

# Egg size, fecundity, and development rate of two introduced New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations

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**Abstract:** Interpopulation differences in several adult phenotypic traits suggest that New Zealand (NZ) chinook salmon (*Oncorhynchus tshawytscha*) are evolving into distinct populations. To further investigate this hypothesis, we compared egg sizes, fecundities, and early development rates of chinook from two NZ streams. The two NZ study populations differed in size-adjusted egg weight and gonadosomatic index, but not in size-adjusted fecundity. Egg weight, fecundity, and gonadosomatic index values for both NZ populations were different than values for chinook from Battle Creek, California, the population regarded as the ancestral NZ stock. In contrast, there was little evidence of divergence in juvenile development. Time to hatching did not differ between the two NZ study populations and heritability estimates were small with large standard errors. Evidence of a small difference in alevin growth rate may have represented an effect of yolk conversion mechanics related to egg size. Despite the similarity in development rates under shared conditions, modeling based on temperature records suggests that emergence dates in the two NZ streams may differ by 4–6 weeks, yielding significant phenotypic differences.

**Résumé :** L'existence de différences entre populations en ce qui a trait à plusieurs caractères phénotypiques adultes laisse penser que le saumon quinnat (*Oncorhynchus tshawytscha*) de Nouvelle-Zélande (N.-Z.) est en train d'évoluer de façon à former des populations distinctes. Pour vérifier cette hypothèse, nous avons comparé les tailles des oeufs, les fécondités et les taux de développement dans les premiers stades de quinnats de deux cours d'eau de la N.-Z. Nous avons observé des différences entre les deux populations étudiées au chapitre du poids des oeufs corrigé selon la taille et de l'indice gonadosomatique, mais pas au chapitre de la fécondité corrigée selon la taille. Les valeurs de poids des oeufs, de fécondité et d'indice gonadosomatique des deux populations étaient différentes des valeurs obtenues chez le quinnat du ruisseau Battle, en Californie, lequel formerait le stock ancestral du quinnat de la N.-Z. Par ailleurs, on dispose de peu d'indices d'une divergence dans le développement des juvéniles. Le délai d'éclosion était le même chez les deux populations de la N.-Z., et les estimations d'héritabilité étaient faibles, avec de fortes erreurs-types. Les données montrant l'existence d'une petite différence dans le taux de croissance des alevins pourraient s'expliquer par la mécanique de conversion du vitellus en rapport avec la taille de l'oeuf. Malgré la similitude des taux de développement dans des conditions similaires, la modélisation fondée sur les données de température laisse penser que les dates d'émergence dans les deux cours d'eau de la N.-Z. peuvent différer de 4 à 6 semaines, ce qui témoigne de différences phénotypiques importantes.

[Traduit par la Rédaction]

## Introduction

Local adaptations of salmonid populations are generally regarded as the product of evolutionary change over millennia, but the rate of adaptation of wild populations remains unclear (Wood 1995). In addition, the interplay between genetic alteration (through deterministic or random genetic effects) and phenotypic plasticity in producing interpopulation

variation in recently established populations is not well known. An understanding of phenotypic divergence and adaptation over short time scales may be important for restoring extirpated populations and for application of the evolutionarily significant unit concept (Waples 1991; Wood 1995).

Introduced populations provide opportunities to study divergence over short time frames in populations whose genetic history is often known and where changed character states and environmental features can be identified. There are only a few documented cases of introduced Pacific salmon populations that have maintained their anadromous habit (Lever 1996). Interpopulation comparisons of life history traits commonly measured on indigenous populations, and characterization of associated environmental factors, present a logical starting point to begin studying these cases (Reznick and Travis 1996).

Egg size, fecundity, and total ova mass are interrelated life history traits that have commonly been used to characterize

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salmon populations (e.g., Healey and Heard 1984; Beacham and Murray 1993). A trade-off between egg size and fecundity occurs within and among salmon populations (Beacham and Murray 1993; Quinn et al. 1995). There is some dispute as to whether egg size or fecundity is the primary character under selection. Fleming and Gross (1990) concluded that egg size is the primary reproductive trait under selection in salmonids and that variation in fecundity reflects compensation for the demand on egg size within a relatively fixed total energy investment. They hypothesized that warm incubation temperatures select for larger eggs because yolk is used less efficiently in warm water; hence, smaller alevins and fry are produced for a given egg size. Another important selective factor on egg size may be the size of incubation substrate. Egg size was positively correlated with gravel size within a suite of sockeye salmon (*Oncorhynchus nerka*) populations (Quinn et al. 1995). This is thought to reflect the importance of surface to volume ratio for respiration under different conditions of substrate porosity (Quinn et al. 1995). Alternatively, Beacham and Murray (1993) hypothesized that fecundity is the primary factor under selection as a result of compensation for reduced survival in populations with older ages at maturity.

