# Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities

**Andrew P. Hendry and Thomas P. Quinn**

**Abstract**: Body size, age composition, and male body depth were compared among five Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations. Two of the populations (Bear and Cottage creeks) were indigenous to the watershed and three (Cedar River, Issaquah Creek, and Pleasure Point) were non-native (from Baker Lake, Washington). To isolate the relative contributions of habitat type and ancestral relatedness to phenotypic variation, we compared populations with (*i*) the same origin and similar habitats, (*ii*) different origins and different habitats, (*iii*) the same origin and different habitats, and (*iv*) different origins and similar habitats. Spawning salmon in the Cedar River were older and larger than those in the native populations, a result consistent with their origin (contemporary Baker Lake fish were also large and old) and with habitat variation (the Cedar River is much larger than Bear and Cottage creeks). Body size and age composition did not differ among the three non-native populations, but the body depth of males spawning on the lake beach (Pleasure Point) was greater than that of males in the Cedar River, suggesting adaptive divergence. Adaptive convergence may also have occurred because the population in Issaquah Creek (intermediate-sized creek) did not differ appreciably from those in Bear and Cottage creeks.

**Résumé** : La taille corporelle, la composition en âge et l'épaisseur corporelle des mâles ont été comparées dans le cas de cinq populations de saumons sockeye (*Oncorhynchus nerka*) du lac Washington. Deux des populations sont indigènes (ruisseaux Bear et Cottage) au bassin hydrographique et trois (rivière Cedar, ruisseau Issaquah et Pleasure Point) ne sont pas indigènes (provenant du lac Baker, en Washington). Pour séparer la contribution relative du type d'habitat et du lien de filiation à la variation phénotypique, nous avons comparé les populations ayant (*i*) des origines semblables et des habitats semblables, (*ii*) des origines différentes et des habitats différents, (*iii*) des origines semblables et des habitats différents et enfin, (*iv*) des origines différentes et des habitats semblables. Les saumons en frai dans la rivière Cedar étaient plus âgés et plus gros que ceux des populations indigènes, résultats qui concordent avec leur origine (les poissons contemporains du lac Baker sont également plus gros et plus âgés) et avec la variation de l'habitat (la rivière Cedar est beaucoup plus grande que les ruisseaux Bear et Cottage). La taille corporelle et la composition en âge n'ont pas différé de manière statistiquement significative chez les trois populations non indigènes, mais l'épaisseur corporelle des mâles frayant sur la plage du lac (Pleasure Point) était plus grande que celle des mâles de la rivière Cedar, ce qui indiquerait une divergence liée à l'adaptation. Une convergence adaptative peut également avoir eu lieu parce que la population du ruisseau Issaquah (ruisseau de taille intermédiaire) n'a pas différé de manière substantielle de celles des ruisseaux Bear et Cottage.
[Traduit par la Rédaction]

## Introduction

Natal homing by Pacific salmon (*Oncorhynchus* sp.) isolates discrete conspecific breeding aggregations (Quinn et al. 1987; Tallman and Healey 1994). Such "populations" are often genetically distinct from one another, owing to mutation, random genetic drift, and natural selection (Ehrlich and Raven 1969; Endler 1986; Altukhov and Salmenkova 1991; Adkison 1995; Wood 1995). Mutation and random genetic drift result in the divergence of reproductively isolated populations only if gene flow is limited (Slatkin 1987). In contrast, natural selection directly affects an organism's fitness and can initiate population divergence even if gene flow is substantial (Ehrlich and Raven 1969; Endler 1986). Different Pacific salmon populations experience different selective regimes, leading to adaptive variation in life history, morphology, and behavior (Ricker 1972; Taylor 1991; Wood 1995).

Local adaptation is difficult to prove but recurring environment–phenotype correlations can provide strong circumstantial evidence for its role in evolution, especially if the trait in question has a genetic basis and a mechanism of selection is known (Endler 1986; Taylor 1991). Body size and age at maturity are positively correlated with stream size in sockeye salmon (*Oncorhynchus nerka*; Rogers 1987; Bishop 1990), chum salmon (*Oncorhynchus keta*; Beacham and Murray 1987), and pink salmon (*Oncorhynchus gorbuscha*; Beacham et al. 1988). These traits have a genetic basis (Hankin et al. 1993; Smoker et al. 1994) and are sensitive to natural and sexual selection (Holtby and Healey 1986; Healey 1987; van den Berghe and Gross 1989; Fleming and Gross 1994; Quinn and

Received November 22, 1995. Accepted June 14, 1996.
J13172

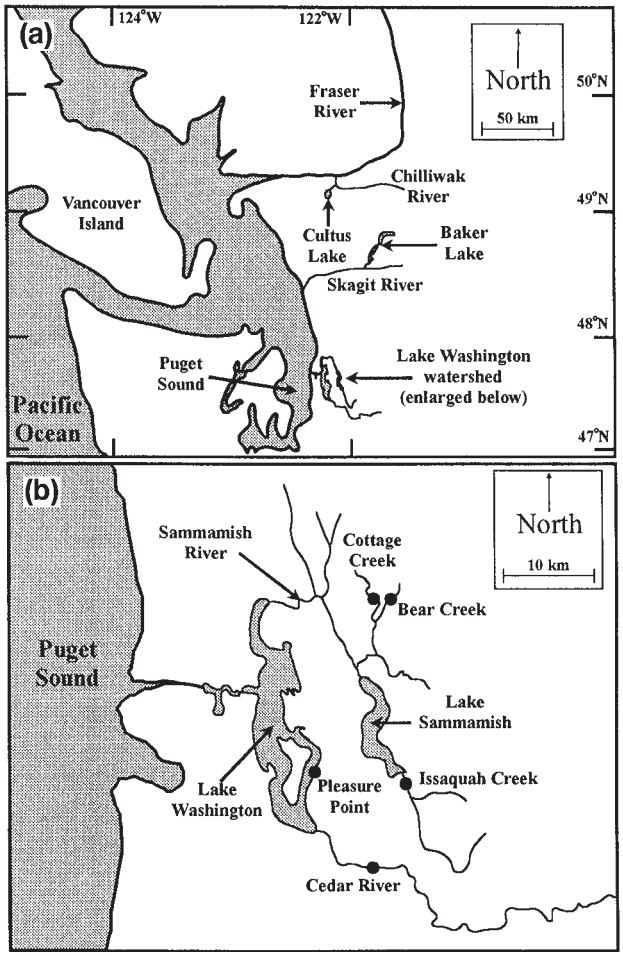
**A.P. Hendry[1] and T.P. Quinn.** University of Washington, Fisheries Research Institute, P.O. Box 357980, Seattle, WA 98195-7980, U.S.A.

[1] Author to whom all correspondence should be addressed.
e-mail: hendry@fish.washington.edu



© 1997 NRC Canada

**Fig. 1.** The locations of Cultus Lake, Baker Lake, and Lake Washington (*a*) and study sites within the Lake Washington watershed, shown as solid circles (*b*).




