

# Population-specific variation in body dimensions of adult chinook salmon (*Oncorhynchus tshawytscha*) from New Zealand and their source population, 90 years after introduction

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**Abstract:** Chinook salmon (*Oncorhynchus tshawytscha*) transplanted from the Sacramento River, California, U.S.A., to New Zealand in the 1900s colonized many South Island rivers, which now show significant population-specific phenotypic variation. To characterize this variation, we conducted a morphometric analysis of two New Zealand populations and the fall-run Battle Creek population at the Coleman Hatchery, the apparent ancestral stock. Variation in length at age, weight at length, fin lengths, hump depth, snout length, and caudal peduncle width was detected among populations. Sexually mature Battle Creek and New Zealand chinook salmon were consistently identifiable from morphometric data (97.7% classification accuracy), largely through differences in caudal peduncle width and hump depth. The two New Zealand spawning populations, although distinguishable in morphology in 1994 (mean of 80% correct classification), did not classify as well using the same discriminant functions in 1995 (mean of 62.7% correct), suggesting interannual multivariate effects. Little variation was observed between the two mainstem river populations in adults collected shortly after entering freshwater. Although the genetic or environmental causes for the differences between populations have yet to be determined, our results provide empirical evidence of phenotypic divergence over decadal time scales. This work may be relevant to considerations in the development and monitoring of salmon recovery and conservation programs.

**Résumé :** Le saumon quinnat (*Oncorhynchus tshawytscha*) qui a été prélevé dans la rivière Sacramento, en Californie (É.-U.), pour être relâché en Nouvelle-Zélande dans les années 1990 a colonisé de nombreuses rivières de l'île du Sud, où l'on observe aujourd'hui une variation phénotypique significative entre populations. Pour caractériser cette variation, nous avons effectué une analyse morphométrique de deux populations néo-zélandaises et de la remonte d'automne de la population du ruisseau Battle à l'écluserie Coleman, qui semble être le stock d'origine. Nous avons détecté parmi les populations une variation dans la longueur selon l'âge, le poids selon l'âge, la longueur des nageoires, la hauteur de la bosse, la longueur du museau et la largeur du pédoncule caudal. Les quinnats arrivés à maturité sexuelle du ruisseau Battle et de la Nouvelle-Zélande pouvaient être identifiées avec un minimum d'erreur à partir des données morphométriques (précision de classification de 97,7 %), en grande partie grâce aux différences dans la largeur du pédoncule caudal et la hauteur de la bosse. Les deux populations reproductrices de la Nouvelle-Zélande, quoique nettement distinctes morphologiquement en 1994 (classification correcte à 80 % en moyenne), se distinguaient moins facilement au moyen des mêmes fonctions discriminantes en 1995 (classification correcte à 62,7 % en moyenne), ce qui laisse penser qu'il y aurait des effets multidimensionnels interannuels. Nous n'avons observé qu'une faible variation entre les deux populations du bras principal des rivières chez les adultes recueillis peu après leur entrée en eau douce. Bien que les causes génétiques ou environnementales des différences entre populations n'aient pas encore été déterminées, nos résultats fournissent des preuves empiriques d'une divergence phénotypique à l'échelle de décennies. Ce travail peut fournir des informations utiles pour l'élaboration et la surveillance de programmes de rétablissement et de conservation du saumon.

[Traduit par la Rédaction]

## Introduction

Interpopulation variation and its genetic basis underlie the protection and management of salmonid fishes (Billingsley 1981; Nielsen 1995). Differences in size at age and adult body

morphology occur within many salmonid species (e.g., chum salmon (*Oncorhynchus keta*): Beacham and Murray 1987; sockeye salmon (*Oncorhynchus nerka*): Blair et al. 1993; chinook salmon (*Oncorhynchus tshawytscha*): Roni and Quinn 1995). Size and shape of adult salmon are thought to reflect

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natural and human-induced variation in rearing regimes (e.g., Taylor and McPhail 1985; Fleming et al. 1994) and genetic changes from the selective forces of migration, spawning site features (such as flow and gravel size), predation risk, and sexual selection (Fleming and Gross 1989; Blair et al. 1993; Quinn and Foote 1994). Researchers have seldom attributed cases of interpopulation differences in size and shape to random genetic effects, but this mechanism is nonetheless possible (Adkison 1996).

Differences among indigenous populations are often considered to represent evolutionary change over millennia, resulting from a long history of genetic processes (Taylor 1991; Wood 1995). However, the need to recover locally adapted populations in the face of recent losses (e.g., Nehlsen et al. 1991) and the need to define evolutionarily significant units for conservation purposes (Waples 1995) require a consideration of the genetic and environmental components of divergence over much shorter time frames. Selective breeding programs (e.g., Hershberger et al. 1990) and investigations of differences between hatchery-produced and wild salmonids (e.g., Berejikian et al. 1996) indicate that genetic changes can arise in populations in a few generations. However, these extreme and highly manipulated conditions may not represent good models for questions concerning mechanisms and time frames of genetic and phenotypic change in complex, natural systems.

Introductions provide systems where the period of isolation and opportunity for subsequent evolution are known, and hence, diverging character states can be identified with a greater resolution of the time frame over which the differences arose. Freshwater populations of salmonids have been established worldwide (Lever 1996), but efforts to establish anadromous salmon populations have had very limited success, even within their native ranges (Withler 1982). Sockeye salmon introduced into Lake Washington, Washington (Hendry and Quinn 1997), and salmon established in the Great Lakes (e.g., pink salmon (*Oncorhynchus gorbuscha*): Berg 1979) have provided opportunities for comparative studies of phenotypic divergence in salmon. However, the chinook salmon introduced into New Zealand (NZ) at the beginning of the twentieth century (see McDowall 1994 for details) provide the longest standing introduction and an opportunity to investigate populations that have maintained their anadromous life cycle and established many self-sustaining spawning groups from a shared introductory gene pool.