Most of the variation in embryo development rates is controlled by temperature (Alderdice and Velsen 1978; Murray and McPhail 1988). However, early development rates have a genetic basis (Beacham 1988) and differ among some salmon populations (e.g., Beacham and Murray 1989). Genetic differences in development may represent compensation for the effects of incubation temperature and spawning time. Populations that incubate under colder conditions or that spawn later tend to develop faster (Beacham and Murray 1987, 1989; Hendry et al. 1998).

### New Zealand chinook salmon

The present-day New Zealand (NZ) chinook salmon (*Oncorhynchus tshawytscha*) populations are thought to have originated from fall-run fish shipped from Battle Creek, a tributary of the Sacramento River, California, between 1904 and 1907 (McDowall 1994; Quinn et al. 1996). All modern runs are unambiguously descended from this introduction group, as there were no subsequent transplants. Previous studies (some using archival data) showed that fish from the Waitaki River and Glenariffe Stream (or its basin, the Rakaia River) differed from each other in age, size at age, morphology, fecundity, and migratory timing of juveniles and adults (Quinn and Bloomberg 1992; Quinn and Unwin 1993; Kinnison et al. 1998). To better investigate the phenotypic divergence of NZ populations, and to determine the relative contributions of genetic and environmental factors, we initiated a research program involving a nested breeding design and rearing under common, controlled conditions. This design provides a more rigorous evaluation of the genetic divergence of a manageable subset of populations based on a diverse array of traits, and it allows estimation of quantitative genetic parameters. By applying this design in the study of NZ chinook salmon populations, we hope to provide a better understanding of the process of salmon population evolution occurring over short time scales.

In this study, we compared the reproductive traits of wild-reared females from Battle Creek and two NZ populations

and the juvenile development of the two NZ populations reared under common conditions. We also quantified related environmental variables and estimated some quantitative genetic parameters to help understand how these traits may interact with the environment to produce the phenotypic variation observed among the NZ populations. We do not assume that all differences reflect adaptation. However, based on research on salmon in their native range, we would expect that (i) populations that experience warmer incubation conditions would have larger eggs, (ii) populations incubating in finer gravel would have smaller egg sizes, (iii) populations with older mean ages of maturity would have higher fecundities, and (iv) populations that experience warmer incubation conditions would have slower incubation and alevin development rates than populations that naturally rear under colder conditions, when reared under common conditions.

## Materials and methods

### Study populations

The two NZ populations chosen for study spawn in the Hakataramea River (a tributary of the Waitaki River, 44°20'S, 170°38'E) and Glenariffe Stream (a tributary of the Rakaia River, 43°19'S, 171°23'E). Their respective river habitats differ in flow regime and channel morphology, and both have weirs for the capture of salmon. The Hakataramea River is rain-fed, joining the Waitaki River 60 km from the sea at an altitude of about 200 m, 7 km below an impassable hydroelectric dam. It has a daily mean discharge of 6.0 m<sup>3</sup>·s<sup>-1</sup> and is prone to sudden and severe flooding with a mean annual flood of 105 m<sup>3</sup>·s<sup>-1</sup> (daily mean discharge). By contrast, Glenariffe Stream is a stable spring-fed tributary joining the Rakaia River 100 km above the mouth at an altitude of 430 m. It flows in a well-defined channel and has a daily mean discharge of 3.4 m<sup>3</sup>·s<sup>-1</sup>. The mean annual flood is 7.9 m<sup>3</sup>·s<sup>-1</sup>. Both populations have consisted of about 2000–3000 spawning salmon in recent years. Battle Creek, the spawning tributary of the putative ancestral lineage, joins the Sacramento River 418 km from Suisun Bay at an altitude of 133 m and has a mean annual flow of 13.5 m<sup>3</sup>·s<sup>-1</sup> (S. Croci, Northern Central Valley Fish and Wildlife Office, Red Bluff, Calif., personal communication).

### Data collection

On April 22 and 23, 1994, we obtained ova mass, egg size, and fecundity data from 33 Hakataramea and 40 Glenariffe females, which were spawned with 16 Hakataramea and 20 Glenariffe males, respectively. In 1995, we collected comparable data on 17 Hakataramea and 23 Glenariffe females on April 30 and May 1, respectively. Similar data were collected on October 18 and 19, 1994 (60 females) and 1995 (59 females), at the Coleman National Fish Hatchery on Battle Creek (40°25'N, 122°10'W). Fish were weighed to the nearest 10 g and their body length (postorbit to hypural flexure) was recorded to the nearest millimetre.