Foote 1994). Some morphological traits also covary with habitat features in a predictable manner. In sockeye salmon, males spawning on lake beaches have deeper bodies, at a common body size, than those in nearby streams (Bishop 1990; Blair et al. 1993; Wetzel 1993; Hamon 1995). The heritability of body depth has not been determined, but some interpopulation differences persist even in a common rearing environment, suggesting some genetic basis for the trait (Moore 1996). Evidence is also accumulating that secondary sexual traits, including male body depth, are influenced by natural and sexual selection (Fleming and Gross 1994; Quinn and Foote 1994; Hamon 1995; Moore 1996). Although some ambiguity remains in certain circumstances (Adkison 1995), local adaptation is undoubtedly important in the evolution of sockeye salmon body size, age at maturity, and morphology (Blair et al. 1993; Wood 1995; Moore 1996).

Most North American salmon populations probably became established after the last glacial retreat but well before the arrival of Europeans (Wood et al. 1994; Wood 1995; Taylor et al. 1996). Evolution in these populations has been the product of at least hundreds and probably thousands of years of selection. Occasionally, however, salmon have recently colonized new areas following transplants (e.g., Royal and Seymour 1940; Blackett 1979; Gharrett and Thomason 1987; McDowall 1994) or the recession of glaciers (e.g., Milner and Bailey 1989). Circumstances such as these provide opportunities to evaluate evolutionary processes within new populations (Endler 1986; Wood 1995). In the Great Lakes, for example, introduced pink salmon have diverged genetically from a common ancestral group in 12–13 generations, primarily because of random genetic drift and founder effects (Gharrett and Thomason 1987). In New Zealand, life-history traits currently differ among populations of chinook salmon (*Oncorhynchus tshawytscha*) introduced from a common source, perhaps reflecting local adaptation in less than 20 generations (Quinn and Unwin 1993).

## Lake Washington sockeye salmon and their origins

The historical distribution and abundance of *O. nerka* within Lake Washington is poorly understood. Nevertheless, substantial numbers of kokanee (the nonanadromous form) and limited runs of sockeye salmon (the anadromous form) were probably present at the turn of the century (see references in Hendry et al. 1996). In 1912 (not 1917 as reported in Hendry et al. 1996), a ship canal was constructed at the lake's western edge, forming a new outlet, and the Cedar River (formerly a tributary to the Duwamish River) was diverted into the southern end of the lake. Associated changes in the drainage pattern (the original outlet dried up) and lake level (a drop of 3 m) were generally assumed to have resulted in the extinction or severe depletion of any native runs (Ajwani 1956; Woodey 1966). In the 1930s and 1940s, sockeye salmon were introduced into Lake Washington from Cultus Lake, British Columbia, and from Baker Lake, Washington (reviewed in Hendry 1995). Analysis of allelic variation at protein-coding (allozyme) loci has indicated that the transplants from Baker Lake, but not those from Cultus Lake, made a substantial contribution to the existing population mixture (Hendry et al. 1996).

Situated in the Skagit River system north of Lake Washington (Fig. 1), Baker Lake contains sockeye salmon for which historical records of abundance, distribution, and propagation are as ambiguous as those for Lake Washington. Although the details are much too convoluted to discuss here, several generalizations are relevant to the present study (for a complete list of pertinent citations contact the primary author of this paper). First, substantial stream and beach spawning populations were present at the turn of the century but the relative abundance of each spawning type is not known. Second, hatchery production was initiated in 1896 using a mixture of stream spawners (captured in the Upper Baker River) and beach spawners (captured in the lake using gill nets). The relative contributions of any such subpopulations to hatchery production cannot be estimated because any detailed records that may have existed were destroyed in a series of fires (Kemmerich 1945). Third, between 1899 and 1933 virtually all sockeye salmon returning to Baker Lake were captured in a weir at the lake's outlet and then spawned in hatcheries (Kemmerich 1945). Fourth, numerous transfers of eggs and fry between the two hatcheries that propagated Baker Lake sockeye salmon (Kemmerich 1945) thoroughly mixed the descendants of any subpopulations that might initially have been present. Juveniles from these hatcheries were subsequently used for the Lake Washington introductions, beginning in 1937 (Royal and

© 1997 NRC Canada

Seymour 1940; Kemmerich 1945; Woodey 1966; Hendry 1995). We conclude that although both beach and stream spawning fish likely contributed to the initial Baker Lake hatchery stock, subsequent artificial propagation for seven or eight generations likely achieved a complete genetic admixture prior to the Lake Washington introductions. Note that this more recent interpretation differs somewhat from that stated in Hendry et al. (1996).

The original Baker Lake transplants gave rise to self-sustaining populations in the Cedar River and Issaquah Creek (Royal and Seymour 1940; Hendry et al. 1996). Strays from these locations apparently then gave rise to several additional populations, including those spawning on beaches within Lake Washington (Hendry et al. 1996). As no recent introductions have occurred, the Baker-derived populations have been isolated from their ancestral group since 1945, more than 12 generations. Despite the numerical predominance of non-native fish, sockeye salmon indigenous to the watershed appear to have persisted in several small streams, reproductively isolated from the Baker-derived groups (Hendry et al. 1996). This rare combination of native and non-native conspecifics reproducing in different environments provided an opportunity to evaluate the interaction between ancestral affinities and habitat features in the evolution of population-specific life history and morphology.

### Approach and objectives

This study examined variation in body size, age composition, and male body depth among five Lake Washington sockeye salmon populations. Consistent interpopulation patterns were interpreted in relation to ancestral relationships and physical features of the spawning environment (stream size, water depth, flow, and discharge). First, we compared populations with a common origin and similar habitats, predicting that they would not differ in their life history or morphology. Second, we compared populations that differed in both origin and spawning habitat, predicting differentiation attributable to selection and (or) ancestry. Third, we compared populations with the same origin and different habitats. If phenotypic differences were evident in this comparison, and such differences were consistent with habitat variation, adaptive population divergence may have occurred. Finally, we tested for differences among populations with different origins and similar habitats. If selection were the predominant evolutionary force, these populations might have converged for some traits despite probable differences in their ancestral genotypes.

## Methods

Study sites within the Lake Washington drainage (Fig. 1) were chosen on the basis of their annual escapement and existing evidence as to their distinctiveness (see references in Hendry 1995). Study sites and their annual escapements included the Cedar River (76 000 – 359 000), Issaquah Creek (707 – 23 979), Bear and Cottage creeks (1795 – 27 533), and the Pleasure Point Beach (54–103). The Cedar River, Issaquah Creek, and Pleasure Point populations were of Baker Lake origin and the Bear Creek and Cottage Creek populations were indigenous to Lake Washington (Hendry et al. 1996). No other large populations (escapement perennially >500) were present within the watershed.

### Habitat features

Habitat surveys within Lake Washington took place in November and December of 1993 at all locations except Pleasure Point, which was surveyed in June of 1994. For the three creeks, 10 equidistant transects were placed perpendicular to the stream's flow through the area from which adults were collected. Five sampling locations, evenly spaced across the wetted width of the channel, were then established along each transect (i.e., 50 total sampling locations per creek). In the Cedar River, most randomly selected locations were too deep and fast for sampling, so only four such transects were established (river km 13, 16, 20, and 22). At Pleasure Point (a beach within Lake Washington), 10 equidistant transects were placed perpendicular to the shoreline across the area used for spawning. These transects, each of which had five evenly spaced sampling locations, extended from the shore (where spawning began) to the point where spawning ceased (9–16 m offshore).