### Objectives

Initial demonstrations of population-specific variation (Quinn and Bloomberg 1992; Quinn and Unwin 1993) were limited by four factors. First, the sampling methods, although similar, were not consistent among all rivers or years. Second, the data set emphasized the years from 1965 to about 1980, but since 1980, hatchery-produced chinook salmon have been released into the Rakaia River system, and thus the patterns revealed in the data from the 1970s may have changed in recent years. Third, morphological features that have proven useful in distinguishing indigenous populations (e.g., Blair et al. 1993) were not recorded. Finally, no direct comparison was made with the likely founder population (or its closest modern equivalent) from Battle Creek, California, U.S.A. Although the Battle Creek salmon have been under a different regime of

natural and artificial selection from the NZ fish and experience different environmental conditions, phenotypic comparisons between the NZ and Battle Creek salmon would nevertheless provide information on the phenotypic divergence resulting from both genetic and environmental forces acting on the isolated populations. The primary objectives of this study were thus to determine (i) if the size and shape of mature NZ chinook salmon differ from the Battle Creek population from which they were apparently derived, (ii) whether size and shape differ between the NZ populations, either at the time of entry from the ocean into the mainstem rivers or at spawning, and (iii) whether differences in length at age between the NZ chinook populations have persisted through the recent period of hatchery operations.

## Materials and methods

### Description of the rivers

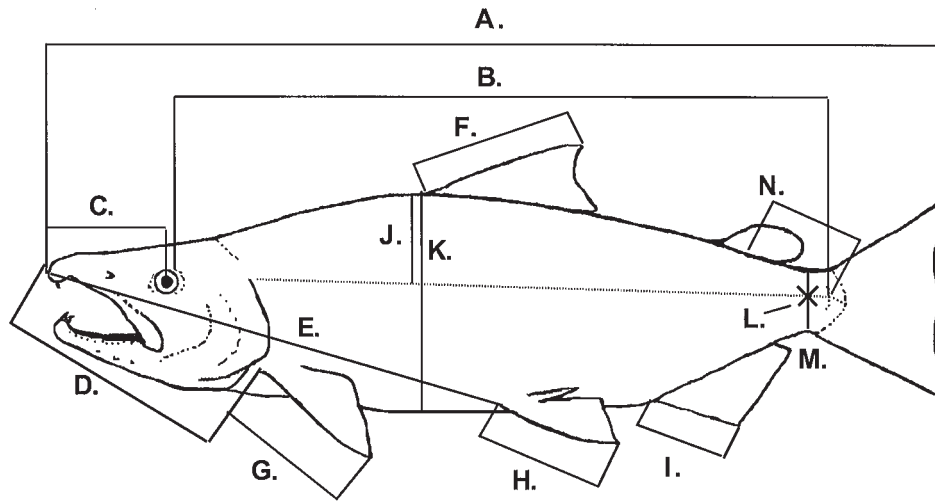
The main rivers inhabited by NZ chinook salmon (Waitaki, Rangitata, Rakaia, and Waimakariri) are primarily fed by snow and ice melt flowing from the Southern Alps of the South Island eastward into the South Pacific Ocean. Peak flows tend to occur in spring and minimum flows in winter, but floods resulting from heavy rainfall in the alpine headwaters can occur at any time of the year (Glova et al. 1985). Over much of their length, the rivers have unstable, braided shingle beds, often more than 1 km wide. The two mainstem study rivers have mean discharges of 350 (Waitaki), and 196 m<sup>3</sup>·s<sup>-1</sup> (Rakaia). An impassable dam (built in 1932) limits spawning in the Waitaki system largely to river margins of the mainstem below the dam and the Hakataramea River, which joins the Waitaki River 60 km from the mouth at 200 m elevation. In the Rakaia River, stable spring-fed streams along the flood plain margins in the upper catchment (90–120 km upriver) provide most of the salmon spawning habitat, including Glenariffe Stream (river km 100, elevation 430 m). Both rivers (and the others producing chinook salmon in NZ) lack estuaries. Battle Creek flows into the Sacramento River 418 km above its mouth at an elevation of 106 m. It has a mean annual discharge of 13.5 m<sup>3</sup>·s<sup>-1</sup>, and some spawning takes place in the creek but a large proportion is now propagated in the Coleman Hatchery, 9 km upstream of the confluence (S. Croci, Northern Central Valley Fish and Wildlife Office, Red Bluff, CA 96080, U.S.A., personal communication).

### Data collection

NZ samples were obtained from two sources: fishing competitions in the lower reaches of the mainstem rivers and weirs on the spawning streams. Fish from the lower reaches were maturing but still in a relatively "oceanic" state and represented the complex of spawning populations in each river. They were sampled during 3- to 5-day fishing competitions, from 1984 to 1995, timed to coincide with peak arrival of salmon at the river mouths (early February and March in the Rakaia and Waitaki rivers, respectively). There is no directed commercial fishing of salmon at sea, so the age and size distributions of salmon entering freshwater represent their true distributions, unbiased by selective fisheries. Mature chinook salmon were collected from weirs on the Hakataramea River and Glenariffe Stream on April 22–23, 1994, and on May 1 and 3, 1995. We used data from only live-captured fish in good condition.