For female chinook from the two NZ populations, the drained weight of the entire freely spawned ova mass was recorded to the nearest gram. At the Coleman Hatchery, the ova mass was weighed undrained to the nearest 10 g and a regression equation, developed from 81 chinook, was used to convert these data to drained weights ( $W_{\text{drained}} = 38.4 + 0.88W_{\text{undrained}}$ ;  $r^2 = 0.99$ ,  $p < 0.001$ ). For all three populations, a drained subsample (about 30 g) of fresh eggs from each female was weighed to the nearest 0.1 g and preserved in 5–10% buffered formalin for later counting. Mean egg weight for each female was determined by dividing the fresh sample weight by the number of eggs; fecundity was calculated by dividing the total ova mass by the mean egg weight.

**Table 1.** Mean (SE) total ova weight, GSI, egg weight, size-adjusted egg weight, fecundity, and size-adjusted fecundity for chinook salmon from the Hakataramea River, Glenariffe Stream, and Battle Creek, 1994 and 1995.

	Year	Hakataramea	Glenariffe	Battle Creek
Total ova weight (g)	1994	1496 (56.2)	1211 (48.6) <sup>a</sup>	1304 (43.7) <sup>a</sup>
	1995	1583 (94.4)	1224 (51.0) <sup>a</sup>	1189 (29.1) <sup>a</sup>
GSI (%)	1994	19.5 (0.29)	18.2 (0.33)	20.3 (0.33)
	1995	18.8 (0.53)	17.6 (0.46)	19.8 (0.22)
Egg weight (mg)	1994	215 (4.36)	185 (3.63)	249 (1.90)
	1995	219 (6.96) <sup>b</sup>	179 (4.25)	227 (2.81) <sup>b</sup>
Egg weight at 660 mm	1994	206 (3.93)	185 (3.03)	258 (4.91)
	1995	203 (5.66)	177 (3.74)	236 (3.05)
Fecundity	1994	7358 (270)	6583 (218)	5238 (127)
	1995	7525 (463)	6896 (228)	5232 (114)
Fecundity at 660 mm	1994	6724 (174) <sup>a</sup>	6577 (162) <sup>a</sup>	5648 (120)
	1995	6490 (332) <sup>a</sup>	6792 (189) <sup>a</sup>	5554 (79)
Sample size	1994	33	40	60
	1995	17	23	59

**Note:** All characters showed significant origin effects ( $p < 0.001$  in all cases).

<sup>a</sup>Two populations did not differ in two-way Tukey's analysis ( $p \geq 0.05$ ).

<sup>b</sup>Two populations did not differ within a year ( $p \geq 0.05$ ).

Experimental families, from the gametes collected in NZ in 1994, were established at the Silverstream Research Station (43° 25'S, 172°36'E) on a tributary of the Waimakariri River. We used a half-sib mating design, in which milt from one male fertilized ova from two females, to create 32 full-sib families nested within 16 half-sib families for the Hakataramea population and 40 full-sib families nested within 20 half-sib families for the Glenariffe population. The time of fertilization for each family was recorded and each full-sib family was incubated in an individual vertical flow-through jar. Temperature regimes during the experiment were monitored using Hobo temperature loggers (Onset Corporation).

After incubating for 24 days ( $T_{\text{mean}} = 12.4^{\circ}\text{C}$ ), family sizes were standardized so that none contained more than 1900 embryos, and the populations were reduced to 30 families each by discarding pairs of half-sib families. After hatching, the embryos from each family were transferred to a screened section (partitioned with metal screen) in one of 10 stainless steel troughs to complete yolk absorption.

We monitored the number of degree-days (sum of daily mean incubation temperatures) to hatching over two temperature regimes: Silverstream Hatchery ambient water ( $T_{\text{mean}} = 12.4^{\circ}\text{C}$ ) and chilled water ( $T_{\text{mean}} = 5.9^{\circ}\text{C}$ ). For the ambient treatment, we placed samples of 100 live embryos from each family in porous hatching trays. These trays were set into a hatchery trough supplied with water at ambient temperature. Once hatching began, the trays were checked at 4- to 6-h intervals and hatched alevins were counted and removed.

For the cold treatment, about 100 embryos per family were collected within 23 h of fertilization. The eggs were half submerged in oxygenated, distilled water in petri dishes and covered with loose-fitting lids. The dishes were incubated in a walk-in cooler, and water was changed twice a week. After 51 days, all surviving eggs were submersed in a chilled, recirculating water bath using the same porous trays. Once hatching began, the trays were checked up to three times daily and newly hatched alevins were removed and counted.