Wetted channel width (width of water at time of survey) was measured along each transect in the four streams. At each sampling location, water depth was recorded and water velocity was determined at the surface and immediately above the substrate, using a model 2100 current velocity meter (Swoffer Instruments, Inc.). Averages and standard errors were calculated for each habitat feature. Mean daily discharge was calculated for the Cedar River, Issaquah Creek, and Bear Creek (over October and November, 1992–1993), using data provided by the U.S. Geological Survey (Pacific Northwest District, Tacoma Field Office, 1201 Pacific Avenue, Suite 520, Tacoma, WA 98402).

### Collection and sampling of adults

In 1992 and 1993, adult sockeye salmon were collected during peak spawning periods from each of the five Lake Washington populations and from Baker Lake. Collection techniques and timing varied among the populations, reflecting limitations imposed by the habitat and by the abundance of spawners. In each case, however, we attempted to minimize capture biases associated with fish size or shape. In 1992 and 1993, live fish were collected from the three creeks using an electroshocker (October and November), from Pleasure Point using hand spears and angling (November), and from the Cedar River using fine-mesh gill nets (October and November, 1992) and a weir (November and December, 1993). At the Cedar River and Bear Creek in 1994, fish were collected from stream banks within several days of their death. At Baker Lake, dead fish were collected from artificial spawning ponds within 12 h of their death.

Otoliths were removed from each fish and used to determine age at maturity, specified as the number of freshwater annuli followed by the number of saltwater annuli. For example, a 4-year-old fish that spent one winter rearing in the lake and two winters in the ocean would be considered age 1.2 (one winter was also spent in the gravel). Calipers were used to measure (*i*) body length (middle of the eye to the end of the hypural plate) to the nearest millimetre on all fish and (*ii*) body depth (anterior insertion of dorsal fin to the bottom of the abdomen, perpendicular to the lateral line) to the nearest 0.1 mm on all live males. To control for possible effects of reproductive condition on male body depth (Quinn and Blair 1992), each was classified as green (not sexually mature, no loose eggs or milt), ripe (sexually mature, no deterioration of body condition), spawned out (deterioration of body condition), or dead.

### Statistical analyses

The data collected in this study fell into three discrete groups: (*i*) age, body length, and body depth for live fish collected from the five Lake Washington populations in 1992 and 1993, (*ii*) age and body length for dead fish from the Cedar River and Bear Creek in 1994, and (*iii*) age and body length for dead fish from Baker Lake in 1992 and 1993. Ideally, all years of data would have been incorporated into a single analysis focusing on each trait. This could not be done for several reasons. First, only two populations were sampled in 1994,

© 1997 NRC Canada

**Table 1.** Summary of habitat features at the sites from which spawning sockeye salmon were collected in Lake Washington.

| | Cedar River | Issaquah Creek | Bear Creek | Cottage Creek | Pleasure Point |
|---|---|---|---|---|---|
| Channel width (m) | 30.75±1.5 | 11.58±0.9 | 5.11±0.6 | 4.66±0.9 | na |
| Water depth (cm) | 52.3±2.7 | 36.9±2.4 | 24.1±1.7 | 29.4±2.4 | 137.3±2.4 |
| Surface velocity (cm/s) | 111.7±3.9 | 58.7±3.5 | 24.1±1.7 | 29.3±3.5 | 0 |
| Bottom velocity (cm/s) | 69.9±3.2 | 32.3±2.9 | 21.2±2.0 | 25.5±2.9 | 0 |
| Discharge ($m^3/s$) | 11.6 | 1.5 | 0.3 | — | na |

**Note**: Values for wetted channel width, water depth, surface velocity, and bottom velocity are given as the mean ± standard error. The discharge data are mean daily values for the months of October and November averaged over 1992 and 1993. na, not applicable.

and so these data could not be included in analysis of variance (ANOVA) with the 1992 and 1993 data. Second, it would have been inappropriate to directly compare current phenotypes in the Baker Lake population with those found within Lake Washington because of extensive hatchery influence in the Baker Lake system (see Introduction). To accommodate the distinctive nature of the three data groups, each was analyzed separately.

Factors affecting age composition were examined using log-linear models that incorporated population (Cedar River, Cottage Creek, Bear Creek, Issaquah Creek, and Pleasure Point), sex (male and female), year (1992 and 1993), and age category (1.1, 1.2, and 1.3). In this type of analysis, low $p$ values accompanied models that did not fit the data well, whereas high $p$ values were associated with models that were needlessly complex (Wilkinson et al. 1992, p. 672). Our goal was to define the simplest model that adequately explained the effects of population, sex, and year on the frequency of fish in a given age category. To this end, backward selection at $\alpha = 0.05$ was used to define a final model.

Body length data were analyzed separately for males and for females using (*i*) fish of all ages and (*ii*) age-1.2 fish only. For 1992 and 1993, two-way ANOVA with fixed effects was used to test for differences among populations and between years. As year effects and interaction terms were commonly significant ($p < 0.05$), variation among populations was further examined with each year using Student–Newman–Keuls tests. For the 1994 data, two-sample $t$ tests were used to test for a difference in body length between the Cedar River and Bear Creek for males and for females.

Reproductive condition can influence adult morphology: males are deeper bodied when ripe than when senescent or dead (Quinn and Blair 1992). Hence, we included only ripe males in the analysis of body depth variation. Simple linear regression revealed that body depth and body length were positively correlated ($r^2 = 0.61$, $F = 380.37$, $p < 0.001$). Therefore, an allometric adjustment was used to standardize male body depth to a common body length, allowing interpopulation comparisons independent of covariation with body size (Reist 1986). Analysis of covariance (ANCOVA) (using $\log_{10}$ values) was used to test for homogeneity of slopes among the different collections (population- and year-specific) in the body depth – body length relationship. The slopes of these relationships did not differ ($F = 0.97$, $p = 0.467$), and the body depth of each male was then standardized to the common body length of all ripe males (445 mm), using Ihssen et al.'s (1981) adjustment equation:

$$D_{std} = D_o(L/L_o)^b$$

where $D_{std}$ was the standardized body depth, $D_o$ was the observed body depth, $L$ was the common body length, $L_o$ was the observed body length, and $b$ was the common within-group slope (Reist 1986) of $\log_{10}$ body depth on $\log_{10}$ body length. The adjustment coefficient ($b = 1.118$) was calculated using ANCOVA to allow for different intercepts while maintaining a common slope (Reist 1986). The effectiveness of the standardizing technique was evaluated using simple linear regression to test for a relationship between standardized body depth and body length. Variation in standardized male body depth was analyzed using two-way ANOVA with fixed effects (population and year). Student–Newman–Keuls tests were used for all pairwise interpopulation comparisons within each year.

