and Holmes 1928). Quinn and Fresh (1984) reported that only 1.4% of the returning spring-run chinook salmon from the Cowlitz River Hatchery were recovered outside of their natal watershed, and it was suggested that straying was more frequent in older fish and in years when the run-size was low. Olfactory cues provided by conspecifics on spawning grounds, especially large aggregations, may be a powerful attractant to returning salmon (Duker 1981). If these spawning aggregations are an attractant, it may explain the negative correlation between run-size and straying as well as explaining the observed straying of naturally-produced salmon into hatcheries. Chapman et al. (1991, 1994) suggested that straying is more common among fall-run fish than among spring-run fish. Quinn et al. (1991) found that straying rates differed considerably (10-27.5%) between hatcheries releasing fall chinook salmon on the lower Columbia River.

The adult returning migratory process has been shown to be under a significant genetic influence. In one experiment, "upriver bright" chinook salmon were captured, spawned, and the subsequent progeny reared and released from a downriver site (McIsaac and Quinn 1988). A significant fraction of the returning adults from the upriver bright progeny group bypassed their rearing site and returned to their "traditional" spawning ground 370 km further upriver.

Hatchery rearing and release procedures may increase the rate of straying. Wild chinook salmon had significantly lower straying rates than did hatchery-reared fish from the Lewis River (McIsaac 1990). Releasing fish even a short distance from the hatchery can dramatically increase the straying rate (Quinn 1993, Heard 1996). Straying rates as high as 86% resulted from the long-distance transportation and release of fall chinook salmon in the Sacramento River (Cramer 1989). Unfavorable conditions (high water temperature and low flow) at hatchery return facilities may further increase straying rates (Quinn 1993). The use of hatchery stocks founded from a composite of wild stocks (e.g., upriver bright fall chinook salmon) may increase straying if the genetic component to homing is more important than the olfactory (learned) component. Chapman et al. (1994) indicated that Columbia River fall chinook salmon upriver bright hatchery stocks did have a relatively high straying rate. However, Pascual and Quinn (1994) found similar homing success rates for local and introduced stocks of chinook salmon

released in the Columbia River.

Any interpretation of straying rates should consider the way in which strays were enumerated. Chapman et al. (1991) made a distinction between "legitimate" strays and "wanderers," those fish that enter non-native streams as a part of their homing search or as a temporary refuge from unfavorable river conditions. Wanderers will normally retreat from these non-native streams and continue their return migration; however, where weirs or hatchery traps are present, wanderers will be unable to return and are often considered strays. Additionally, straying rates can be influenced by the effort placed on surveying sites other than the release site.

The use of cut-off dates by hatcheries to separate run-times can result in "temporal" straying. Cope and Slater (1957) found that 16% of the fish returning as "spring-run" adults to Coleman NFH were produced from fall-run parents, and 19% of the returning "fall-run" adults came from spring-run parents. The use of fixed return or spawning dates to distinguish runs at adult collection facilities may have resulted in the introgression of previously distinct stocks (Mullan 1987, WDF et al. 1993, Waknitz et al. 1995).

Straying by hatchery fish, especially those from non-native hatchery stocks, increases the potential for interbreeding and genetic homogenization. This may result in the loss of regionally distinct life-history characteristics.

Fecundity and Egg Size

Fecundity and egg size differences between stocks of salmon occur on a geographic basis. In salmon, fecundity tends to increase while egg size decreases with latitude (Healey and Heard 1984, Kaev and Kaeva 1987, Fleming and Gross 1990). Variation between and within regions can be considerable.

The anadromous life history of salmon is thought to be a response to the relatively poor productivity of glacially influenced or unstable freshwater environments relative to the nearby marine habitat (Neave 1958, Miller and Brannon 1982). In order to maximize the success of their emigration to saltwater, salmon juveniles must obtain a relatively large size in productivity-limited freshwater environments. One strategy for accomplishing this is through the production of large eggs and thereby large embryos (Taylor 1991, Kreeger 1995). Larger eggs produce larger fry (Fowler 1972), which may be more successful at migrating to saltwater than smaller fry (Kreeger 1995). Ocean-type chinook salmon stocks in British Columbia were reported to have larger eggs than stream-type stocks (Lister 1990). Rich (1920b) found that some chinook salmon returning to coastal streams in Oregon and Washington had larger eggs than fish returning to the Columbia River. In general, Smironov (1975) suggested that latitudinal differences existed in egg size, with southern stocks having larger eggs. Furthermore, he speculated that this was because embryonic development at higher temperatures is less efficient; southern stocks need more energy stores (larger eggs) to complete development. Alternatively, this trend may be related to the need for more southerly, predominantly ocean-type, chinook salmon to produce larger-sized fry for migration to estuary areas. In general, stream-type stocks of chinook salmon have smaller eggs than ocean-type stocks. However, there is no apparent latitudinal cline in egg size among stream-type nor ocean-type stocks ([Appendix C](#)).