We recorded dried (oven-dried at  $95^{\circ}\text{C}$  for 24 h) alevin yolk and body weights of five formalin (5% buffered) preserved individuals,

and wet values on one preserved individual, from each family on four occasions over the yolk absorption period (40, 52, 64, and 73 days after fertilization, corresponding to about 1, 13, 25, and 34 days after hatching at a mean temperature of  $12.1^{\circ}\text{C}$ ). The final collection approximated the time when remaining yolk became enclosed within the body cavity ("button-up"). This period is associated with the final stage of yolk absorption (Beacham et al. 1985), the time of maximum alevin wet weight, the beginning of exogenous feeding, and timing of emergence from the redd (Heming 1982; Rombough 1985).

### Data analysis

Fecundity and egg weight were transformed to compensate for interpopulation variation in mean adult body size. The data for each female were adjusted to a body length of 660 mm, the mean for both populations, using the common within-groups slope estimated by regressing  $\log(\text{trait})$  on  $\log(\text{length})$  (Reist 1986). We characterized total ova mass relative to body size using the gonadosomatic index ( $\text{GSI} = \text{drained ova mass}/\text{body mass}$ , expressed as a percentage and arcsine-square root transformed). Two-way ANOVAs with population and year as factors were performed on both the raw and size-adjusted measures. Tukey's analysis was run as a post hoc test on the two-way ANOVA results, using techniques outlined in Neter et al. (1990) to handle two-factor designs with unequal sample sizes. When the interaction effect was significant, we ran separate one-way ANOVA models and Tukey's analysis for each year.

Hatching times were converted to degree-days by summing the mean daily incubation temperatures over development. ANOVA with dams nested within sires nested within population was used to determine whether embryos of Hakataramea and Glenariffe origin differed in the mean number of degree-days to hatching. In performing this analysis, the data for two and three sires were removed at random from the Glenariffe data in the ambient and cold temperature data sets, respectively, to balance the design with the number of Hakataramea families (creating 32 families nested within 16 sires for each of the populations under the warm conditions and 28 families nested within 14 sires for each of the popula-

tions under the cold conditions). Because sample sizes for each population were modest with respect to separate quantitative genetic analyses (and because analyses did not evidence significant differences in the trait means or significantly different separate heritability estimates), this design was also used to estimate quantitative genetic parameters (Becker 1984) for the NZ chinook populations in combination. Restricted maximum likelihood (Shaw 1987) was employed to obtain variance components under the ambient and cold conditions. Maternal effects were estimated as in Beacham (1988). We performed bivariate correlations between family estimates of degree-days to hatching at the two different temperatures, and linear regressions of mean degree-days on family mean egg weights, to further investigate potential genotype by environment interactions and maternal effects relating to egg size.

Alevin yolk weight, body weight, total weight, and yolk proportion were compared between populations at each of the four sampling times. We also compared the specific alevin growth rate (daily percent change in alevin weight), specific yolk use rate (daily percent change in yolk weight), and yolk conversion efficiencies between each successive collection and over the period from the first collection to the last collection. Rates and conversion efficiency were calculated on the dried tissue data set using 30 family means per population. Specific rates were calculated using natural logarithms and conversion efficiency was calculated as the difference in dry body weight between collections divided by the difference in dry yolk weight (expressed as a percentage and arcsine-square root transformed). Nested ANOVA (dams within sires within populations for dry data and sires within populations for wet data and rates) was used to compare population means and evaluate sire effects.

### Environmental measures

Two years of daily mean stream temperatures were obtained using Hobo loggers installed in the lower reaches of each stream in April 1994. Time to hatching was modeled using the simple thermal sums model (Alderdice and Velsen 1978). Rombough's (1985) model was employed to estimate time to maximum alevin wet weight (MAWW) from the temperature records from each river and initial mean egg weights. We chose this stage as a surrogate for timing of emergence from the gravel (Heming 1982).