## Results

Bear Creek and Cottage Creek were the narrowest, shallowest, and slowest flowing of the study streams (Table 1). At the other extreme, the Cedar River was the widest, deepest, and fastest (Table 1), with actual averages for these features probably greater because many locations were too deep and fast for sampling. Average daily discharge from the Cedar River was almost 10 times that of the next largest stream, Issaquah Creek, which had a discharge 5 times that of Bear Creek (Table 1). Bear and Cottage creeks were similar in all respects, but their average discharge could not be compared because Cottage Creek lacked a gauging station. The Pleasure Point Beach spawning area was deep (never <1 m) and had no measurable current (Table 1).

Log-linear analysis of age composition revealed that main effects alone (population, sex, year, and age category) were not sufficient to explain the observed variation ($G = 432.06$, df = 51, $p < 0.001$) but that a model containing all three-way interactions was needlessly complex ($G = 8.69$, df = 8, $p = 0.369$). Simplification by serial removal of terms generated the final model, which included population, year, and sex; a three-way interaction between population, year, and age; and a two-way interaction between population and sex ($G = 31.53$, df = 25, $p = 0.172$). The complexity of even this final model underscored the confounding influence of interannual variation and differences between males and females.

Age-1.2 fish predominated in 1992 (89%) and 1994 (97%) but age-1.3 fish were almost as common in 1993 (46% age 1.2 versus 42% age 1.3). Age composition varied the most between years in Issaquah Creek: not one age-1.3 salmon was collected in 1992 but 89% age-1.3 males and 90% age-1.3 females were collected in 1993 (Table 2). The highest proportion of age-1.1 spawners was found in Bear and Cottage creeks (14%), whereas only one age-1.1 fish was collected from the Cedar River ($N = 350$), and not one was collected from Issaquah Creek ($N = 147$). The proportion of age-1.3 spawners varied greatly among years and populations but, within a given year, Bear and Cottage creeks were usually among the populations having the fewest fish of that age (Table 2).

For males of all ages combined, body length differed among the populations ($F = 6.36$, $p < 0.001$) but not between the years ($F = 0.44$, $p = 0.507$), with an interaction between population and year ($F = 9.03$, $p < 0.001$). In 1992, Cedar River males were the largest, and in 1993, Issaquah Creek males were the largest (Fig. 2). In 1994, males from the Cedar River were larger than those from Bear Creek (493.7 versus 453.7 mm;

© 1997 NRC Canada

**Table 2.** Sample sizes (*N*) and the proportion (%) of males and females in each age category, within each population and year.

| | 1992 | | | | 1993 | | | | 1994 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *N* | 1.1 | 1.2 | 1.3 | *N* | 1.1 | 1.2 | 1.3 | *N* | 1.1 | 1.2 | 1.3 |
| Males | | | | | | | | | | | | |
| Pleasure | 27 | 4 | 56 | 41 | 24 | 17 | 70 | 13 | — | — | — | — |
| Bear | 33 | 3 | 91 | 6 | 27 | 48 | 32 | 20 | 50 | 0 | 100 | 0 |
| Cedar | 41 | 0 | 80 | 20 | 40 | 3 | 79 | 18 | 49 | 0 | 92 | 8 |
| Cottage | 28 | 7 | 93 | 0 | 23 | 48 | 17 | 35 | — | — | — | — |
| Issaquah | 54 | 0 | 100 | 0 | 40 | 0 | 11 | 89 | — | — | — | — |
| Females | | | | | | | | | | | | |
| Pleasure | 13 | 8 | 83 | 8 | 17 | 0 | 63 | 38 | — | — | — | — |
| Bear | 30 | 0 | 90 | 10 | 26 | 35 | 27 | 38 | 49 | 0 | 100 | 0 |
| Cedar | 93 | 0 | 86 | 14 | 77 | 0 | 53 | 47 | 50 | 0 | 94 | 6 |
| Cottage | 20 | 0 | 100 | 0 | 16 | 31 | 38 | 31 | — | — | — | — |
| Issaquah | 29 | 0 | 100 | 0 | 24 | 0 | 8 | 92 | — | — | — | — |

**Note**: In 1994, fish were collected only from the Cedar River and Bear Creek.

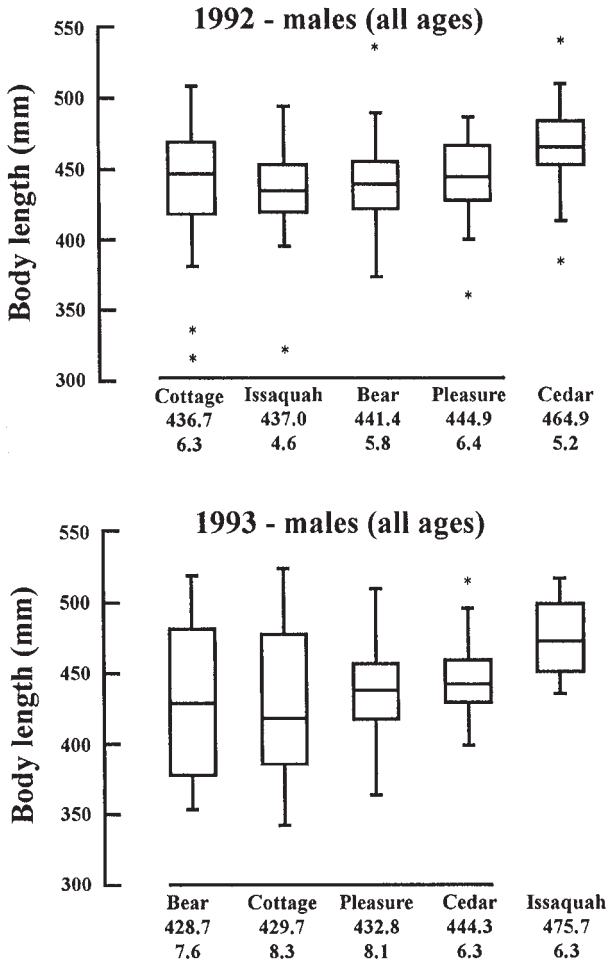
$t = 8.63$, df = 98, $p < 0.001$). For age-1.2 males, body length did not differ consistently among populations ($F = 0.98$, $p = 0.417$; Fig. 3) or between the years ($F = 0.55$, $p = 0.459$), but there was an interaction between these factors ($F = 3.13$, $p = 0.016$). In 1994, age-1.2 Cedar River males were larger than age-1.2 Bear Creek males (490.5 versus 453.7 mm; $t = 7.75$, df = 92, $p < 0.001$).

For females of all ages, body length differed among the populations ($F = 22.56$, $p < 0.01$) and between the years ($F = 18.15$, $p < 0.001$), with an interaction between these factors ($F = 5.71$, $p < 0.001$). In 1992, Cedar River females were largest, and in 1993 they were larger than females from all populations except Issaquah Creek (Fig. 4). In 1994, Cedar River females were larger than those in Bear Creek (487.7 versus 440.6 mm; $t = 9.20$ df = 98, $p < 0.001$). For age-1.2 females, body length differed among populations ($F = 11.82$, $p < 0.001$) and between years ($F = 9.33$, $p = 0.003$), with an interaction between these factors ($F = 6.35$, $p < 0.001$). In 1992, age-1.2 Cedar River females were larger than those from all of the other populations, but in 1993, they were only larger than those in Cottage Creek and at Pleasure Point (Fig. 5). In 1994, age-1.2 Cedar River females were larger than those from Bear Creek (486.4 versus 440.9 mm; $t = 8.78$, df = 95, $p < 0.001$).