Older (larger) year classes of salmon tend to produce larger sized eggs but not proportionately larger numbers of eggs than their younger (smaller) counterparts; this may be a life-history strategy to improve the survival of individual progeny rather than producing more of them (Gray 1965, Iwamoto 1982, Beacham and Murray 1985, Healey 1986, Nicholas and Hankin 1988). Factors affecting egg size in chinook salmon appear to be operating on a between- and within-population basis. Variability in egg

size within populations appears to be most directly related to fish size and, to a lesser extent, age (Healey and Heard 1984, Hankin and McKelvey 1985), whereas between-population differences may represent an adaptation to regional environmental and geographic conditions.

Physiological and ecological factors have been identified that may limit the potential minimum and maximum egg sizes, 0.12 and 0.47 g, respectively (Quinn and Bloomberg 1992). The physical limitations of large eggs in absorbing oxygen due to a reduced surface area-to-volume ratio and the generally high physiological oxygen demands of salmonids may limit the maximum size of chinook salmon eggs. Stream flow, gravel quality, and silt load all significantly influence the survival of developing chinook salmon eggs. Therefore, behavioral traits such as spawning site selection would need to be correlated with physical fecundity traits. Healey (1991) showed that suboptimum habitat conditions delay or discourage spawning at a specific site.

Variation in fecundity and egg size among different stocks of chinook salmon appears to be related to geography and life-history strategy. Chinook salmon females sampled from the Sacramento River had 68% more eggs than females from the Klamath River, after adjusting for differences in body size (Snyder 1931, Healey and Heard 1984). Fecundity is related to body size, although this relationship is also dependent on a number of other factors--age, migration distance, latitude--and varies between stocks (Healey and Heard 1984, Kaev and Kaeva 1987, Fleming and Gross 1990). Galbreath and Ridenhour (1964) found that linear length-fecundity regressions for the Columbia River chinook salmon stocks were not significantly different when compared on a seasonal (monthly) run timing, total age, or smolt age basis; however, differences in body size and a small sample size may have obscured racial differences in fecundity. A further complication in the analysis of fecundity traits is the difference in body weight devoted to gonadal tissue in coastal and inland populations. Populations which undertake extended migrations may not be able to devote the same percentage of body weight toward gonad (especially ovary) development (Lister 1990). Linley (1993) found a significant negative correlation for adult sockeye salmon between the percentage of body weight devoted to gonads and the length and duration of the freshwater migration. Ivankov (1983) determined that differences in the fecundity of masu salmon (*O. masu*) females within and among rivers were correlated with juvenile growth rate and the rate of gonadal development prior to saltwater emigration, although he did not specifically evaluate the relative contributions of genetic and environmental effects.

Correlations between fecundity and body size and age, in addition to environmental fluctuations over several years, complicate the interpretation of fecundity differences. Furthermore, the majority of fecundity information comes from hatchery populations. Differences in selection on fecundity and egg size traits under hatchery conditions relative to the natural environment may limit the representative value of hatchery populations for their wild counterparts (Fleming and Gross 1990).

Other Life-History Traits

Information concerning the variability, adaptiveness, and heritability of other life-history traits in salmon is extremely limited. Genetically based differences in the rate of Pacific salmon embryonic and alevin development between run times in the same river (Tallman 1986), and between rivers (Iwamoto 1982, Beacham and Murray 1987, 1989) represent important adaptations to ensure emergence occurs at a time for optimal survival. The heritability estimates for embryonic development to hatch in chinook salmon range from 0.25 to 0.40 (Hickey 1983). Smirnov (1975) suggested significant differences in the embryonic development exist between Asian and North American stocks of chinook salmon.

Pathogen resistance is another locally adapted trait. Chinook salmon from the Columbia River drainage exhibited reduced susceptibility to *Ceratomyxa shasta*, an endemic pathogen, relative to stocks from

coastal rivers where the disease is not known to occur (Zinn et al. 1977). Differences in susceptibility to the infectious hematopoietic necrosis virus (IHNV) were detected between Alaskan and Columbia River stocks of chinook salmon (Wertheimer and Winton 1982). Variability in temperature tolerance between populations is also probably due to adaptation to local conditions; however, information on the genetic basis of this trait is lacking (Levings 1993).

[Go to next section](#)

[Table of Contents](#)