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Geographic Variation in Size and Age of North American Chinook Salmon

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Abstract.-Patterns of mean length and length at age were characterized and compared for 108 populations of chinook salmon Oncorhynchus tshawytscha located between 42 and 65° north latitude in western North America. Mean overall fish length in populations ranged over 45.5 cm for adult males and 28.8 cm for females. Mean length at a given marine age and freshwater life history type varied by up to 26 cm. Mean length at marine age did not differ between stream-type and ocean-type life histories, which indicates that differences in size and date of ocean entry had little effect on final size. Hatchery-reared fish were significantly smaller at a given age than naturally produced fish. Chinook salmon from the Kenai, Kitsumkalum, and Wannock rivers had the largest total mean lengths of the 108 populations, and were also the largest at marine ages 4 and 5. These populations appear to represent extremes in both body size and reproductive life history. There are many selective advantages of large body size, but no consistent relationship was detected between latitude or migration distance and length. Therefore, local adaptations of body size in chinook salmon are probably the result of other factors in the freshwater portion of their life history. This large variation in length among populations further emphasizes the need for stockspecific fisheries management and nonselective fisheries to protect unique stocks of chinook salmon and diversity within these stocks.

North American populations of chinook salmon Oncorhynchus tshawytscha range from central California to Kotzebue Sound, Alaska, and migrate to spawning areas in streams from near tidewater to 3,200 km upstream (Major et al. 1978). They are the largest Pacific salmon and exhibit great variation in such life history traits as duration of juvenile residence in freshwater, size at age, age at maturity, ocean distribution, migration time, and spawning time (Ricker 1972; Healey 1991). Chinook salmon are generally categorized as oceantype or stream-type based on the freshwater residence patterns of juveniles (Gilbert 1913; Healey 1983; Taylor 1990a, 1990b). Ocean-type chinook salmon begin to migrate to the sea as newly emerged fry or after about 2-3 months of freshwater residence; stream-type fish migrate to the sea after a year or more in freshwater. Taylor (1990a) suggested that the increasing predominance of stream-type chinook salmon in higher latitudes and altitudes was related to the less-productive nature of these rearing environments. In Washington, Oregon, and California most streamtype chinook salmon return as adults in the spring and most ocean-type adults return to their natal streams in late summer or fall (Healey 1991).

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North American chinook salmon have experienced dramatic declines in size and age at maturity over the past five decades. Since the 1930s, the average size of chinook salmon taken in fisheries has declined by over half, and the average age at maturity has declined by more than a year (Ricker 1980, 1981). The longevity of chinook salmon and the generally coastal nature of their ocean distribution make them susceptible to exploitation by commercial and sports fisheries for longer periods of time than other species of Pacific salmon (Ricker 1980). Age at maturity and growth are partly heritable in chinook salmon (Hard et al. 1985; Withler et al. 1987; Hankin et al. 1993), and there has been selection against fish that mature at an older age, against fish of greater size, and against fish of certain migration patterns (Ricker 1980). More populations of chinook salmon have been extirpated than of other species of Pacific salmon and at least 64 populations in the lower 48 states may be in danger of extinction (Nehlsen et al. 1991). The Washington Department of Fisheries (WDF) et al. (1993) reported that 35 stocks of chinook salmon in Washington state were depressed and that another 5 were at production levels low enough that permanent damage to the stock has probably already occurred.

Despite declines in size and age at maturity, there is still considerable variation in size among populations, and some individuals of exceptional size are still produced. While a great deal of data exist on individual populations of chinook salmon, there is no comprehensive assessment of the variation in size and age at maturity throughout the species' range. The objective of this study was to characterize this variation and assess the influence of geographic location, freshwater life history, freshwater migration distance, and origin (natural or hatchery) on overall length and length at age. Knowledge of the relationships among these factors can be important to fisheries managers in determining the effects of size-selective fisheries on size and age of chinook salmon populations.

We compiled and analyzed data on 108 populations of North American chinook salmon between 42 and 65° north latitude. Initial examination of data revealed that three populations (Kenai River, Alaska, and the lower Kitsumkalum and Wannock rivers, British Columbia) exhibited exceptionally large body size. Additional analysis focused on the life history of these three populations, which appeared to represent evolutionary extremes.

Methods

Length and age data recorded from escapement samples from over 30,000 chinook salmon representing 97 populations were obtained from the Alaska Department of Fish and Game, the WDF, and Canada's Department of Fisheries and Oceans (DFO). The populations were sampled during 1987–1991, and fish were collected by carcass recovery, beach seine, drift gill net, and sport fishing. Information was supplemented with data from Nicholas and Hankin (1989) and Shepherd et al. (1986). The focal populations of large-bodied chinook (from the Kenai, Kitsumkalum, and Wannock rivers) were sampled in 1991 (Roni 1992).

The different length measurements used by the agencies were converted to postorbital-hypural length (POH). Mideye to fork lengths (MEF) were converted by means of a formula derived from samples collected from four different populations in 1991. Fork length (FL) was converted by means of equations derived from a combination of the 1991 data and escapement data collected by WDF in 1988–1990. The equations used to convert FL to POH were POH = 0.748FL + 2.382 (N = 1,216; $r^2 > 0.97$) for males and POH = 0.777FL + 2.020 $(N = 800; r^2 > 0.96)$ for females. The equations used to convert MEF to POH were POH = $0.920MEF - 3.686 (N = 168; r^2 > 0.99)$ for males and POH = 0.921MEF - 3.690 (N = 211; $r^2 >$ 0.99) for females.

The decimal age designation system was used (Koo 1962). For example, a fish classified as age 1.4 spent one winter in freshwater and four winters in saltwater, for a total age of 6 years. Life history type and age were determined from the pattern and numbers of scale annuli.