Data on fork length (FL) and (or) postorbit to hypural flexure length (POH), weight, and age (freshwater and marine residence periods, inferred from scale analysis) were recorded and measurements (to the nearest 1 mm) were made on a suite of morphological features (Fig. 1). We also took an identical set of measurements from mature chinook salmon at the Coleman Hatchery on Battle Creek on October 18, 1994, and October 19, 1995. For some analyses, we drew on an

**Fig. 1.** Morphometric measures made on adult chinook salmon collected in New Zealand and at Battle Creek, California, U.S.A.: A, fork length (FL); B, postorbit to hypural flexure length (POH); C, snout length (SNOUT); D, snout to pectoral fin distance (SNAP); E, snout to pelvic fin distance (SNAPE); F, dorsal fin length (DFL); G, pectoral fin length (PECF); H, pelvic fin length (PELV); I, anal fin length (AFL); J, hump depth (HUMP); K, body depth (BD); L, caudal peduncle width (CPW); M, caudal peduncle depth (CPD); N, tail length (TAIL).



updated archival data set for the Rakaia and Waitaki rivers and Glenariffe Stream from 1967 to 1993.

#### Data analysis

We scanned the data for outliers using bivariate regressions between length and each morphometric character. When mature individuals had extreme outliers ( $>3$  studentized residuals from the regression relationship) for a given character, we estimated a value using multiple regression from the other measures to prevent loss of entire cases in multivariate analyses (Tabachnick and Fidell 1989). If a reasonable multiple regression estimate could not be obtained (i.e., an  $r^2 > 0.60$  could not be obtained), or the individual appeared to have a number of outliers, the values were removed from the data set. For fish obtained in the competitions, extreme outliers were deleted from the analysis without an attempt to obtain a regression estimate.

Length at age and the weight to length relationship were examined for angler-caught salmon from the Rakaia and Waitaki rivers from 1967 to 1995. During this period, data were available for 16 years on the Rakaia River (3008 fish) and 16 years on the Waitaki River (3021 fish), with 8 years in common between the two rivers. NZ fish identified as being of hatchery origin on the basis of scale pattern analysis (Unwin and Lucas 1993) were excluded from this analysis. We calculated mean FL at age, for each life history type and age-class, for the two NZ rivers and also for the Battle Creek fish sampled in 1994 and 1995. We used Battle Creek fish measured at spawning for this comparison, since fish closer to freshwater entry were not available. One-, two-, and three-factor ANOVAs of FL by river of origin, life history type, year, age, and sex were then performed to quantify differences. Log-transformed weight to log-transformed length relationship data were analyzed using ANCOVA with year, age, and river of origin as grouping variables or additional covariates in different models.

Morphological measurements were standardized to the average length of the fish in the combined sample being analyzed (FL = 800 mm for both males and females from the fishing competitions, and POH = 660 and 670 mm for mature females and males, respectively). Allometric adjustment (allowing for nonlinear relationships between traits and length) was performed using the common within-groups slope from the regression of  $\log_{10}(\text{trait})$  on  $\log_{10}(\text{length})$  as recommended by Reist (1986). Adjustment coefficients ranged from 0.800 (for caudal peduncle depth of competition females) to 1.231 (for snout length of spawning ground females).

Adjusted morphometric characters were subsequently compared using multivariate techniques. Principle components analyses (PCAs) with Varimax rotation and pairwise deletion of missing values were performed on the variance-covariance matrix of the logged, size-adjusted morphometric character set. Factor scores obtained for individuals were then used as variables in two-way ANOVAs of population and year. Sequential Bonferroni correction (SBC) was used to estimate the  $\alpha$ -level for testing population and year effects (Rice 1989). Tukey's multiple comparison tests for two-factor designs were used as post hoc analyses to determine where significant differences occurred between populations when this effect was significant (Neter et al. 1990). The PCAs sought to determine if the morphological measures could be reduced into logical and correlated character sets and the extent to which these character sets differed between populations.

Linear discriminant functions, based on the original log-transformed, size-adjusted variables, were derived using data from 1994 (larger sample size than in 1995 and greater homogeneity of within-population variance-covariance matrices). These functions were used to classify the 1994 and 1995 fish separately to river of origin. The 1994 samples were classified using jackknifing to prevent bias from classification of individuals used to derive the discriminant functions. This analysis provided an overall multivariate measure of the ability to distinguish these populations based on morphological characters and the robustness of the distinction over time. We excluded snout length (Fig. 1) in the discriminant functions analysis (DFA) for mature fish because data were missing for 35 of the 1994 California salmon (would have severely reduced the sample size in a DFA, but has little effect on PCA). Classification success was assessed by comparing the mean percent of correct classification with the percent expected under random classification conditions. Univariate, two-factor ANOVAs (river and year as factors) of some traits were used to aid in the interpretation of the DFA.

## Results

### Length at age

Results of one-, two-, and three-factor ANOVAs of FL by river of origin, life history type, year, age, and sex showed substantial interannual variation, particularly among 3- and 4-year-old fish ( $p < 0.001$  in all cases). Mean FL for Rakaia River chinook

of each life history type ranged from 737–859 mm for 3-year-old ocean-type fish, 698–793 mm for 3-year-old stream-type fish, 794–923 mm for 4-year-old ocean-type fish, and 772–945 mm for 4-year-old stream-type fish. Similar levels of variation (120–180 mm among years) were apparent for Waitaki fish.

There were consistent differences between the Rakaia and Waitaki rivers (Table 1). For all but 2-year-old ocean-type fish, Waitaki chinook were larger at age than Rakaia chinook, although only for 3-year-old ocean-type fish and 4-year-old stream-type fish were the observed differences significant (nested ANOVA of FL by river and sex,  $p < 0.001$  in both cases). The most recent data (1989–1995 for both rivers) indicated that these trends were still apparent despite releases of hatchery-produced fish (of Glenariffe origin), as Waitaki fish were larger than Rakaia fish at ages 3 and 4 ( $p = 0.02$  for age 4 ocean-type fish,  $p < 0.001$  in all other cases). The differences were particularly marked among age 4 stream-type fish; mean FLs were 853 versus 786 mm for Waitaki and Rakaia females, respectively, and 897 versus 804 mm for males.