The body depth of ripe males was positively correlated with body length before ($r^2 = 0.61$, $F = 380.37$, $p < 0.001$) but not after ($r^2 = 0.00$, $F = 0.63$, $p = 0.426$) standardizing to a common body length of 445 mm. Therefore, Ihssen et al.'s (1981) adjustment equation using the common within-group coefficient (Reist 1986) was effective at removing the effects of body size. The standardized body depth of males differed among populations ($F = 26.63$, $p < 0.001$) and between years ($F = 9.62$, $p = 0.002$), with no interaction between these factors ($F = 1.55$, $p = 0.188$). In both years, Cedar River males had the shallowest bodies (Fig. 6). Pleasure Point males had the deepest bodies in both years, although not always significantly so (Fig. 6).

In the Baker Lake collections, age-1.2 fish predominated in 1992 (97% of the 31 males and 100% of the 28 females) and in 1993 (62% of the 29 males and 76% of the 35 females). The remainder of these collections was comprised of age-1.3 fish. Baker Lake males of all ages averaged 463.0 ± 4.3 mm (mean ± SE) in 1992 and 488.3 ± 5.1 mm in 1993. Age-1.2 Baker Lake males averaged 461.7 ± 4.3 mm in 1992 and 479.6 ± 5.5 mm in 1993. Baker Lake females of all ages averaged

**Fig. 2.** Body length (millimetres) of male sockeye salmon from each population (all ages pooled). For the box plots, the horizontal line is the median value, the boxes contain 50% of the data, and the whiskers contain the remainder of the data excluding outliers, which are denoted with an asterisk. Below the box plots are the results of Student–Newman–Keuls pairwise comparisons within each year following ANOVA. A horizontal bar above populations indicates nonsignificant differences ($p > 0.05$). Below each population is the mean and the standard error for measurements in that year.




© 1997 NRC Canada

**Fig. 3.** Body length (millimetres) of male sockeye salmon from each population (age-1.2 fish only). For details see the caption of Fig. 2.

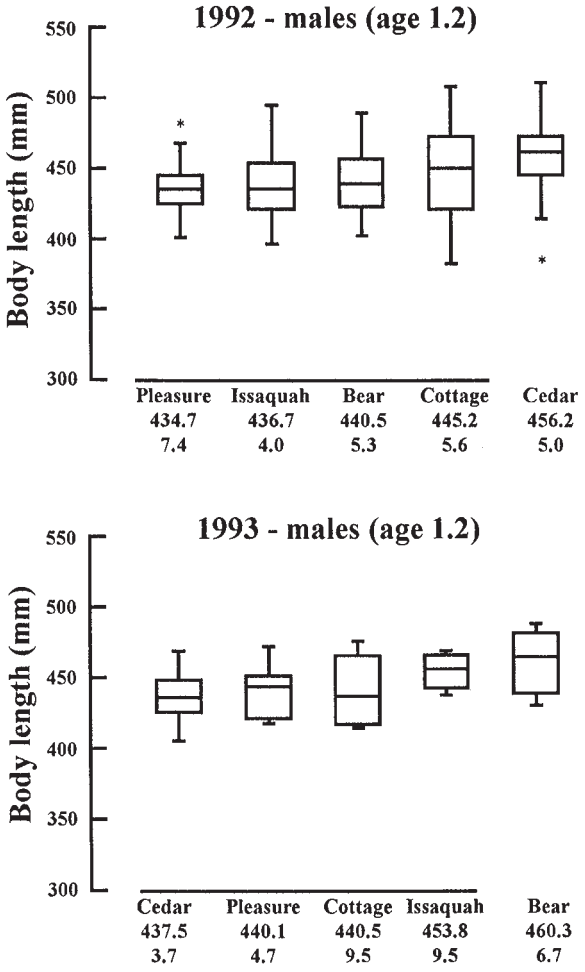
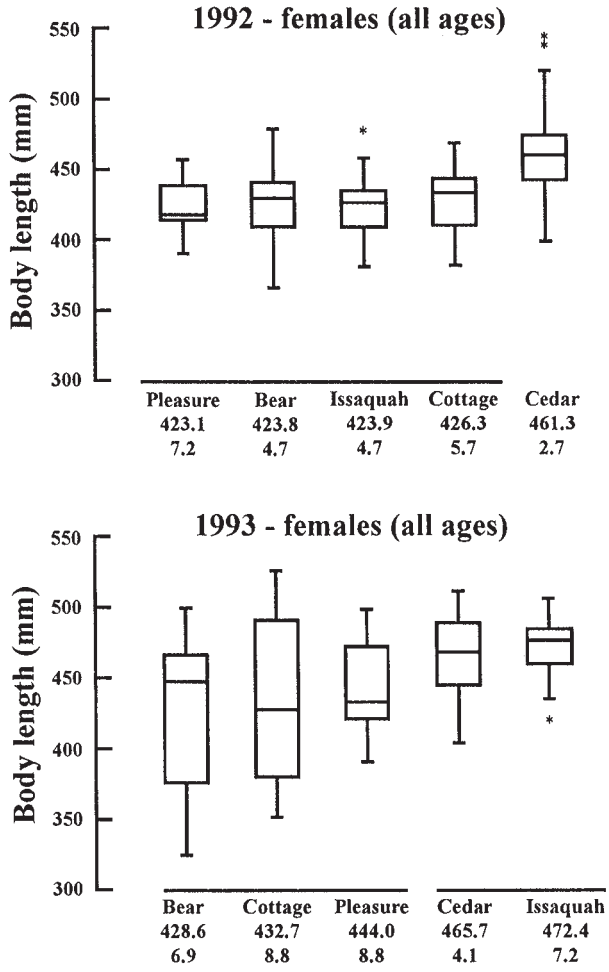



**Fig. 4.** Body length (millimetres) of female sockeye salmon from each population (all ages pooled). For details see the caption of Fig. 2.




444.6 ± 4.2 mm in 1992 and 478.0 ± 5.1 mm in 1993. Age-1.2 Baker Lake females averaged 444.6 ± 4.4 mm in 1992 and 465.5 ± 4.7 mm in 1993.

## Discussion

### Populations with the same origin and similar habitats

The two populations with a common origin and similar spawning habitats (Bear and Cottage) did not differ in age composition, body length, or male body depth. These two populations also did not differ in allelic frequencies at allozyme loci (Hendry et al. 1996) or in their hatching time under controlled rearing conditions (Hendry 1995). The overall similarity between these two populations was consistent with their geographic proximity (Fig. 1), which would facilitate straying and gene flow, and with their similar selective regimes (Table 2), which would favor similar adaptations. An equivalent comparison could not be made within the non-native lineage because each of the three Baker-derived populations spawned in a distinct habitat (a river, a creek, and a beach).