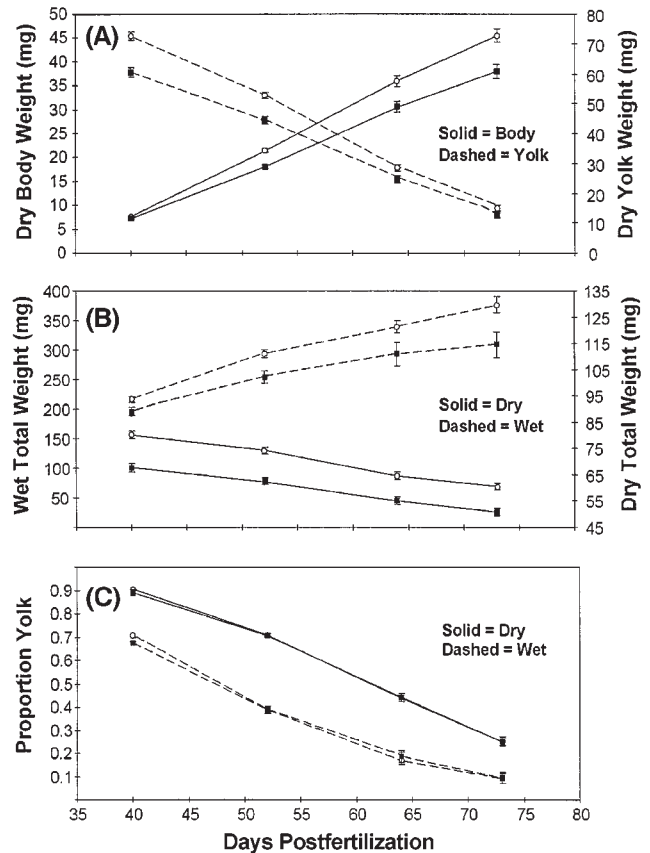
Substrate was sampled at four spawning sites in both the Hakataramea and Glenariffe systems. At each site, surface substrate was characterized using a pebble count technique (Kondolf and Li 1992), and five to eight bulk samples of about 10 kg each were taken by spade and bucket. Samples were air-dried and then sifted through a halving series of wire screens. Two-sample Kolmogorov-Smirnov tests were calculated on both the surface substrate and the bulk samples to compare gravel size distributions. The median substrate size ( $D_{50}$ ) and the arcsine-square root transformed proportions in the different gravel particle size classes were estimated to aid in interpreting differences.

## Results

### Variation in reproductive traits

Total ova weight differed among populations (Table 1). Hakataramea females had larger ova masses than either Glenariffe or Battle Creek females, but Glenariffe did not differ from Battle Creek. There were significant differences between all populations in GSI (Table 1), and there was a significant year effect ( $p = 0.04$ ). Battle Creek fish had the largest GSI and the Glenariffe fish had the smallest. Both the raw and size-adjusted egg size data indicated an interaction between origin and year. In 1994, all three groups differed from each other; Battle Creek fish had the largest

**Fig. 1.** (A) Mean alevin dry body weight and yolk weight, (B) wet and dry total weights, and (C) wet and dry yolk proportions for Hakataramea River (open circles) and Glenariffe Stream (solid squares) chinook salmon incubated at a mean temperature of 12.1°C. Vertical bars indicate 95% confidence intervals.



unadjusted egg size and Glenariffe had the smallest. In 1995 the pattern was similar, except Battle Creek fish did not differ from Hakataramea fish. For the size-adjusted egg size data, all three populations differed from each other within each year; Battle Creek had the largest eggs and Glenariffe had the smallest (Table 1). The interaction effect appears to have been caused by a difference in mean egg size between years at Battle Creek. All three populations differed in mean fecundity (Table 1); Hakataramea salmon had the highest fecundity and Battle Creek fish had the lowest. The NZ fish also had more eggs for their length than those from Battle Creek, but the NZ populations did not differ from each other.

### Variation in development

The number of degree-days to hatching did not differ between populations at 12.4°C (Hakataramea = 480.3, SE = 0.75; Glenariffe = 480.3, SE = 0.36; based on 16 sires each,  $p = 0.96$ ) or under colder conditions (Hakataramea = 487.2, SE = 1.70; Glenariffe = 491.4, SE = 2.65; based on 14 sires each,  $p = 0.34$ ). Hatching distributions are often skewed with long tails, so we also compared the family median hatch times, but they showed the same patterns (ambient: mean median = 479 degree-days for each,  $p = 0.78$ ; cold:

**Table 2.** Mean (SE) specific growth rate (%/day), yolk use rate (%/day), and yolk conversion efficiency for chinook salmon from the Hakataramea River and Glenariffe Stream estimated from samples of five alevins per family taken 40, 52, 64, and 73 days after hatching.

Days after fertilization	Specific growth rate		Yolk use rate		Yolk conversion efficiency	
	Hakataramea	Glenariffe	Hakataramea	Glenariffe	Hakataramea	Glenariffe
40–52	8.7 (0.1)	8.3 (0.2)	2.7 (0.1)	2.8 (0.1)	72 (2)	70 (3)
52–64	4.2 (0.3) <sup>a</sup>	4.2 (0.3) <sup>a</sup>	5.3 (0.2)	5.2 (0.3)	58 (4) <sup>a</sup>	59 (4) <sup>a</sup>
64–73	2.6 (0.2)	2.4 (0.2)	7.4 (0.3)	8.0 (0.5)	70 (5)	64 (5)
40–73	5.4 (0.1) <sup>a</sup>	4.9 (0.2) <sup>a</sup>	4.9 (0.2)	5.0 (0.0)	66 (2) <sup>a</sup>	63 (3) <sup>a</sup>

**Note:** There were no differences detected between populations for any of these measures except for specific growth rate over the entire period ( $p = 0.055$ ). Sample size was 30 families per population.