Battle Creek chinook were predominantly aged 3 and 4, with only three 2-year-old fish among the 213 fish examined. Battle Creek fish did not differ in mean FL from Rakaia River ocean-type chinook at age 3 or 4 ( $p > 0.1$  for both age-classes) but were smaller than Waitaki River ocean-type fish ( $p \leq 0.003$  for both age-classes); however, the Battle Creek fish were measured at a later state of maturity (more snout development) that may have obscured a difference when compared with Rakaia/Glenariffe fish. ANOVA comparing age 3 fish (age with largest sample sizes) collected on the spawning grounds in 1994 and 1995 indicated that Battle Creek salmon were shorter in POH (which excludes the snout) at age than both of the NZ populations ( $p < 0.001$ ).

### Weight at length

Waitaki chinook were heavier for their length than Rakaia fish, based on fishing competition data (ANCOVA models,  $p < 0.001$ ). These differences were greatest among 4-year-old chinook. For 2- and 3-year-old fish, ANCOVA showed no significant interaction term ( $p = 0.15$ ), and weight at length differed by 2.8%. For chinook aged 4 years or older, there was an interaction between rivers ( $p = 0.01$ ). Separate weight ( $W$ ) – length ( $L$ ) regression models for each river (Rakaia:  $W = 10^{-4.53}L^{2.87}$ ,  $N = 460$ ; Waitaki:  $W = 10^{-5.24}L^{3.11}$ ,  $N = 527$ ) indicated that weight at length differed by 3.2% at FL = 872 mm (mean FL for NZ 4-year-old chinook), increasing to 5.2% at 950 mm. We detected a significant year effect over and above variations due to interannual changes in age structure, as ANCOVA models of  $\log(W)$  on  $\log(FL)$  with year as a covariate showed interaction between year and slope for all age-classes and both rivers, singly and in combination ( $p \leq 0.001$  in all cases). Mean weights were correlated between rivers for 8 years of angler-caught fish ( $r = 0.831$ ).

Weight at length of mature salmon consistently differed between all three populations for both sexes. There was no interaction between river of origin and slope for ANCOVA models of  $\log(W)$  on  $\log(FL)$  for either sex ( $p > 0.05$ ), but there were significant differences between rivers in elevation ( $p < 0.01$ ) for ANCOVA models incorporating a common slope. For both sexes, weight at length was lightest for Glenariffe fish, intermediate for Hakatamea fish, and heaviest for Battle

**Table 1.** Mean fork length (FL, mm) at maturity versus total age for ocean- and stream-type chinook salmon from the Rakaia and Waitaki rivers (1967–1995) and Battle Creek (1994–1995).

Origin		Total age (years)			
		2	3	4	5
<b>Ocean life history type</b>					
Rakaia River	Mean FL	593	800	862	971
	SD	52	67	78	11
	<i>N</i>	168	882	74	2
Waitaki River	Mean FL	585	810	887	1050
	SD	57	62	91	0
	<i>N</i>	63	708	95	1
Battle Creek	Mean FL	605	793	839	70
	SD	33	74	87	0
	<i>N</i>	3	155	54	1
<b>Stream life history type</b>					
Rakaia River	Mean FL	450	750	857	870
	SD	69	70	83	20
	<i>N</i>	22	438	184	2
Waitaki River	Mean FL	470	758	886	1025
	SD	62	69	79	0
	<i>N</i>	21	379	321	1

Creek fish. The greatest differences in mean weight at length were between Glenariffe and Hakatamea females (5.4%) and Hakatamea and Battle Creek males (5.2%).

The NZ fish on the spawning grounds were lighter for their length than members of their population measured in the fishing competitions, likely reflecting secondary sexual character development (snout lengthening) and energy consumption associated with migration and cessation of feeding in freshwater. ANCOVA models of  $\log_{10}(W)$  on  $\log_{10}(FL)$  for both NZ rivers and sexes combined, with location of capture (angler or upstream trap) as the covariate, yielded a common slope of 2.724 and a difference in elevation of 0.066 ( $p < 0.001$ ). This difference is equivalent to a 16% decrease in weight to length relationship as the fish matured and moved upstream.

### Morphology at spawning

PCA resulted in four-factor solutions for both sexes, and in both cases, a factor combining fin measures (PC factor 2 for females; PC factor 1 for males) was obtained (Table 2). These factors lacked significant year by population interaction and demonstrated significant population effects ( $p \leq 0.001$ ,  $\alpha = 0.013$  by SBC) as well as a potential year effect in the case of males ( $p = 0.015$ , near rejection with SBC:  $\alpha = 0.013$ ). Although there were some differences between sexes with regard to the pattern of differences and similarities (Table 2), Glenariffe salmon had the largest mean score on the fin factors and were consistently different from the Battle Creek fish for both sexes. Hakatamea River females differed from Glenariffe Stream females but not from Battle Creek females whereas the opposite was true for males. The second factor for males, combining caudal peduncle width, snout to pelvic fin distance, and snout length, varied between the NZ populations and Battle Creek ( $p = 0.001$ ,  $\alpha = 0.013$  by SBC). This factor may reflect head size and tail robustness variation, with Battle Creek having larger factor scores than the two NZ populations.

**Table 2.** Results of PCA and two-way ANOVAs on PCA factor scores for 12 length-adjusted morphometric measures for female and male spawning-condition chinook from Battle Creek (B), Glenariffe Stream (G), and Hakataramea River (H).