### Populations with different origins and different habitats

Several traits varied consistently between non-native fish spawning in the largest river (Cedar) and native fish spawning in the smallest creeks (Bear and Cottage). First, the Cedar River population typically had fewer young spawners (age 1.1) and more old spawners (1.3) than either Bear Creek or Cottage Creek. Large interannual variation in age composition (probably reflecting variation in recruitment and growth) often confounded interpopulation comparisons, but the above trend was evident within each year (except for age-1.3 males in 1993). Second, Cedar River females, and to a lesser extent males, were larger than those in Bear and Cottage creeks. Size at age and age at maturity were positively correlated (Hendry 1995), but Cedar River females were larger even when analysis was limited to the most common age category (1.2). Potential effects of phenotypic plasticity on age and size were not known, but there was also no evidence that the populations differed appreciably in their feeding opportunities, migration patterns, or migration timing.

Positive relationships between body size, age at maturity, and the size of spawning streams have been attributed to natural selection (Beacham and Murray 1987; Rogers 1987; Beacham et al. 1988; Bishop 1990). Large rivers are often characterized by large gravel, high flows, and periods of bedload movement (i.e., gravel scour). Large spawners, especially

© 1997 NRC Canada

**Fig. 5.** Body length (millimetres) of female sockeye salmon in each population (age-1.2 fish only). For details see the caption of Fig. 2.

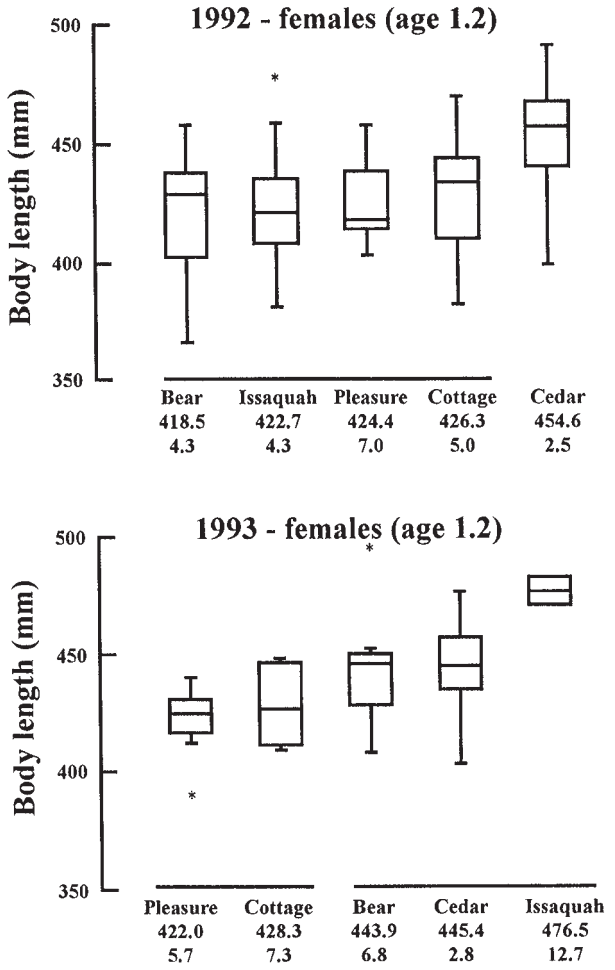
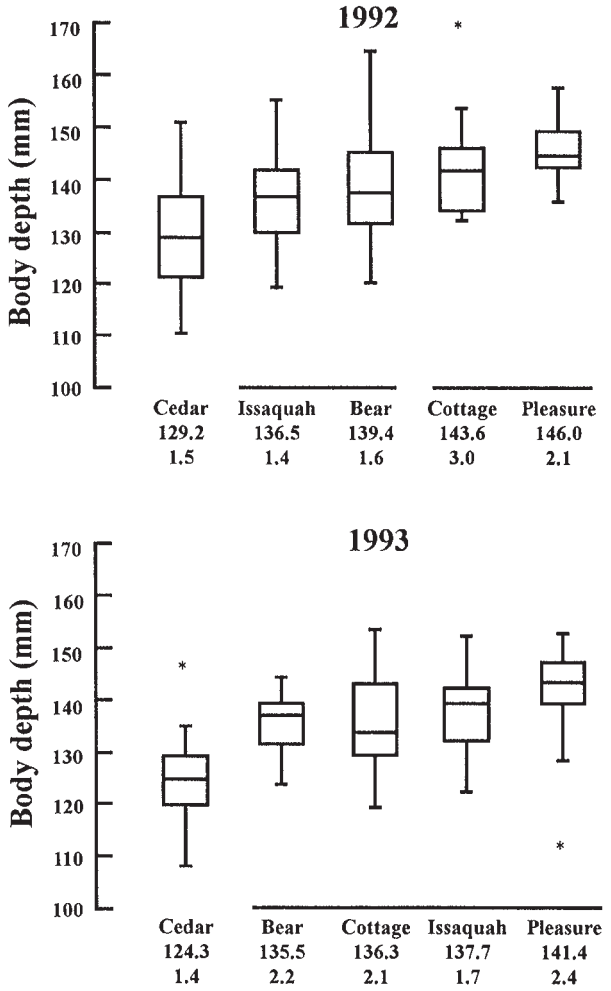



**Fig. 6.** Standardized body depth (millimetres) of ripe male sockeye salmon in each population (all ages pooled). For details see the caption of Fig. 2.




females, should be favored in such environments because they can (*i*) build their redds in larger gravels (cf. Beacham and Murray 1987), (*ii*) negotiate higher flows during upriver migration (Brett and Glass 1973), and (*iii*) bury their eggs below the depth of scour (van den Berghe and Gross 1984). Extensive flooding and scour were common in the Cedar River, often resulting in periods of very high embryo mortality (Thorne and Ames 1987). Hence, older females (and larger females for a given age) might be favored in the Cedar River but not in the much more stable environment of Bear and Cottage creeks.

Fish with different origins and different habitats could also be contrasted by comparing the non-native beach population (Pleasure Point) with the native creek populations (Bear and Cottage). Unlike the previous contrast, these groups were largely indistinguishable from each other on the basis of their phenotypes. This was not unexpected for age at maturity and body size because lake beaches would also lack selection associated with strong water flow. However, one trait that was expected to differ between these groups was male body depth. Sexual selection favors deep bodies in beach spawning males (Quinn and Foote 1994). In small streams, however, males with deep bodies may be more susceptible to stranding or terrestrial predation. As a result, beach spawning males commonly have deeper bodies than their stream spawning counterparts (Bishop 1990; Blair et al. 1993; Wetzel 1993; Hamon 1995). In Lake Washington, however, Pleasure Point males did not have significantly deeper bodies than Bear and Cottage creek males, perhaps because bear predation was nonexistent and access would not be difficult for even the largest and most dimorphic males.