The sampling may have been size or sex selective. Gill nets are highly size selective and may select for males or fish with well-developed teeth (Hamley 1975; Healey 1986). In the Kitsumkalum River, for example, very small chinook salmon may have passed through gill nets, and fish of 35 kg or more occasionally tore through the nets. Sport fishery samples can be biased towards larger fish (Holtby et al. 1992); however, sports fisheries may not catch the largest specimens. Carcass recovery samples are biased towards larger fish and especially towards females, which guard their redds before they die (Neilson and Geen 1981; Neilson and Banford 1983) and are therefore more likely to be recovered. In addition to possible biases inherent in freshwater recoveries, the true age structure of a population is not easily obtained because chinook salmon are subject to fisheries throughout most of their lives (Ricker 1980). Because it was not possible to quantify these biases for even a small fraction of the stocks, length frequency and age structure have been analyzed qualitatively but not statistically. Ranking of size at age included only those stocks from which five or more fish were sampled at the particular age designation and sex. Data for precocious males that mature at ages 0.0 or 1.0 were not available for the populations we examined and are rarely collected for other populations (Taylor 1989; Mullan et al. 1992).

Mean marine age was calculated by summing the marine ages (number of winters at sea) of all fish from a population and dividing by the sample size. The age composition for each region was estimated by calculating the age structure for each population and then averaging these data for each region. Therefore, the age structure was not influenced by differences in sample sizes among populations.

Comparisons of mean length of stream-type and ocean-type chinook salmon at a given marine age could not be made within populations because most populations have predominantly either a stream-type or ocean-type life history. However, comparisons between stream-type and ocean-type length at marine age were made with a two-sample *t*-test that used population means. A similar method was used to compare the mean lengths of hatchery-produced and wild fish.

Upriver distance to spawning areas was used as an indication of the difficulty of migration. The midpoint of spawning distribution for each stock was determined through discussions with area fisheries scientists. The distance of spawning grounds from salt water was estimated from scale maps with a map wheel. Yukon River tributary migration distances were taken from Shultz et al. (1993), and spawning areas for stocks from Washington state were determined from Williams et al. (1975) and WDF et al. (1993). Approximate latitude in degrees for each population was determined either as the point the stream entered the ocean or, in the case of tributaries to larger rivers such as the Columbia and Yukon, the point of confluence with the major river. Regression analysis was used to test the relationship of mean population length to migration distance and latitude.

Results

Initial comparisons examined interannual variation in length within a population. Results for males and females within populations and from population to population were inconsistent. For example, there were significant interannual variations in length of Kenai River males and females at marine age 3 and marine age 4 (P < 0.001). Interannual variation was observed in length of Tahini River males of marine age 3 (P < 0.001) but not marine age 4, and females showed little variation among years. Although differences in length were detected among years for some populations, ages, and sexes, data were not always available from the same years or for more than 1 year for many populations. Hence all data from different years were pooled for each population.

Mean overall length (regardless of age) was calculated for each population, and the populations were ranked (Appendix). Kitsumkalum River chinook salmon of both sexes were larger than all 107 other populations (Appendix). The range in mean length among populations was 45.5 cm (86.4-40.9 cm) for males and 28.8 cm (86.4-57.6 cm) for females. Due to variation in age structure and possible sampling biases, mean length can be misleading. Therefore, data were sorted by freshwater and marine age and ranked by mean length at each age. The range of mean length at age was more than 20 cm in most age-groups and up to 26 cm for males at age 1.2. This analysis included only those populations with five or more fish for a given age-group and sex. The range at a given age is

even larger when groups with sample sizes of less than five fish are compared (Appendix). Mean length of stream-type and ocean-type chinook salmon, averaged among populations, differed for males at marine age 2 (P = 0.012), but not for females or males of any other age.

Mean overall length for each population was positively correlated (weakly) with latitude for females ($r^2 = 0.22$, P < 0.001), but not males (P =0.1; Figure 1). For ages 1.3 and 0.3, the most numerous groups, there was a negative correlation for age-1.3 males ($r^2 = 0.31$, P < 0.001), but no trend was detected for females at ages 1.3 (P =0.17), 0.3 (P = 0.21), or males at age 0.3 (P =0.30). Northern populations tended to have greater marine age and to have spent 1–2 years in freshwater prior to emigration, compared with southern populations (Table 1).

Regression of mean overall length against migration distance was not significant for females (P = 0.87) or males (P = 0.29; Figure 2). Length at age 1.3 was negatively correlated with migration distance for females ($r^2 = 0.07$; P = 0.02) and males $(r^2 = 0.17; P < 0.001)$, but not for females (P = 0.55) or males (P = 0.41) at age 0.3. A weak negative relationship was also detected for females $(r^2 = 0.11; P = 0.02)$ and males $(r^2 = 0.16; P =$ (0.004) at age 1.4, but in neither sex at age 0.4 (P > 0.50). We also examined the relationship between body length and migration distance for Yukon River populations, which were represented by migration distances that ranged from 167 to 2,879 km. A significant positive correlation was detected for mean overall length of males $(r^2 = 0.63; P =$ 0.006) but not of females (P = 0.53). However, a similar analysis of length at age 1.3 and length at age 1.4 was not significant for males or females (P > 0.25).

Differences in mean length at age between hatchery-reared and wild fish were examined at age 0.3, which had the largest number of hatchery-reared (24) and wild (26) populations of any age group. Wild fish were larger than hatchery fish (70.3 versus 68.3 cm for males and 71.2 versus 69.2 cm for females; P < 0.05). No difference in variance between hatchery and wild populations was detected (7.87 and 11.93 cm for hatchery and wild females, 12.26 and 12.93 cm for males; Figure 3).