Factor	Highest loading traits	Loading	% of variation	River by year	River	Year
<b>Females<sup>a</sup></b>						
1	BD	0.842	30.0	0.000	na	na
	SNAPE	0.823				
	CPD	0.575				
2	PELF	0.816	19.0	0.084	0.001 $\overline{HB}$ G	0.425
	AFL	0.715				
	DFL	0.697				
	PECF	0.640				
3	HUMP	0.860	11.4	0.000	na	na
	SNAP	0.605				
	CPW	-0.572				
4	TAIL	0.881	9.5	0.000	na	na
	SNOUT	0.692				
<b>Males<sup>b</sup></b>						
1	DFL	0.802	34.8	0.422	0.000 B $\overline{HG}$	0.015
	AFL	0.682				
	PECF	0.597				
	PELF	0.588				
	SNAP	0.584				
2	CPW	0.808	17.7	0.058	0.000 $\overline{HG}$ B	0.444
	SNAPE	0.782				
	SNOUT	0.598				
3	HUMP	0.845	9.2	0.000	na	na
	BD	0.784				
	CPD	0.722				
4	TAIL	0.819	8.4	0.000	na	na

**Note:** ANOVA results are presented as *p*-values for each effect. Populations are listed in order of increasing mean, with those that did not differ (Tukey's multiple comparisons) indicated by a common line. Traits are defined in Fig. 1.

<sup>a</sup>1994 sample sizes: H = 35, G = 40, B = 60; 1995 sample sizes: H = 16, G = 25, B = 59.

<sup>b</sup>1994 sample sizes: H = 20, G = 26, B = 50; 1995 sample sizes: H = 15, G = 16, B = 50.

The use of 1994 data to obtain discriminant functions, for subsequent classification of 1994 and 1995 data, provided two functions for both sexes (Table 3). For females the first function explained 94.5% of the total between-group variance and the second function explained 5.5%; the corresponding values for males were 91.9 and 8.1%. For both sexes the first functions, which were most correlated with caudal peduncle width and hump depth, best distinguished the NZ and Battle Creek fish (Fig. 2). By noting the direction of group centroid differences and using Table 3, one can infer that hump depth was generally smaller in Battle Creek than in NZ whereas the opposite trend was apparent for caudal peduncle width. For males, pelvic fin length also contributed to the discrimination between countries. The second functions best separated the NZ populations (Fig. 2). For females, snout to pectoral fin distance, some fin measures, and tail length contributed most to the discrimination within NZ whereas for males, caudal peduncle width, pelvic fin length, and hump depth were again most correlated with the discriminating function.

For both sexes, DFA significantly discriminated between the populations, based on chi-square-transformed tests of

Wilks' lambda ( $p < 0.001$  in all cases). For females, discriminant functions derived using the 1994 data correctly classified a mean of 85.8% of the 1994 females and 71.8% of the 1995 females; corresponding figures for males were 85.6 and 75.0% (Table 4). For each year and sex, classification accuracy exceeded that expected by chance (i.e., a mean of 33.3%). When classification results for the two NZ populations were combined to assess classification of country of origin, mean percent accuracy was 97.7% (a mean of 98.7% in 1994 and 96.6% in 1995).

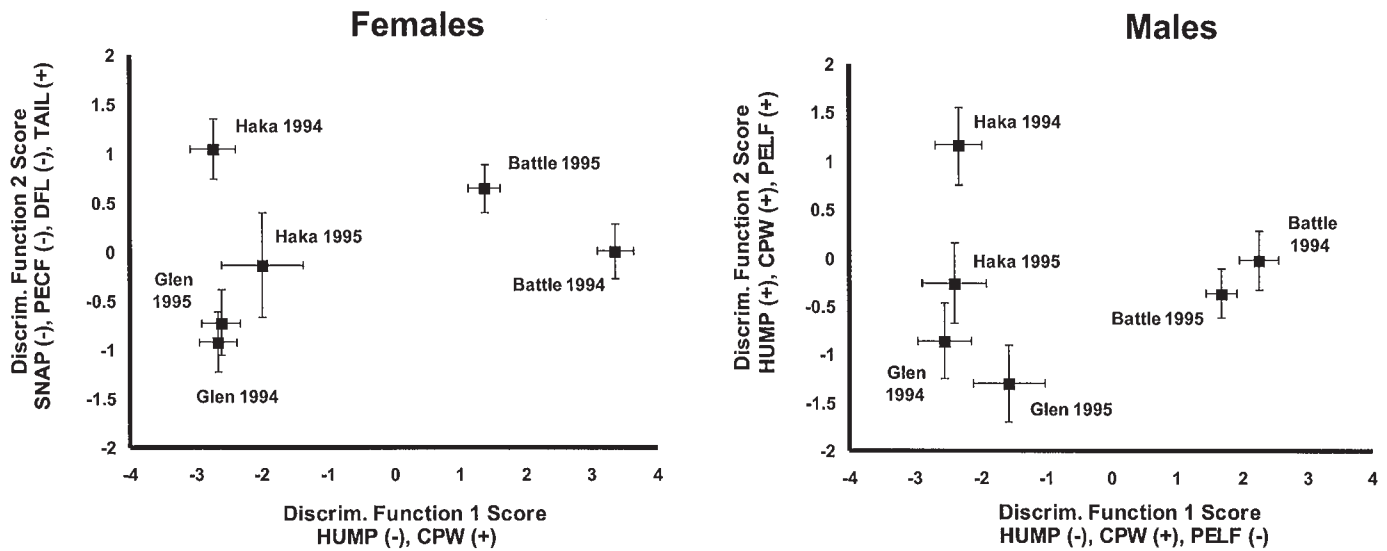
Some patterns were discernible in the misclassification results, particularly for 1995 fish using the 1994 discriminant functions. Only two NZ salmon (a male and a female) were misclassified as being from Battle Creek, and misclassification of Battle Creek fish was only slightly higher (3.7%, or 8/219 fish for both years and sexes combined), indicating a clear separation between salmon from NZ and Battle Creek. Within NZ, classification of 1995 Hakataramea fish was poor for both sexes compared with the classification obtained in 1994 (worse classification in 1995 than expected by chance, Table 4). In 1995, more Hakataramea fish were misclassified as

**Table 3.** Standardized canonical discriminant function coefficients (coeff. F1 and coeff. F2) and correlations between the functions and the morphometric traits (corr. F1 and corr. F2) for males and females collected at weirs.