<sup>a</sup>Significant sire effect ( $p \leq 0.001$  in all cases).

Hakataramea = 485 mean median-degree days, Glenariffe = 488 mean median-degree days,  $p = 0.27$ ). Sire effects were not significant at both temperatures ( $p > 0.28$ ), but dam effects were ( $p < 0.001$ ). Estimated heritability was higher under the ambient conditions ( $h^2 = 0.23$ , SE = 0.34) than under the colder conditions ( $h^2 = 0.05$ , SE = 0.34), although standard errors were large in both cases. Total phenotypic variance was higher under the colder conditions (ambient = 20.3, cold = 317.3), while estimated maternal effects were similar at the two temperatures (ambient = 0.36, cold = 0.41).

Families that developed relatively quickly in warm water did not also tend to develop quickly in colder water (Pearson correlation:  $|r| < 0.16$ ,  $p > 0.41$ ), suggesting a genotype by environment interaction. This was further supported by ANOVA of family and temperature; the interaction effect was significant ( $p < 0.001$ ) and accounted for about 36% of the variation. Regression of degree-days to hatching on mean egg weight was not significant ( $p = 0.19$ ); thus, egg size did not appear responsible for dam effects on time to hatching.

One day after hatching (40 days postfertilization), Hakataramea alevins had more dry yolk (Hakataramea = 72.7 mg, Glenariffe = 60.5 mg,  $p < 0.001$ ), higher total dry alevin weight (Hakataramea = 80.3 mg, Glenariffe = 67.8 mg,  $p < 0.001$ ), and slightly more dry body tissue (Hakataramea = 7.58 mg, Glenariffe = 7.28 mg,  $p = 0.059$ ). By the final collection (73 days postfertilization, or approximately the time of yolk absorption) the Hakataramea fry had larger dry body weights (Hakataramea = 45.5 mg, Glenariffe = 38.0 mg,  $p = 0.006$ ) (Fig. 1). The two populations differed in proportion of yolk at the first collection ( $p < 0.001$ ), but not at subsequent collections ( $p > 0.83$ ). The Hakataramea alevins started with a larger percentage of dried yolk weight (Hakataramea = 91%, Glenariffe = 89%), but this difference disappeared by the next collection (52 days postfertilization: Hakataramea = 71%, Glenariffe = 71%). Wet weight data indicated the same patterns of total weight, body weight, yolk weight, and proportion of yolk.

Specific alevin growth rate was slightly greater (about 10%,  $p = 0.055$ ) for the Hakataramea alevins over the entire period between collections 1 and 4 (40–73 days postfertilization) (Table 2). ANCOVA of specific alevin growth rate, with origin as a factor and dry yolk to body proportion as the covariate, indicated, however, that this effect may be related to interpopulation differences in yolk to body proportion, as the covariate was significant ( $p = 0.01$ ) and the ori-

gin effect was greatly reduced ( $p = 0.39$ ). Conversion efficiencies did not differ for the two populations between any of the consecutive collections or over the entire collection period ( $p > 0.37$  in all cases) (Table 2). Significant sire effects were found for alevin growth rate and for conversion efficiencies over the period from collection 2 to collection 3 (52–64 days postfertilization) and over the entire time period (Table 2).

#### Environmental variables

The Hakataramea had a higher mean temperature than Glenariffe over most of the year (Fig. 2). The difference averaged 2.3°C over the normal incubation period. This resulted in a difference of 13.6 days in 1994 and 16.4 days in 1995 in modeled hatching time for embryos spawned in these systems on the same date (using 480 degree-days to hatch). The modeled time to emergence (Fig. 2) differed between the NZ rivers by 27.5 days in 1994 and by 41.5 days in 1995.