The three focal populations were larger than other populations at specific ages. Kenai River males were larger than only 53.2% (N = 64) of the populations at age 1.3 but larger than all (N = 43) other populations at age 1.4. Kenai River females





FIGURE 1.—Relationship between mean length (regardless of age) and latitude for (A) female (N = 108) and (B) male (N = 108) chinook salmon. Regression was significant for females ($r^2 = 0.22$) but not for males ($r^2 = 0.01$).

were larger than 72.5% (N = 69) of the populations at age 1.3 and all (N = 43) other populations at age 1.4. Kitsumkalum River males were larger than 95.3% (N = 64) of the populations at age 1.3, 97.7% (N = 43) at age 1.4; females were larger than 88.4% of the populations at age 1.3 and 97.7% at age 1.4. Wannock River males were larger than 94.4% (N = 18) and females were larger than all (N = 29) populations at age 0.4. While these three populations were the largest in mean length, no populations were consistently the smallest. In addition to being larger for their age, the age structure of these three populations differed slightly from other populations in their regions. All Kenai River fish were stream-type, Kitsumkalum River samples averaged 92.3% stream-type, and Wannock River samples averaged 0.52% stream-type. Mean age composition was calculated for all other populations in each region for comparison to the three focal populations. A higher percentage of Kitsumkalum River and Kenai River fish matured at marine ages 4 and 5 than other populations in

TABLE 1.—Age composition of chinook salmon populations from different North American rivers or areas. Number of stocks for each area is in parentheses; M is male and F is female. Central Alaska includes populations north of Prince William Sound (inclusive); southeast Alaska includes all populations south of Prince William Sound in Alaska. Regional groups do not include study populations.

						Pe	rcent of	f popul	ation ir	age-cl	ass:						Mean
River or area	Sex	0.1	0.2	0.3	0.4	0.5	1.1	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	age
Central Alaska (21)	M F						0.8	21.8 1.6	31.3 18.5	36.0 62.3	4.9 11.5		0.2 0.0	2.3 0.3	2.4 3.9	0.3 1.8	3.3 3.9
Kenai River	M F						0.4	14,4 3.1	17.7 8.7	58.8 79.1	8.2 8.9	0.1	0.1	0.4			3.6 3.9
Southeast Alaska (19)	M F		2.0 0.2	0.3 0.7	0.2 1.4		15.8 0.0	30.6 0.8	30.8 40.9	19.1 53.8	0.4 1.4	0.1	0.4 0.4	0.3 0.2	0.2		2.6 3.6
British Columbia (29)	M F	0.5	2.9 0.9	10.7 14.1	3.2 3.5	0.1	6.7 0.1	25.9 9.8	40.6 58.1	9.3 13.2	0.1 0.1		0.1				2.7 3.1
Kitsumkalum River	M F			1.6	3.1 2.1	0.8 1.1		7.0	21.9 20.3	53.9 68.4	11.7 8.0						3.8 3.9
Wannock River	M F		15.6	43.3 24.0	37.8 74.0	1.1 2.1			1.1	1.1							3.3 3.8
Washington (37)	M F	3.0	12.8 3.0	27.8 32.5	11.9 15.9	1.6 4.7	2.3 0.0	28.5 23.9	11.9 19.5	0.1 0.4							2.6 3.0
Oregon (24)	M F	12.3	21.3 8.4	35.5 36.7	14.6 35.1	2.4 5.9	0.1	10.6 8.4	2.4 4.2	0.1							2.6 3.3

their regions (British Columbia and Alaska, respectively). Wannock River fish more often matured after 4 years at sea than other British Columbia populations. Thus the focal populations were both larger for their age and older than most populations in their regions.

Discussion

No consistent relationship was found between length at age and latitude for the 108 populations of chinook salmon examined. In contrast, weight has been negatively correlated with latitude for both pink salmon Onchorhynchus gorbuscha and chum salmon O. keta (Heard 1991; Salo 1991). A positive relationship between marine age at maturity and latitude has been found for Atlantic salmon Salmo salar and chum salmon (L'Abée-Lund 1991; Salo 1991). Differences in exploitation rates of chinook salmon make it difficult to determine if a true relationship exists or if the observed size and age at maturity are a product of differences in fishing pressure and gear selectivity.

A significant difference in length between ocean-type and stream-type chinook salmon existed only for males at marine age 2 (ocean-type fish being slightly larger), but not for females or for males of any other age. Quinn and Unwin (1993) indicated that stream-type fish maintain a size advantage for the first 1-2 years at sea, but that this is apparently not the case after longer periods at sea. Stream-type chinook salmon enter the ocean at a larger size and generally earlier in the year than ocean-type fish (Healey 1991), though data on the specific dates of seawater entry were not available for comparative analysis. The two types also differ in marine distribution (Healey 1983) and often differ in the date of return to freshwater; stream-type fish generally return earlier than ocean-type fish. These complex differences between the two types confound comparisons of size at age.

Our findings on juvenile life history are consistent with Taylor's (1990a) evidence that northern populations and those in less productive areas (e.g., higher elevations) are more often streamtype than populations in southern latitudes and more productive areas. However, this does not explain overall patterns of length at age. While general trends in ocean distribution are available for chinook salmon, little information is available on specific migration patterns of individual populations throughout their marine residence. Our results indicate the latitude where chinook salmon enter the ocean has relatively little effect on length at age or overall body size for a population. Blair et al. (1993) reported large variation in size at age, age structure, and morphology of populations of sockeye salmon Oncorhynchus nerka originating from the same latitude. Those fish originated from the same lake and river system and had similar





FIGURE 2.—Relationship between mean length (regardless of age) and freshwater migration distance (river kilometers) for (A) females (N - 95) and for (B) males (N - 95).

outmigration size, timing, period of ocean residence, migration distances, adult entry into freshwater, and spawning dates. Variation in size at age among chinook salmon populations within a given geographic area is considerable, supporting the hypotheses of Holtby and Healey (1990) and Blair et al. (1993) that the spawning environment selects for different body sizes.

The finding that mean lengths of male and female hatchery-reared fish were significantly smaller than wild fish at age 0.3 was unexpected, as hatchery fish are usually larger at release than their wild counterparts. Although we did not have data on wild and hatchery-reared fish from the same populations, such pairings would be a more powerful way to examine differences in growth. Furthermore, differences in rearing and release strategies and fishing pressure could influence the size of fish in the escapement in complex ways.