Trait	Females				Males			
	Coeff. F1	Coeff. F2	Corr. F1	Corr. F2	Coeff. F1	Coeff. F2	Corr. F1	Corr. F2
SNAP	-0.010	-0.762	-0.031	-0.543*	0.085	-0.204	0.030	-0.232*
SNAPE	0.025	0.208	0.242*	-0.204*	0.190	-0.641	0.196	-0.288*
BD	0.471	0.033	0.234*	-0.087	0.641	0.544	0.060	0.290*
HUMP	-0.903	0.100	-0.458*	0.029	-1.058	0.185	-0.353*	0.351*
PECF	0.021	-0.462	0.082	-0.453*	-0.024	0.025	0.032	0.119
PELF	-0.269	0.083	-0.112	-0.224*	-0.401	0.489	-0.330*	0.421*
DFL	0.185	-0.455	0.082	-0.313*	-0.013	-0.276	-0.104	-0.165
AFL	-0.068	0.614	-0.069	0.158	0.129	0.231	-0.051	0.209*
CPD	-0.173	0.226	0.034	0.019	-0.299	-0.405	-0.049	0.092
CPW	0.774	0.149	0.548*	0.052	0.781	0.514	0.534*	0.547*
TAIL	0.119	0.455	0.005	0.410*	0.087	-0.037	-0.055	0.024

**Note:** Asterisks indicate the characters most correlated with a function. Traits are defined in Fig. 1.

**Fig. 2.** Population centroids of discriminant function scores for spawning-condition females and males by year, with 95% confidence intervals for both dimensions (Haka, Hakataramea River; Glen, Glenariffe Stream; Battle, Battle Creek). The direction of correlation for the most strongly correlated characters on each function is shown in parentheses. Characters are defined in Fig. 1 and complete sets of function correlations are shown in Table 3.



Glenariffe fish than were correctly classified. In contrast, classification accuracy for Glenariffe fish, using the 1994 discriminant functions, was at least as good in 1995 as in 1994 (77.5 and 80%, respectively, for females; 81 and 94% for males) and significantly better than expected by chance. The 1995 classification results for the two NZ populations indicated an overclassification towards a “more Glenariffe” form based on the 1994 functions, suggesting interannual variation in multivariate morphology (separate from that due to body size). The basis for this classification result can be seen in Fig. 2, where the 95% confidence intervals for the 1995 Hakataramea females and males overlapped considerably with the 1994 and 1995 Glenariffe intervals.

This reduction of classification accuracy within NZ in 1995 suggests potential year and year by population interaction effects of the individual morphological traits comprising the multivariate discrimination. Univariate ANOVAs (only the

NZ populations) indicated that, of the traits most correlated with the second female discriminant function (that distinguishing Hakataramea from Glenariffe), snout to pectoral fin distance, snout to pelvic fin distance, and pectoral fin length showed year effects ( $p \leq 0.001$ ) and tail length showed an interaction of year and population ( $p < 0.001$ ). For male traits most correlated with the second discriminant function, snout to pelvic fin distance, anal fin length, and hump depth showed year effects ( $p \leq 0.07$ ) and body depth, caudal peduncle width, and pelvic fin length showed evidence of year by population interactions ( $p \leq 0.08$ ). The multivariate and univariate interannual effects do not, however, indicate that the NZ populations may not be distinguishable in any given year based partly on the same traits. For example, a DFA using the 1995 female data (our largest set for spawning fish in 1995) to develop discriminate functions found significant differences between the NZ populations ( $p < 0.001$ ) and obtained good classification

**Table 4.** Classification results for 1994 and 1995 spawning-condition females and males using the 1994 canonical discriminant functions.

	Origin	N	No. classified (%)			Significance test ( <i>p</i> )
			Hakataramea River	Glenariffe Strem	Battle Creek	
<b>Females</b>						
1994	Hakataramea River	35	28 (80)	7 (20)	0 (0.0)	<0.001 (+)
	Glenariffe Strem	40	8 (20)	31 (77.5)	1 (2.5)	<0.001 (+)
	Battle Creek	60	0 (0.0)	0 (0.0)	60 (100)	<0.001 (+)
Mean % correct = 85.8%						
1995	Hakataramea River	16	7 (44)	9 (56)	0 (0.0)	0.03 (-)
	Glenariffe Strem	25	5 (20)	20 (80)	0 (0.0)	<0.001 (+)
	Battle Creek	59	3 (5.0)	2 (3.0)	54 (92)	<0.001 (+)
Mean % correct = 71.8%						
<b>Males</b>						
1994	Hakataramea River	20	16 (80)	4 (20)	0 (0.0)	<0.001 (+)
	Glenariffe Strem	26	5 (19)	21 (81)	0 (0.0)	<0.001 (+)
	Battle Creek	50	0 (0.0)	2 (4.0)	48 (96)	<0.001 (+)
Mean % correct = 85.6%						
1995	Hakataramea River	15	5 (33)	10 (67)	0 (0.0)	0.013 (-)
	Glenariffe Strem	16	0 (0.0)	15 (94)	1 (6.0)	<0.001 (+)
	Battle Creek	50	0 (0.0)	1 (2.0)	49 (98)	<0.001 (+)
Mean % correct = 75.0%						

**Note:** For each year and river of origin, the table shows the actual number of individuals (*N*) and the number (percentage in parentheses) classified to each river of origin and a *p*-value (based on a  $\chi^2$  test) together with a plus or minus sign indicating whether classification was better or worse than expected by chance.

(mean of 85.5% correct in NZ). Likewise, five out of six of the traits (excluding tail) most correlated with the function separating the two NZ populations in the 1994-based DFA remained correlated with the analogous function in the 1995-based DFA.