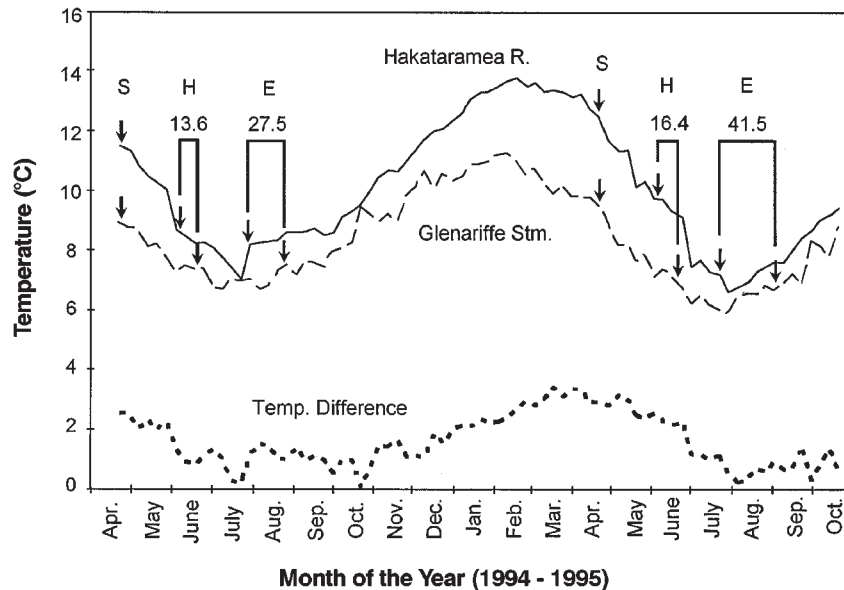
Kolmogorov–Smirnov tests indicated that the gravel of the rivers differed in both bulk and surface composition ( $p < 0.005$ ). The Hakataramea had more fine particles (<0.5 mm) and more very large (16–32 mm) material whereas the Glenariffe system had more material of intermediate sizes (0.5–2 mm). The surface pebble count data were consistent with these results. The Hakataramea had more large particles (32 to 48 mm) whereas Glenariffe had more intermediate (1–8 mm) particles. Surface samples did not measure finer material.

## Discussion

#### Egg size and incubation conditions

The NZ salmon had smaller eggs and higher fecundities at a common body size than the Battle Creek fish. Battle Creek and Hakataramea River fish had larger eggs and appear to experience warmer incubation temperatures than Glenariffe Stream fish, consistent with the pattern described by Fleming and Gross (1990). Mean temperatures at the Coleman Hatchery (and in Battle Creek; data obtained from U.S. Fish and Wildlife Service, Red Bluff, Calif.) were about 10.5°C over the incubation period, warmer than those in Glenariffe (about 8.5°C) but similar to those in the Hakataramea. However, NZ and Battle Creek chinook incubate under warmer conditions but have smaller eggs than most North American populations (Healey and Heard 1984), inconsistent with the

**Fig. 2.** Temperature regime (7-day running average) in Glenariffe Stream and the Hakataramea River and modeled times of hatching (H; Alderdice and Velsen 1978) and emergence (E; based on MAWW, Rombough 1985) based on a common spawning date (S) in both years. Numbers over brackets indicate estimated difference in days between the rivers.



hypothesized influence of temperature on egg size on a different scale.

If egg size were positively correlated with incubation gravel size, as found by Quinn et al. (1995), we would have expected smaller eggs in the Hakataramea because they incubate in substrate with a higher proportion of fine material. However, they were larger than chinook salmon eggs from Glenariffe. The differences in gravel size distributions between the NZ rivers, however, were small compared with the range of gravel sizes reported by Quinn et al. (1995).

### Fecundity and age at maturation

Most chinook salmon populations in North America (Roni and Quinn 1995) have an older mean age at maturity than those in NZ (Quinn and Unwin 1993). Thus, early age at maturation and high fecundity in NZ may be related to lower survival rates (see Unwin 1997 for Glenariffe estimate). However, some populations from the southern portion of the range in North America, including fall-run Battle Creek fish, have relatively high fecundity and mature early (Healey and Heard 1984; Kinnison et al. 1998). Thus the expression of these traits in NZ chinook may also reflect only minor modification of a character state that evolved in California. Within NZ, Waitaki/Hakataramea fish had a slightly higher mean age of maturity than Rakaia/Glenariffe fish (Quinn and Unwin 1993: males, 3.32 versus 2.96 years; females, 3.35 versus 3.18 years), but fecundity for a given size did not differ between the populations.

### Other sources of variation in reproductive traits

The temperature/egg size and age at maturity/fecundity hypotheses were both at least partly consistent with the variation detected here, but other factors or interactions among factors may also have contributed to the variation. From a phenotypic plasticity perspective, rapid growth is associated

with high fecundity and small eggs (Thorpe et al. 1984; Jonsson et al. 1996). The high size-specific fecundity of the NZ fish is consistent with their larger size at age than most North American populations (Quinn and Unwin 1993; Roni and Quinn 1995) including Battle Creek fish (Kinnison et al. 1998). The mean fecundities of Rakaia and Waitaki chinook reported by Quinn and Bloomberg (1992) were significantly smaller than the values found here, but this may also reflect an effect of growth rate on fecundity. The fish from both NZ rivers were larger and heavier for their length in the present study than those analyzed by Quinn and Bloomberg (1992).