The three focal populations of large-bodied chi-





FIGURE 3.—Percent of populations of age-0.3 hatchery and wild chinook salmon (A) females (52 stocks) and (B) males (53 stocks) in each of five size-classes.

nook salmon were geographically distant from each other and differed in juvenile life history, although they shared other traits. The Kenai River and Kitsumkalum River fish were almost exclusively stream-type, whereas the Wannock River fish were almost all ocean-type, which indicates that large final body length may not necessarily be related to life history type. Chinook salmon from the Kenai, Kitsumkalum, and Wannock rivers were larger for their age and had a higher percentage of older fish (marine ages 4 and 5) than most populations in their regions. The combination of large length at age and delayed maturity explains the large overall length of fish from these populations. Both growth and age at maturity are heritable in salmonids (Ricker 1972; Hard et al. 1985; Withler et al. 1987; Tipping 1991; Hankin et al. 1993). Rapid growth in chinook salmon is often associated with individuals that mature at an early age (Healey 1991). However, fish from the Kenai, Kitsumkalum and Wannock rivers appear to grow rapidly but delay age at maturity. Moreover, females from these three stocks have a higher fecundity for their length than other populations of chinook salmon, and females from the Kitsumkalum and Wannock rivers also produce larger eggs (Roni 1992). It is unclear why these particular stocks have not seen declines in size and age, but limited coded wire tag data did not reveal unique migration patterns (Roni 1992).

Ricker (1980) suggested that large chinook salmon are more successful than smaller fish in constructing redds in large streams with large substrate, but the depths, velocities, and substrates on which Chinook salmon from the Kenai, Kitsumkalum, and Wannock rivers spawned were within the range reported for other populations with smaller fish (Roni 1992). Moreover, Burner (1951) indicated the largest substrate in Columbia River tributaries was found in the Ohanapecosh River, a mountain stream utilized by spring-run chinook salmon, which average about 6.8 kg, further evidence that the correlation between body size and substrate is weak.

Adult chinook salmon migrate to spawning areas that range from just above tidewater to as far as 3,200 km upstream (Major et al. 1978). Unlike Atlantic salmon (Schaffer and Elson 1975; Thorpe and Mitchell 1981) and brown trout Salmo trutta (L'Abée-Lund 1991), length was not positively correlated with distance of migration for chinook salmon. Our analysis suggests a weak negative correlation between size and migration distance for stream-type populations of chinook salmon. Similarly, Fleming and Gross (1989) found a negative correlation between size and migration distance for coho salmon Oncorhynchus kisutch. The three populations of very large-bodied chinook salmon find few or no points of difficult ascent and spawn in the lower main stem of their natal streams (Roni 1992). Chinook salmon that spawn in the Kenai and Wannock rivers migrate from 16 to 80 km (Burger et al. 1985) and 3 to 5 km, respectively. Kitsumkalum River chinook salmon migrate approximately 100 km up the Skeena River before they enter the Kitsumkalum River and spawn between river km 0 and 21. Snyder (1931) found that chinook salmon returning to the Klamath River became progressively larger for a given age as the season progressed. The largest fish returned at the end of the spawning run, were relatively mature upon entering freshwater, and spawned in the lower river. Beacham and Murray (1987) and Beacham et al. (1988) found that pink salmon and chum salmon that spawned in large rivers were larger than those that spawned in small streams. The Kenai, Kitsumkalum, and Wannock rivers have mean annual discharges of 168, 123, and 328 m^3/s , respectively, which are not unusually large in comparison with other chinook salmon rivers.

Spawning habitats utilized by the largest chinook salmon in the Kenai, Wannock, and Kitsumkalum rivers have certain similarities. These large glacial rivers have large lakes that buffer the flow and temperature regimes. The populations of large-bodied chinook salmon spawn in the main stem of the rivers below these lakes during some of the highest flows of the year. Smaller-bodied populations of chinook salmon are found elsewhere in the watersheds of the Kenai (Hammarstrom 1981), Kitsumkalum (Roni 1992; see Cedar River, Appendix 1) and Wannock rivers (Sandy J. MacLaurin, DFO, personal communication). Escapement size of Kenai River late-run chinook salmon (the large-bodied population) has ranged from 19,581 to 48,037 fish for 1981-1989, and the total return (escapement plus harvest) has ranged from 39,656 to 79,837 fish (Sonnichsen and Alexandersdottir 1991). Estimates of escapement to the Kitsumkalum River below Kitsumkalum Lake ranged from 8,308 to 24,508 fish from 1984 to 1988 (Andrew and Webb 1988; Carolsfeld et al. 1990). Wannock River escapement is believed to range from 2,000 to 17,000 fish (S. J. MacLaurin, DFO, personal communication). Most chinook salmon populations in British Columbia number fewer than a thousand individuals (Healey 1982), and this is probably the case elsewhere in North America (Healey 1991). The three focal populations are thus large in total run size compared with most other populations. This could result in intense competition for mates and redd sites, depending on the amount of spawning habitat available. Hartman (1969) hypothesized that high levels of competition lead to selection for large body size in rainbow trout Oncorhynchus mykiss. Furthermore, there is a positive correlation between fish size and redd depth for salmonids (van den Berghe and Gross 1984; Crisp and Carling 1989). If larger female chinook salmon dig larger and deeper redds, then these redds are less likely to be disturbed by later spawning females, smaller females, or scouring floods (Hankin and McKelvey 1985). In addition, large females are likely to secure the best spawning areas.