In 1992 and 1993, the Baker Lake population was most similar in size and age to the Cedar River population and least similar to the Bear and Cottage creek populations. Thus, ancestral genotypes may have predisposed the Cedar River fish to be larger and older than the native Lake Washington fish. However, the Baker Lake fish were spawned in hatcheries from 1896 to 1933 and in man-made ponds since 1957. Therefore, current phenotypes may not reflect those in the original donor group and inferences about life history and morphology in the ancestral populations are purely speculative.

### Populations with the same origin and different habitats

Sockeye salmon spawning in streams and on beaches often represent divergent population groups (Blair et al. 1993; Varnavskaya et al. 1994; Burger et al. 1995; Quinn et al. 1995; Wood 1995). In Alaskan lake systems, beach spawning males

© 1997 NRC Canada

have deeper bodies, for a given length, than stream spawning males, probably because deep bodies are favored by sexual selection on beaches but opposed by natural selection in small streams (see above). In fast-flowing streams, deep bodies might also increase hydraulic drag, which would be energetically disadvantageous during spawning and migration (cf. Fleming and Gross 1989; Moore 1996). Stream and beach spawning areas in Lake Washington were both occupied by fish derived from Baker Lake, and the beach spawning males (Pleasure Point) had deeper bodies than the stream spawning males (except for Issaquah Creek in 1993). Phenotypic plasticity may have contributed to this pattern (although there is as yet no evidence for this), but body depth has at least some genetic basis (Moore 1996). Therefore, variation in male body depth within Lake Washington may reflect the rapid adaptation (12–14 generations) of populations to their spawning habitat. Morphological divergence despite probable gene flow (Hendry et al. 1996) is in accord with the view that natural selection can cause divergence more rapidly than genetic drift (Ehrlich and Raven 1969).

Body size and age composition did not differ consistently among the three Baker-derived populations. The lack of differences in these traits could have been due to (*i*) inadequate time for differences to arise, (*ii*) substantial gene flow that prevented divergence, and (*iii*) the absence of a sufficient selection differential. The first two possibilities were unlikely because other traits could delineate Pleasure Point (male body depth, the present study) and Issaquah Creek (allozyme allelic frequencies, Hendry et al. 1995). Finally, habitat variation may have been insufficient to select for differences in age at maturity and body size. These traits differ between beach and stream populations in some lakes (Blair et al. 1993) but not in others (Wetzel 1993; Burger et al. 1995). We suggest that the contrasting environments of beaches and streams may have a greater effect on male body depth than on body size and age at maturity, at least in some instances.

**Populations with different origins and similar habitats**

When populations with different origins become established in habitats with similar selective regimes, local adaptation and (or) phenotypic plasticity could cause their phenotypic convergence. Adaptive convergence is evident in the parallel life-history evolution of kokanee derived independently from anadromous populations in different lake systems (Wood 1995; Taylor et al. 1996). Similarly, the adaptive convergence of anadromous populations probably maintains environment–phenotype correlations that are evident at varying geographical scales. In male sockeye salmon, for instance, migration distance is negatively correlated with body depth and body size, perhaps owing to hydrodynamic constraints and variation in patterns of energy allocation (Moore 1996). In female sockeye salmon, egg size is positively correlated with the size of incubation gravels, probably in response to dissolved oxygen availability and surface to volume ratio constraints for developing embryos (Quinn et al. 1996).

For Lake Washington, it was difficult to evaluate adaptive convergence because both native populations were found in small creeks, whereas the introduced populations were in a larger creek, in a river, and at a beach. Nonetheless, Bear and Cottage creeks were more similar in their habitat to Issaquah Creek than they were to the Cedar River or Pleasure Point (Table 1). Consistent differences in body size and male body depth were not evident between the Issaquah Creek population and the Bear and Cottage creek populations. Cedar River females, on the other hand, were consistently larger than those in Bear and Cottage creeks. Hence, the similarity in the body sizes of the Bear and Cottage creek fish to that of fish in Issaquah Creek, but not to that of fish in the Cedar River, was consistent with the general character of their habitats and might reflect adaptive convergence.

**Summary**

The Lake Washington drainage supports several anadromous sockeye salmon populations, isolated from each other to varying degrees. This study examined variation in life history and morphology among two adjacent populations that were indigenous to the watershed (Bear and Cottage creeks) and three other discrete groups that all had their origin in transplants from Baker Lake (Cedar River, Issaquah Creek, and Pleasure Point). Within these populations, age at maturity, body size, and male body depth varied interannually, but consistent differences were still evident among several of the groups. For instance, young and small spawners were rare in the largest river (Cedar) whereas old and large spawners were rare in the smallest creeks (Bear and Cottage). These differences may reflect adaptation to local selective regimes or the persistence of ancestral phenotypes (contemporary Baker Lake sockeye salmon were also old and large). Apparent adaptive divergence of non-native populations (Pleasure Point males were deep bodied and Cedar River males were shallow bodied) provided supporting evidence for the role of natural selection in the rapid evolution of population-specific traits.

## Acknowledgments

Field collections were assisted primarily by Jay Hensleigh, Burt Lewis, Laura Hartema, and Denise Hawkins. Logistical support and valuable advice were provided by Jim Ames, Ron Egan, Kurt Fresh, Rick Gustafson, Paul Seidel, and Gary Sprague. The otoliths were read by Carol Lidstone and Holly Derham (Pacific Salmon Commission) and by John Sneva (Washington Department of Fish and Wildlife). Comments on earlier drafts by Chris Foote, Mike Kinnison, Steve Schroder, Fred Utter, and two anonymous reviewers substantially improved the manuscript. This research was funded by the H. Mason Keeler Endowment. A.P.H. was supported by a Natural Sciences and Engineering Research Council postgraduate scholarship and an H. Mason Keeler fellowship.

## References

Adkison, M.D. 1995. Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment? Can. J. Fish. Aquat. Sci. **52**: 2762–2777.

Ajwani, S. 1956. A review of Lake Washington watershed, historical, biological and limnological. M.S. thesis, University of Washington, Seattle, Wash.

Altukhov, Y.P., and Salmenkova, E.A. 1991. The genetic structure of salmon populations. Aquaculture, **98**: 11–40.

Beacham, T.D., and Murray, C.B. 1987. Adaptive variation in body size, age, morphology, egg size, and developmental biology of chum salmon (*Oncorhynchus keta*) in British Columbia. Can. J. Fish. Aquat. Sci. **44**: 244–261.

© 1997 NRC Canada

Beacham, T.D., Withler, R.E., Murray, C.B., and Barner, L.W. 1988. Variation in body size, morphology, egg size, and biochemical genetics of pink salmon in British Columbia. Trans. Am. Fish. Soc. **117**: 109–126.

Bishop, S.M. 1990. Morphometric differences among spawning populations of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake System. M.S. thesis, University of Washington, Seattle, Wash.

Blackett, R.F. 1979. Establishment of sockeye (*Oncorhynchus nerka*) and chinook (*O. tshawytscha*) salmon runs at Frazer Lake, Kodiak Island, Alaska. J. Fish. Res. Board Can. **36**: 1265–1277.

Blair, G.R., Rogers, D.E., and Quinn, T.P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. Trans. Am. Fish. Soc. **122**: 550–559.

Brett, J.R., and Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. J. Fish. Res. Board Can. **30**: 379–387.