### Morphology at river entry

Four-factor PCA solutions were obtained for both sexes consisting of a robustness factor (hump depth, body depth, caudal peduncle depth, and caudal peduncle width), a fin factor (dorsal fin length, pectoral fin length, pelvic fin length, and anal fin length), a snout and snout to fin factor (snout length, snout to pectoral fin distance, and snout to pelvic fin distance), and a tail factor (tail length). The difference between the two sexes was that factors 1 and 2 were transposed between the two sexes. No factors indicated significant population effects ( $p \geq 0.05$ ,  $\alpha = 0.013$  with SBC) for both sexes.

DFA produced a single function for each sex (Table 5). For both sexes, chi-square-transformed tests of Wilks' lambda indicated significant discrimination between the 1994 populations ( $p < 0.001$  in all cases). Mean classification accuracy for the 1994 females was 89.4%, significantly better than the 50% expected by chance, but was only 47.1% applying the same functions for the 1995 data (Table 6). The corresponding figures for males were 76.7 and 41.1%. The misclassification trend was similar to that obtained for spawning fish (Table 4) and suggests that the 1994 functions were of little value in discriminating the 1995 NZ populations. Both of the variables most correlated with the female discriminant function, dorsal fin length and tail length, showed interaction effects ( $p \leq 0.06$ ). Among the male traits most correlated with the discriminant function, pectoral fin length, anal fin length, and caudal peduncle width showed evidence of year by population interaction

**Table 5.** Standardized canonical discriminant function coefficients and the correlations between the functions and the morphometric traits for males and females collected in fishing competitions.

Trait	Females		Males	
	Coefficients	Correlations	Coefficients	Correlations
SNOUT	-0.170	-0.015	-0.102	-0.107
SNAP	-0.196	0.107	-0.066	-0.069
SNAPE	-0.133	-0.071	0.119	0.055
BD	0.154	0.118	-1.109	-0.352*
HUMP	-0.151	-0.067	0.588	0.121
PECF	-0.115	-0.049	0.205	0.229*
PELF	-0.170	0.036	-0.267	-0.062
DFL	0.516	0.232*	0.042	0.071
AFL	-0.050	-0.026	0.145	0.217*
CPD	0.510	0.191	-0.038	-0.029
CPW	-0.224	-0.086	0.801	0.488*
TAIL	0.882	0.795*	-0.267	-0.096

**Note:** Asterisks indicate the traits most correlated with the functions. Traits are defined in Fig. 1.

effects ( $p \leq 0.08$ ), consistent with the decreased classification success of 1995 individuals using functions derived with 1994 data.

### Discussion

As expected, the most pronounced differences in morphology, and thus the best classification results, were between the Battle Creek and NZ populations. DFA based on length-standardized morphological characters correctly classified 98% of spawning-condition fish by country of origin (99.5% in 1994 and 97% in

**Table 6.** Classification results for 1994 and 1995 fishing competition fish from the Waitaki and Rakaia rivers using the 1994 canonical discriminant functions.

	Origin	N	No. classified (%)		Significance test ( <i>p</i> )
			Waitaki River	Rakaia River	
<b>Females</b>					
1994	Waitaki River	59	54 (91.5)	5 (8.5)	<0.001 (+)
	Rakaia River	55	7 (13)	48 (87)	<0.001 (+)
Mean % correct = 89.4%					
1995	Waitaki River	47	6 (13)	41 (87)	<0.001 (-)
	Rakaia River	43	8 (19)	35 (81)	<0.001 (+)
Mean % correct = 47.1%					
<b>Males</b>					
1994	Waitaki River	46	35 (76)	11 (24)	0.001 (+)
	Rakaia River	44	10 (23)	34 (77)	0.001 (+)
Mean % correct = 76.7%					
1995	Waitaki River	80	34 (43)	46 (57)	0.438
	Rakaia River	47	9 (19)	38 (81)	0.001 (+)
Mean % correct = 41.1%					

Note: See Table 4 for details.

1995). The variables most associated with these differences were caudal peduncle width and hump depth. DFA was less successful in separating fish from the two NZ populations, particularly when the 1995 data were subjected to the discriminant functions derived using the 1994 data. This overlap was apparent for fish caught in the fishing competitions as well as for mature fish intercepted at hatcheries or weirs. PCA identified some differences in fin lengths between all three populations, Glenariffe fish had the largest fins and Battle Creek fish the smallest. Waitaki fish were consistently longer at age than Glenariffe fish, and Battle Creek salmon were generally shorter at age than the NZ salmon. Waitaki River fish were also heavier for their length than those from the Rakaia, particularly for 4- and 5-year-olds. In nearly all comparisons between the NZ populations, year effects were noted as well as population effects.

Adaptation through natural selection is, of course, one explanation for the phenotypic differences between populations; however, differences could also arise through genetic changes from random genetic effects and through environmentally induced variation. Some combination of these influences are probably responsible for the differences detected; further genetic and functional experiments would be required before more precise estimates of the significance of these effects could be concluded. However, it is informative to compare the patterns of trait variation that we observed with patterns documented or hypothesized for North American salmon.

Maturing Battle Creek fish tended to have a more robust tail (wider caudal peduncle) but a less pronounced hump than fish from either NZ population. Salmon from large rivers tend to be larger and have larger heads, fins, caudal peduncles, and tails than those from smaller rivers (e.g., Beacham and Murray 1987). The wider caudal peduncles of Battle Creek fish would fit this pattern, given the larger volume and length of the Sacramento River relative to the NZ rivers. Likewise the higher scores of the Battle Creek males on PCA factor 2 (incorporating head size and caudal peduncle width) would be consistent. Fin length patterns, however, were inconsistent with that

expected based on river size. The braided study rivers in NZ drop more than twice the elevation to the sea in less than half the distance compared with the Sacramento River. Thus the upriver migration of NZ salmon may be less arduous in the sense of the distance to the spawning grounds, but braiding and higher current speeds may require larger fins for improved holding and maneuverability. Higher current speeds have been correlated with longer fins in juvenile salmonids, and this trait has a genetic basis (Riddell et al. 1981).