Upriver migration can also affect reproductive traits, both as a selective force for differences among populations and as a proximate factor (i.e., energetic cost) influencing gonad size. Sockeye salmon populations with more arduous migrations up the Fraser River had lower GSI values than populations with easier migrations (Linley 1993), and Beacham and Murray (1993) found that longer migrating salmon populations had smaller eggs. The lower GSI of Glenariffe females than Hakataramea females is consistent with this trend, as Glenariffe is at a higher elevation and farther inland. Additionally, Rakaia (and presumably Glenariffe) fish enter freshwater about a month earlier than Waitaki fish (Quinn and Unwin 1993); hence the lower GSI of Glenariffe fish may also reflect the metabolic demand resulting from time in freshwater (i.e., without feeding) prior to spawning. However, GSI and egg size differences between NZ and Battle Creek chinook would not be consistent with the river size/length hypothesis, as the Sacramento is much longer than either NZ river. Time in the river, temperatures, and the braided nature of the NZ rivers may partly account for this.

### Genetic and phenotypic effects on hatching time

Although the NZ populations differed in some reproductive traits, no statistically significant differences were de-

tected in degree-days to hatching under common rearing conditions. Embryo development rate (measured as time or temperature units to hatching) differs among some North American salmon populations, but the differences tend to be small and some investigators have suggested that it is generally a conserved character (e.g., Murray and McPhail 1988). Hendry et al. (1998) also found that hatching time did not diverge appreciably among populations of sockeye salmon established in Lake Washington, Wash. (though it did differ appreciably over the course of one run). The developmental rate of NZ chinook salmon is rapid compared with reported values for North American populations (Beacham and Murray 1989).

Quantitative genetic analyses indicated primarily dam effects and generally low heritabilities with large standard errors for embryo development, suggesting limited potential for selection to modify degree-days to hatching at present in NZ. The lack of correlations between incubation times for embryos from the same families at different temperatures indicated a genotype by environment interaction in both populations. That is, families did not have similar reaction norms at different temperatures, similar to Beacham's (1988) findings. The lack of a relationship between egg size and time to hatching is also consistent with other studies (e.g., Beacham et al. 1985).

#### Alevin development and thermal regime

Amount of yolk at hatching and body size near to yolk absorption were influenced by egg size, consistent with other investigations (e.g., Beacham et al. 1985; Rombough 1985). Dry yolk weight differed between populations at all collections, but yolk proportion converged soon after hatching and remained similar through yolk absorption, the Hakataramea alevins having a slightly higher specific growth rate. The difference in growth rate, however, could be related to growth mechanics resulting from differences in surface area of the yolk reserves (maternal effect of yolk size) relative to alevin body sizes (Beer 1996). ANCOVA of specific alevin growth rate, with origin as a factor and dry yolk to body proportion as the covariate, supports this hypothesis. Overall, the NZ populations performed similarly under common environmental conditions with respect to alevin development, although significant sire effects suggest that additive genetic variation is available for alevin growth rate and conversion efficiency. Hakataramea salmon are thought to spawn a short time later, on average, than the Glenariffe population, and this spawning time divergence may have mitigated factors that would otherwise promote divergence in egg or alevin development rate.

The larger fry size at the end of yolk absorption of Hakataramea fish found under experimental conditions may be more pronounced for wild fish. Hakataramea embryos and alevins appear to experience warmer temperatures (with perhaps slightly less efficient yolk conversion; Heming 1982) and may emerge as fry 4–6 weeks earlier than Glenariffe fish (given similar spawning dates; Fig. 2), obtaining an earlier start on exogenous feeding. Thus, there is considerable potential for environmental variation and maternal effects to produce phenotypic differences between juveniles in the two NZ rivers.

## Summary

For a newly established population to succeed, the phenotype must be sufficiently suited to local conditions that the population can at least replace itself in the following generations. Persistence then opens the possibility of adaptation to the new environment, leading to increased survival rates, abundance, and possible range extension. Chinook salmon introduced into NZ in the 1900s persisted, increased in abundance, and expanded their range. Our data support previous work demonstrating significant phenotypic divergence in adult traits in NZ, but suggest that genetic differences in early development rates are slight or have not developed between the NZ populations investigated. Trends in reproductive traits were consistent with some hypotheses for salmon in their native range (Fleming and Gross 1990; Beacham and Murray 1993), although we cannot conclude an adaptive genetic basis for this recently derived variation. Future comparisons of the reproductive characters of these populations under common rearing conditions are planned to determine the roles of environmental induction and genetic control in the phenotypic divergence that has arisen in these traits over the past 90 years.

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