Holtby and Healey (1986) suggested that the mixture of body sizes of coho salmon in a stream is determined primarily by competition for nest sites, gravel quality, and scour during incubation. Their model predicted that good quality gravel, high competition, and deep scour would select for large females with a low variance in size. Mate choice is size selective, and selection for large females may lead to selection for large males because females find males of similar or greater size the most attractive (Hanson and Smith 1967; Foote 1990). Large males are usually dominant (Hanson and Smith 1967). If selection for large females has occurred in the Kenai, Kitsumkalum, and Wannock rivers, this might explain the large size of males in these populations.

Declines in size and age at maturity may lead to populations of chinook salmon that are less well suited to their environment than their predecessors and less likely to adapt to or survive large disturbances, either natural or anthropogenic. Given the large number of chinook salmon populations that have been listed at risk (Nehlsen et al. 1991), it is important that less selective forms of harvest or reduced harvest rates be examined. Most fisheries for chinook salmon do not target specific populations. Furthermore, fisheries such as ocean troll fisheries are size selective and tend to remove not only fish that grow rapidly but also the oldest individuals (Ricker 1980). River fisheries for chinook salmon that target specific stocks or stock groups are typically gill-net fisheries, which are highly selective (Hamley 1975; Healey 1986). The result of these different fisheries is the removal of fish of specific sizes, particularly the oldest and largest fish. Reducing the natural range of sizes and age in the species may lead to populations that are ill suited to spawn in their natural habitats. Miller and Kapuscinski (1994) reported that the effects of size-selective fisheries can be complex and that characteristics of a population must be well understood to assess the genotypic and phenotypic changes that may result from these fisheries. Furthermore, by reducing the overall fitness of a population through removal of the largest and potentially most successful spawners, selective fisheries may reduce the overall biomass and harvest (Forbes and Peterman 1994).

While it was not possible to quantify the effects of selective and mixed stock fisheries on the length and age of chinook salmon, it is unlikely that it could explain the variation in length observed among populations from a given region. Considerable evidence indicates that size-selective fisheries may have complex and deleterious effects on Pacific salmon populations. The weak or nonexistent relationships of length with latitude, migration distance, and juvenile life history type suggest that variation in length among chinook salmon populations may represent unique adaptations to local spawning conditions or other aspects of freshwater life history. These findings, along with the tremendous variation in length among chinook salmon populations, further emphasize the need for stock-specific fisheries management and nonselective fisheries to protect unique populations of chinook salmon and genetic diversity within populations.

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Appendix follows on page 336

Appendix: Length at Age in Chinook Salmon Populations

TABLE A1.—Mean postorbit-hypural (POH) length (cm) at age, sample size, and latitude in degrees for 108 populations of North American chinook salmon. Ocean-type life history is denoted by age 0.x, stream-type by ages 1.x and 2.x; M is male; F is female; NA is not available.

	Latituda			Length (POH, cm) at age:								
Population location	(degrees)	Sex	N	0.1	0.2	0.3	0.4	0.5	1.1			
Chena River	64.5	M F	782 811						44.7			
Salcha River	64.3	M F	887 806						30.0			
Anvik River	62.4	M	871 530						30.4			
Sheep Creek	62.2	M F	102						31.3			
Talkeetna River	62.2	M E	160						23.0			
Tatchun Creek	62.2	г М Е	130									
Gulkana River	62.1	г М Б	27									
Little Salmon River	62.0	r M	37 171									
Andreafsky River	62.0	F M	1,020						39.9			
Ross River	61.6	F M	497 72									
Klutina River	61.6	F M	106 90									
Lake Creek	61.5	F M	86 147						31.3			
Big Salmon River	61.5	F M	143 178									
Willow Creek	61.5	F M	223 220									
Deshka River	61.4	F M	277 320						29.6			
	(1.2	F	219						29.0			
Alexander Creek	61.2	M F	203 158									
Little Susitna River	61.2	M F	244 355						29.4			
Tahkini River	60.5	M F	30 40									
Kenai River (late)	60.3	M F	959 966									
Nisutlin River	60.1	M F	102 166									
Kluckshu River	60.1	M F	201 233									
Tahini River	59.4	M F	364 82						35.2			
Situk River	59.3	M F	65 65		41.5 42.4	66.2 69.6	76.8 77.7		33.4			
Nakina River	58.5	M F	600 320						27.8			

TABLE A1.—Extended.

······		Length (POH, cm) at age:										
Population location	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	ages		
Chena River	47.5 66.3	64.2 69.3	74.9 75.9	85.3 81.0		44.7	60.7	73.0	82.2	63.1 75.8		
Salcha River	49.5 57.6	64.8 70.6	78.1 77.5	87.3 83.5		56.1	66.3		89.2	65.1 77.1		
Anvik River	49.1	63.1 68.1	71.4 73.5	77.9 80.0		61.4	62.1	82.8		61.1 72.5		
Sheep Creek	54.3 63.1	69.5 74.3	81.3 83.3	89.3 87.1			82.4			70.6 81.7		
Talkeetna River	48.1 50.5	66.3 67.4	79.9 77.1	89.4 78.1						66.9 73.2		
Tatchun Creek	52.0 51.6	62.8 66.8	71.5 71.8	79.6						62.7 71.1		
Gulkana River	81.3	79.6 71.2	84.4 80.7	87.4 80.3						83.5 77.9		
Little Salmon River	47.6 48.0	60.0 62.5	76.7 74.7	83.7 82.0			63.9 70.0	79.6 73.2	82.2	64.2 75.6		
Andreafsky River	48.5 55.7	63.2 68.1	73.3 76.1	80.8 81.5		52.9				60.4 75.1		
Ross River	47.4	62.8 69.4	76.1 76.0	83.8 81.0			60.3	75.5	78.3	72.8 78.5		
Klutina River	54.1	74.1 75.7	86.1 83.4	90.6 82.1						81.2 81.8		
Lake Creek	49.5 51.4	71.0 72.3	85.4 82.0	92.9 87.2			78.7			66.9 78.8		
Big Salmon River	48.0	60.8 67.3	74.9 75.5	83.1 80.9		50.6	61.3 55.7	82.3 75.4	85.1 80.6	68.8 77.2		
Willow Creek	51.7	67.6 74.3	81.3 80.5	89.7 79.1				81.4 82.7		73.0 79.8		
Deshka River	47.2 59.0	68.3 70.2	79.9 75.1	90.2 91.3		61.6	67.2 71.1	85.2		63.2 72.5		
Alexander Creek	49.9 53.6	67.4 67.9	81.8 77.0				73.6 73.7			54.5 71.3		
Little Susitna River	52.5 53.4	71.7 73.6	86.5 81.8	92.8 87.7			80.1			79.1 80.5		
Tahkini River		64.3 72.5	76.2 74.2	95.2 85.9			69.4	73.9 75.6	85.6 81.3	70.5 77.3		
Kenai River (late)	56.3 57.7	68.7 73.3	91.8 87.7	93.2			80.8 69.3	91.2		82.8 86.0		
Nisutlin River	50.6	63.7 68.7	73.5 72.3	82.8 76.4		53.8	60.5 65.4	70.9 72.2	78.2 77.5	68.1 72.3		
Kluckshu River	50.7 63.6	72.8 71.5	81.0 76.1							68.3 71.6		
Tahini River	54.4 58.0	67.4 72.9	79.2 78.8	85.7 88.4		58.0	62.6	79.0		62.3 76.5		
Situk River	44.8 47.4	69.3 67.9	75.8 76.9			53.4				53.1 73.7		
Nakina River	47.1	63.8	76.2 73.6	78.0 73.4						60.1 73.7		