Sexual selection is believed to favor large size and hump and snout development (Fleming and Gross 1994; Quinn and Foote 1994). In their native habitats, salmon spawning in shallow streams may experience selection against large size from predation or the inability to access certain areas (Blair et al. 1993; Quinn and Foote 1994). NZ lacks predators on adult salmon, and both spawning streams are sufficiently deep that access is not likely to be a selective factor restricting body size. Sexual selection may differ between the NZ rivers and Battle Creek due to the predominance of wild spawning in NZ compared with the hatchery propagation in Battle Creek, which may have relaxed sexual competition and selection (Fleming and Gross 1989, 1994). This may have contributed to the tendency for the Battle Creek fish to have shallower hump depths as indicated by the analysis. Alternatively, the smaller hump depth of the Battle Creek population may be a streamlining adaptation for the longer river migration that they undergo (Taylor and McPhail 1985) or a phenotypic expression of energy expended during migration.

Differences among salmon populations in mean age and size at maturity are thought to reflect different threshold points for trade-offs associated with mortality and incremental benefits of size at maturity (e.g., Healey 1987) or different balancing points in a mixed evolutionarily stable strategy (Gross 1985). The Battle Creek and NZ populations are relatively young at maturity (modal age of 3) compared with most North American populations, but are large for their age (Quinn and Unwin 1993; Roni and Quinn 1995). This is consistent with the general trend among salmonids for age at maturity to be

inversely correlated with growth rate (Thorpe et al. 1983; Healey 1991) and also with the trend for younger maturation at lower latitudes (Beacham and Murray 1987). The two NZ populations lie at a slightly higher relative latitude (44–45°S) than Battle Creek (40°21'N), but are colatitudinal with central Oregon, where a modal age of 3 is common among coastal fall-run chinook (Roni and Quinn 1995). The rapid growth shown by all three populations may reflect growing conditions that the NZ and Battle Creek fish experience, similar selective regimes of the populations, or retention of a shared ancestral state.

The two NZ rivers are generally similar to each other in migratory length, elevation, temperature, and flow compared with the range of chinook salmon rivers in North America. For example, spawning in North America ranges from nearly tidal to 3200 km up the Yukon River, and mean spawning river discharge ranges from about 4.28 to more than 566 m<sup>3</sup>·s<sup>-1</sup> in British Columbia (Healey 1991). It is not clear how the more subtle (and in many cases undocumented) freshwater habitat differences between the NZ study sites would be reflected in particular life history traits, and relatively little is known about the marine ecology of NZ chinook. Nevertheless, it is clear that the environments experienced by Waitaki and Rakaia chinook are much more similar to each other than either is to the upper Sacramento River. The relatively high level of morphological differentiation between the NZ salmon and the Battle Creek population, compared with that between the NZ populations, is consistent with what we would expect based on environmental similarity and potential levels of gene flow. Battle Creek fish may have undergone significant genetic changes since the time of the transplants to NZ, and the loss of some hatchery records allows that Battle Creek fish may not have been the sole ancestral lineage (McDowall 1994). Nonetheless, the differences we observed and the persistence of the NZ populations in such a novel ecosystem reveal a considerable ability of this lineage of salmon to acclimate to new and different environments.

NZ salmon from the two river systems examined near the time of river entry did not differ. Two factors may have contributed to this result. First, the size and shape of salmon taken in the lower reaches during fishing competitions may reflect selection for a common body shape adapted to foraging and predator avoidance at sea rather than a more river-specific morphology. If so, differences in shape at river entry would be less likely than differences at maturity, which might be more closely linked to physical features of the migratory route and spawning grounds, or to sexual selection. Such stage-dependent divergence has been hypothesized for Atlantic salmon (*Salmo salar*) parr and smolts (Nicieza 1995). Second, fish taken during the fishing competitions would have included individuals destined for spawning grounds other than the Hakataramea River and Glenariffe Stream. This mixture may have varied more in degree of maturity (and hence, development of maturity related characters) than those measured on entry to spawning grounds or may have consisted of morphologically diverged subpopulations (Quinn and Unwin 1993).

The most recent fishing competition data (post-1989) indicated that the tendency for Waitaki chinook to be larger at age than Rakaia fish (Quinn and Unwin 1993) has persisted in recent years and perhaps magnified. For 4-year-old stream-type fish, we recorded differences between the two rivers of

67 and 93 mm for females and males, respectively, compared with a difference of 49 mm (both sexes combined) for data collected prior to 1980. For 2- and 3-year-old fish the trend was similar to earlier findings. Thus, hatchery releases into the Rakaia River since the early 1980s appear to have had little impact on the pattern of differences between the two rivers. Phenotypic changes observed among Glenariffe Stream chinook over the last decade, potentially as a result of hatchery releases, have been largely confined to males and are most pronounced among 2-year-old fish, which appear to now be shorter and more abundant (Unwin and Glova 1997).

In summary, our study revealed phenotypic differences between Battle Creek chinook and the present-day NZ populations and (on a smaller scale) between the two NZ populations. These differences have emerged after only about 90 years of separation from a believed common ancestral lineage. The large number of environmental factors that could have selective or phenotypic plasticity effects and the potential for random genetic effects make it difficult to ascribe these differences (and those between the Battle Creek and NZ populations) to a particular cause at this time. Nevertheless, our results help to quantify which traits and to what degree phenotypic characters are altered, over decadal time scales, under natural conditions in new environments. This information may be useful in developing and monitoring salmon recovery and reintroduction programs.

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