Burger, C.V., Finn, J.E., and Holland-Bartels, L. 1995. Pattern of shoreline spawning by sockeye salmon in a glacially turbid lake: evidence for subpopulation differentiation. Trans. Am. Fish. Soc. **124**: 1–15.

Ehrlich, P.R., and Raven, P.H. 1969. Differentiation of populations. Science (Washington, D.C.), **165**: 1228–1232.

Endler, J.A. 1986. Natural selection in the wild. Princeton University Press, Princeton, N.J.

Fleming, I.A., and Gross, M.R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**: 141–157.

Fleming, I.A., and Gross, M.R. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution, **48**: 637–657.

Gharrett, A.J., and Thomason, M.A. 1987. Genetic changes in pink salmon (*Oncorhynchus gorbuscha*) following their introduction into the Great Lakes. Can. J. Fish. Aquat. Sci. **44**: 787–792.

Hamon, T. 1995. Artificial selection in the wild: selection on spawner morphology of wild sockeye salmon (*Oncorhynchus nerka*) by a gillnet fishery. M.S. thesis, University of Washington, Seattle, Wash.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**: 347–358.

Healey, M.C. 1987. The adaptive significance of age and size at maturity in female sockeye salmon (*Oncorhynchus nerka*). Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 110–117.

Hendry, A.P. 1995. Sockeye salmon (*Oncorhynchus nerka*) in Lake Washington: an investigation of ancestral origins, population differentiation and local adaptation. M.S. thesis, University of Washington, Seattle, Wash.

Hendry, A.P., Quinn, T.P., and Utter, F.M. 1996. Genetic evidence for the persistence and divergence of native and introduced sockeye salmon (*Oncorhynchus nerka*) within Lake Washington, Washington. Can. J. Fish. Aquat. Sci. **53**: 823-832.

Holtby, L.B., and Healey, M.C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **43**: 1946–1959.

Ihssen, P.E., Evans, D.O., Christie, W.J., Reckahn, J.A., and DesJardine, R.L. 1981. Life history, morphology, and electrophoretic characteristics of five allopatric stocks of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. **38**: 1790–1807.

Kemmerich, J. 1945. A review of the artificial propagation and transplantation of the sockeye salmon of the Puget Sound area in the State of Washington conducted by the Federal Government from 1896 to 1945. Report to the Regional Director, U.S. Fish and Wildlife Service. Available from the Washington Department of Fish and Wildlife, 600 Capitol Way North, Mail Stop 43151, Olympia, WA 98501-1091.

McDowall, R.M. 1994. The origins of New Zealand's chinook salmon, *Oncorhynchus tshawytscha*. Mar. Fish. Rev. **56**: 1–7.

Milner, A.M., and Bailey, R.G. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. Aquacult. Fish. Manage. **20**: 179–192.

Moore, K. 1996. The adaptive significance of body size and shape in sexually mature male sockeye salmon (*Oncorhynchus nerka*). M.S. thesis, University of Washington, Seattle, Wash.

Quinn, T.P., and Blair, G.R. 1992. Morphological changes in senescing adult male sockeye salmon (*Oncorhynchus nerka* Walbaum). J. Fish Biol. **41**: 1045–1047.

Quinn, T.P., and Foote, C.J. 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. Anim. Behav. **48**: 751–761.

Quinn, T.P., and Unwin, M.J. 1993. Variation in life history patterns among New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. Can. J. Fish. Aquat. Sci. **50**: 1414–1421.

Quinn, T.P., Wood, C.C., Margolis, L., Riddell, B.E., and Hyatt, K.D. 1987. Homing in wild sockeye salmon (*Oncorhynchus nerka*) populations as inferred from differences in parasite prevalence and allozyme allele frequencies. Can. J. Fish. Aquat. Sci. **44**: 1963–1971.

Quinn, T.P., Hendry, A.P., and Wetzel, L.A. 1995. The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). Oikos, **74**: 425–438.

Reist, J.D. 1986. An empirical evaluation of coefficients used in residual and allometric adjustment of size covariation. Can. J. Zool. **64**: 1363–1368.

Ricker, W.E. 1972. Hereditary and environmental factors affecting certain salmonid populations. *In* The stock concept in Pacific salmon. *Edited by* R.C. Simon and P.A. Larkin. H.R. MacMillan lectures in fisheries. University of British Columbia, Vancouver, B.C. pp. 27–160.

Rogers, D.E. 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 78–89.

Royal, L.A., and Seymour, A. 1940. Building new salmon runs. Prog. Fish-Cult. **52**: 1–7.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. Science (Washington, D.C.), **236**: 787–792.

Smoker, W.W., Gharrett, A.J., Stekoll, M.S., and Joyce, J.E. 1994. Genetic analysis of size in an anadromous population of pink salmon. Can. J. Fish. Aquat. Sci. **51**(Suppl. 1): 9–15.

Tallman, R.F., and Healey, M.C. 1994. Homing, straying, and gene flow among seasonally separated populations of chum salmon (*Oncorhynchus keta*). Can. J. Fish. Aquat. Sci. **51**: 577–588.

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture, **98**: 185–207.

Taylor, E.B., Foote, C.J., and Wood, C.C. 1996. Molecular genetic evidence for parallel life-history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). Evolution, **50**: 401–416.

Thorne, R.E., and Ames, J.J. 1987. A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Can. J. Fish. Aquat. Sci. **44**: 1791–1795.

van den Berghe, E.P., and Gross, M.R. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **41**: 204–206.

van den Berghe, E.P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**: 125–140.

Varnavskaya, N.V., Wood, C.C., Everett, R.J., Wilmot, R.L., Varnavsky, V.S., Midanaya, V.V., and Quinn, T.P. 1994. Genetic differentiation of subpopulations of sockeye salmon (*Oncorhynchus*

© 1997 NRC Canada

*nerka*) within lakes of Alaska, British Columbia, and Kamchatka, Russia. Can. J. Fish. Aquat. Sci. **51**(Suppl. 1): 147–157.

Wetzel, L.A. 1993. Genetic, morphometric, and life history characteristics of sockeye salmon (*Oncorhynchus nerka*) in the Wood River Lake system, Alaska. M.S. thesis, University of Washington, Seattle, Wash.

Wilkinson, L., Hill, M., Welna, J.P., and Birkenbeuel, G.K. 1992. SYSTAT for Windows: statistics, version 5 edition. SYSTAT Inc., Evanston, Ill.

Wood, C.C. 1995. Life history variation and population structure in sockeye salmon. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J.L. Neilsen. Am. Fish. Soc. Symp. **17**: 195–216.

Wood, C.C., Riddell, B.E., Rutherford, D.T., and Withler, R.E. 1994. Biochemical genetic survey of sockeye salmon (*Oncorhynchus nerka*) in Canada. Can. J. Fish. Aquat. Sci. **51**(Suppl. 1): 114–131.

Woodey, J.C. 1966. Sockeye salmon spawning grounds and adult returns in the Lake Washington watershed, 1965. M.S. thesis, University of Washington, Seattle, Wash.

© 1997 NRC Canada