TABLE A1.—Continued.

-	Latitude				L.	ength (POI	I, cm) at a	ge:	
Population location	(degrees)	Sex	N	0.1	0.2	0.3	0.4	0.5	1.1
Tatsamenie River	58.5	M F	77 49						29.7
Dudiontu River	58.5	M F	41 42						30.8
Nahlin River	58.5	M F	1,081 916						30.7
Kowatua River	58.5	M	383 219						29.3
Naknek River	58.4	Mi	270						33.6
Tatsamenie Lake	58.2	M F	1,222						31.1
Hackett River	58.2	M F	106						34.0
Little Tahitan River	58.1	M F	155			69.0	75 5		30.9
King Salmon River	58.0	M F	203 25 23			07.0	15.5		
Damdochax River	56.3	M	40			68.2			
Bear River	56.2	г М Г	40 82			69.7			30.8
Genes Lake Creek	56.1	г М Б	90 28						31.4
Clear Creek	56.1	г М Г	- 38 109 75						32.3
Eulachon River	56.1	г М Г	99 121						32.9
Cripple Creek	56.1	г М Б	1,303						29.7
Unuk River	56.0	и М Е	91 56						29.8
South Fork Chickamin River	55.5	M F	100						33.1
Chickamin River	55.5	M F	172						31.2
Babine River	55.4	M F	33						31.8
Cranberry River	55.3	M F	20 32				75 4		
Bulkley River	55.2	, M F	46 64				, .,.4		
Kitwanga River	55.1	M	39 67						
Cedar River	54.5	M	32				84.0		
Kitsumkalum River	54.3	n M F	129			66.0	89.2 87 2	84.0 88 0	

TABLE A.1-Extended.

				Length	(POH, cm	i) at age:	-			A 11
Population location	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	ages
Tatsamenie River	49.1	67.3 64.4	74.2 73.3				61.6			61.8 67.1
Dudiontu River	47.3	67.6 67.8	81.2 75.1							66.7 71.6
Nahlin River	49.9 54.3	65.6 66.3	76.5 73.5	83.9 78.5	31.6	49,4	70.9 67.9	92.0 73.8		62.6 70.7
Kowatua River	47.0	65.5 69.1	78.1 76.3	83.1 78.3		49.4	68.5 68.6	85.1		59.4 75.0
Naknek River	41.4 52.8	67.8 72.0	79.7 76.5	84.3 79.4		34.6				62.3 75.4
Tatsamenie Lake	49.5 61.0	64.3 68.7	77.9 75.8	82.9 69.8	29.2	55.7				53.4 73.7
Hackett River	44.5 55.3	62.4 63.4	80.2 69.4							57.2 66.9
Little Tahltan River	42.0	66.7 69.7	79.1 75.6	82.6			80.0 73.2			68.1 74.0
King Salmon River	49.6	60.1 73.7	74.8 77.5							59.4 76.9
Damdochax River	50.9	69.7 71.8	90.6 84.0							68.9 80.6
Bear River	55.8 58.4	70.3 72.5	78.0 80.7							67.7 74.4
Genes Lake Creek	51.1	67.2 73.8	86.5 82.9	91.6						40.9 78.1
Clear Creek	50.9	69.1 74.8	83.0 81.7							50.3 79.0
Eulachon River	53.0	68.8 74.5	86.4 83.1	94.8 82.0						61.6 79.0
Cripple Creek	49.7	68.8 72.9	85.0 81.1	87.7 85.4						52.1 78.1
Unuk River	50.1 69.5	62.9 71.4	82.6 79.5	89.3						45.7 75.6
South Fork Chickamin River	50.6	66.1 76.2	78.2 84.1	85.0						51.2 80.1
Chickamin River	51.6	67.5 73.9	84.0 82.0	87.7		80.8				63.5 77.8
Babine River	56.5 58.8	62.4 73.3	84.9 79.9	84.7						57.8 75.5
Cranberry River		70.4 73.2	81.9 80.0							76.8 76.3
Bulkley River	56.8 60.8	68.5 65.8	80.5 71.3							62.4 66.2
Kitwanga River	53.8 57.5	67.5 72.9	80.8 81.5							66.7 76.8
Cedar River	57.0	73.7 73.7	86.8 82.4							76.8 77.9
Kitsumkalum River	60.7	78.6 80.7	91.3 87.6	95.9 89.4						86.4 86.4

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TABLE AI.—Continued.

	Latitude			Length (POH, cm) at age:							
Population location	(degrees)	Sex	N	0.1	0.2	0.3	0.4	0.5	1.1		
Morice River	54.3	M F	50 47								
Kitimat River	54.0	M F	23 56			79.1 77.8	82.7 85.2				
Atnarko River	52.5	M F	37 37		56.0 59.0	66.3 67.7	76.0 77.7	86.0			
Wannock River	51.4	M F	91 94		53.7	73.8 79.2	87.5 87.5	97.4 91.8			
Harrison River ^a	49.1	M F	NA NA	36.1	60.8 64.5	73.6 73.2	80.5 77.3				
Nooksack Hatchery	48.5	M F	84 166	43.5	56.1 56.3	64.1 66.5	69.0 66.9		45.1		
Samish Hatchery	48.3	M F	17		51.0 59.3	67.1 66.0	70.4				
Winthrop Hatchery	48.3	л М Б	11			00.0	70.4				
Skagit Hatchery	48.2	M	175	37.7	55.5	74.8	82.6 79.5				
Suiattle River	48.2	r M E	105	35.3	52.8	67.3	85.0		39.0		
North Fork Stilliguamish River	48.1	г М Г	28		55.1	69.7	73.1				
Elwah River	48.1	г М Б	98		65.3	71.7	78.8				
Soleduck Hatchery	47.5	r M F	90		45.0	66.9	69.0		42.0		
Wallace River	47.5	M	30		55.0	67.8	74.0	82.0			
Skykomish Hatchery	47.5	M	96 25		57.6 55.2	66.6 68.7	67.5 78.6	02.0	48.8		
Skykomish River	47.5	M F	23 41		55.8 56.0	67.3 71.5	75.0 72.9				
Snoqualamie River	47.5	M F	42		50.0	69.1 71.0	77.6		39.0		
Bridal Veil Creek	47.5	M F	40 29	42.8	54.7	66.7 68.7	80.2 75.5		40.4		
Shale Creek	47.4	M F	34 24			67.0 73.0	76.5 79.5	74.0			
Winfield Creek	47.5	M	40		58.0	68.0 71.5	75.4 78.1	87.0 82.5			
Leavenworth Hatchery	47.3	M	85 78		58.0	(1.5	70.1	82.5	49.7		
Green River Hatchery	47.3	r M F	149	41.4	58.0	68.8	74.1		52.5		
Wenatchee River	47.3	г М Б	182	39.0	54.1 54.3	68.4	74.1 78.2	017	42.0		
Quinault Hatchery	47.2	г М F	225 45 27	36.0	53.0	69.5 72.3	74.9 77 6	81.6 84.0			

TABLE A.1-Extended.

				Length	(POH, cm	n) at age:				A11
Population location	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	ages
Morice River	57.5	75.6 74.4	85.4 79.7	87.0						73.0 75.8
Kitimat River		75.1	86.0							80.5 79.0
Atnarko River	59.3	73.4 75.6	81.0							69.7 75.6
Wannock River		77.5	92.1							76.4 85.6
Harrison River ⁴										71.0 74.2
Nooksack Hatchery	58.8 61.1	63.4								61.1 65.4
Samish Hatchery										66.1 65.7
Winthrop Hatchery	63.6 60.1	70.6 70.1								66.2 62.0
Skagit Hatchery	67.7 67.8	79.5 78.6	70.4							70.8 73.0
Suiattle River	57.2 63.4	72.9 72.1	80.0 71.7							60.2 69.6
North Fork Stilligaumish River	65.0	68.2 70.4								63.2 70.9
Elwha River	67.4 66.3	74.0 75.0	71.0 78 <i>.</i> 5							70.7 72.2
Soleduck Hatchery	58.8 64.1	68.8 69.1	67.5 73.8							63.3 68.3
Wallace River	71.5 67.2	74.0 66.8								63.9 68.8
Skykomish Hatchery	62.4 66.3	74.7 74.0								63.8 68.0
Skykomish River	65.3 64.8	74.3 69.4	80.0							67.6 70.4
Snoqualamie River	57.8 66.2	75.8 74.5								64.4 72.6
Bridal Veil Creek	56.9 64.0	71.2 72.2								56.3 70.2
Shale Creek										73.9 80.0
Winfield Creek										75.1 79.2
Leavenworth Hatchery	64.0 61.5	72.7 70.2								65.4 63.0
Green River Hatchery	62.8 64.9	73.2 72.4								64.5 69.8
Wenatchee River	61.6 61.9	75.7 71.4								66.3 72.6
Quinault Hatchery										71.3 79 I

TABLE A1.-Continued.

	1 atituzka			Length (POH, cm) at age:								
Population location	(degrees)	Sex	N	0.1	0.2	0.3	0.4	0.5	1.1			
Cle Elum River	47.1	M F	34 71				67.0					
Humptulips River	47.0	M F	45 21			67.0 63.0	78.0 77.0	81.0 83.5				
Deschutes River	47.0	M F	47 52		54.6 63.8	65.1 65.3	70.8		46.5			
American River	46.6	M F	79 84						40.0			
Priest Rapids Hutchery	46.4	M F	78 109	42.5	57.7 59.8	72.3 71.8	82.0 77.8	85.0	49.5			
Naches River	46.4	M F	90 80						44.7			
Hanford Reach (Columbia River)	46.4	M F	27 58	38.3	58.2 59.0	74.7 73.7	79.6 78.7					
Lyons Ferry Hatchery	46.4	M F	46 151	45.3	66.3 70.4	79.7 70.2	81.3		45.1			
Tucannon River	46.3	M F	104 148						43.5			
Naselle Hatchery	46.3	M F	215 210	43.0	55.4 57.0	65.8 69.7	74.0 75.3	77.7				
Yakima River	46.2	M F	244 251	38.9	52.6 58.8	70.4 68.6	79.0 75.2		42.4			
Big Creek Hatchery	-46.1	M F	23 73	54.0	66.6 61.8	72.3 70.9	76.7 73.8					
Cowfitz Hatchery	46.1	M F	139 72		54.1 64.2	67.5 68.1	76.4 81.3					
Kalama Falls Hatchery	46.0	M F	96 91		48.0	71.1 73.3	79.9 77.8					
Little White Salmon Hatchery	45.4	M F	45 47	38.3	55.7 58.5	73.8 71.7	82.4 77.4	85.0				
Carson Hatchery	45.4	M F	42 48						45.0			
Klickitat River	45.4	M F	92 84						35.0			
Lewis River	45,4	M F	123 146	34.7	53.2	67.6 68.2	76.1 74.9	82.0 78.0	38.6			
Bonneville Hatchery	45.4	M F	46 44		55.1 58.3	71.0 71.4	76.6 76.7					
Round Butte Hatchery	45,4	M F	40 46		49.0	57.0 58.0			39.7			
Spring Creek Hatchery	45.4	M F	117 288	53.0	66.5 64.3	74.3 71.3	70.8					
Sandy River	45.3	M F	18 32		55.8 60.0	63.4 69.3	85.3 79.1	83.0 80.0				
Trask River	45.3	M F	74 59		59.3	72.6 77.5	83.1 85.4	78.7 89.0				
Clackamas Hatchery	45.2	M F	33 51		51.8	66.6 63.7	76.4 69.2					

TABLE A.1-Extended.

	Length (POH, cm) at age:											
Population location	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	ages		
Cle Elum River	58.0 57.6	72.5 64.5								58.9 57.9		
Humptulips River										75.6 79.1		
Deschutes River	66.1	70.0								59.4 65.7		
American River	59.3 61.0	75.0 72.8	75.0							67.6 71.6		
Priest Rapids Hatchery		71.0								69.4 70.8		
Naches River	57.2 60.8	74.9 72.0								63.9 67.5		
Hanford Reach (Columbia River)	53.0									68.4 75.3		
Lyons Ferry Hatchery	60.5 63.5	77.2 70.1								64.3 67.5		
Tucannon River	55.6 57.7	69.9 67.4								57.5 61.0		
Naselle Hatchery	58.0 59.0									66.1 73.0		
Yakima River	55.0 56.4	70.3 66.6								53.3 61.2		
Big Creek Hatchery										69.8 69.7		
Cowlitz Hatchery	58.7 57.3	67.5 65.2								62.3 67.0		
Kalama Falls Hatchery	59.9 64.7	70.3 72.0								69.1 73.2		
Little White Salmon Hatchery		73.5								56.9 72.5		
Carson Hatchery	61.4 59.8	75.3 70.3								62.0 60.5		
Klickitat River	59.4 62.4	74.9 70.6	67.0							59.6 67.7		
Lewis River	57.1 62.5	67.8 68.9								68.7 68.7		
Bonneville Hatchery	69.0	68.0 67.0	82.0							70.0 72.0		
Round Butte Hatchery	55.9 57.7	58.0								53.5 57.6		
Spring Creek Hatchery										66.5 66.1		
Sandy River										66.8 75.2		
Trask River										72.0 83.0		
Clackamas Hatchery	69.6									66.0 64.8		

TABLE A1.—Continued.

<u> </u>	Latitude				L	ength (POI	I, cm) at a	ge:	
Population location	(degrees)	Sex	N	0.1	0.2	0.3	0.4	0.5	1.1
Siletz River ^b	44.5	M F	NA NA		55.2	71.0 77.6	79.4 78.6	87.7 80.5	
Marion Forks Hatchery	44.5	M F	43 44			59.9 63.0	75.7 71.7		
Yaquina River ^b	44.4	M F	NA NA	40.3	58.6 61.6	69.8 70.9	76.8 75.4		
Alsea River ^b	44.3	M F	NA NA	41.7	50.0	63.6 69.8	77.2 80.5	85.2	
McKenzie Hatchery	44.1	M F	42 47			66.2 67.3	79.1		48.0
Dexter Hatchery	44.0	M F	14 64			64.9 64.4	72.7 74.6		
Siuslaw River ^b	44.0	M F	NA NA	42.1	59.9 58.5	72.1 72.8	81.8 77.4	80.5	
Coquille River ^b	43.1	M F	NA NA	40.1	58.5 58.4	69.8 69.2	78.5 75.6		
Sixes River ^b	42.5	M F	NA NA	43.0	57.1 60.0	70.6 69.5	79.2 74.7	78.6	
Elk River ^b	42.5	M F	NA NA	41.3	58.0 61.7	70.0 69.9	78.8 75.2	80.9 78.2	
Rogue Hatchery	42.3	M F	35 49		55.8 56.6	65.9 66.3	70.0 77.0		52.5
Chetco River ^b	42.0	M F	NA NA	43.8	56.4 61.5	68.0 70.6	72.5 75.4		

^a From Starr and Schubert (1990).

^b From Nicholas and Hankin (1989).

TABLE A.1-Extended.

	Length (POH, cm) at age:										
Population location	1.2	1.3	1.4	1.5	2.1	2.2	2.3	2.4	2.5	ages	
Siletz River ^b										72.7 78.3	
Marion Forks Hatchery	59.2 62.0	68.5 70.2								61.6 66.9	
Yaquina River ^b										62.0 72.3	
Alsea River ^b										49.7 77.1	
McKenzie Hatchery	61.7 64.9	78.8 74.()								65.6 68.0	
Dexter Hatchery	60.6 61.8	74.2 69.9								65.9 66.1	
Siuslaw River ^b										61.8 75.2	
Coquille River ^b Sixes River ^b										56.6 69.8 65.9 71.0	
Elk River ^b										53.9 70.6	
Rogue Hatchery	63.3 68.7									59.8 64.3	
Chetco River ^h										53.2 72.4	

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