Growth and salinity tolerance of juvenile chinook salmon (*Oncorhynchus tshawytscha*) from two introduced New Zealand populations

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Abstract: Self-sustaining populations of chinook salmon (*Oncorhynchus tshawytscha*) were established in New Zealand, from a common introduction group, near the turn of the 20th century. To investigate possible population divergence over this relatively short time scale we compared size, growth, and hypersalinity tolerance of families from two populations over their first year of rearing under shared conditions. Differences in initial fry mass were consistent with egg-size differences, but there was also evidence of genetic differences in early growth rates. Size differences between the populations decreased over time and rank correlations of mean family mass with initial egg and fry masses degraded over increasing intervals to nearly zero by the end of the year. Population effects on hypersalinity tolerance were not apparent after 4, 6, or 10 months of rearing (from yolk absorption), but family effects were suggested by ANOVAs and by the existence of groups of families with seemingly different relative seasonal optima for tolerance. Thus far, investigation of juvenile traits under common environmental conditions has shown less genetic divergence between the two New Zealand populations than is suggested by the range of differences found for phenotypic traits measured on wild adults in previous investigations.

Résumé : Des populations auto-suffisantes de Saumons quinnats (*Oncorhynchus tshawytscha*) ont été établies en Nouvelle-Zélande à partir d'un groupe commun d'introduction environ depuis le début du 20e siècle. Pour évaluer la possibilité de divergences entre les populations au cours de cette période relativement courte, nous avons comparé la taille, la croissance et la tolérance à l'hypersalinité chez des familles provenant de deux populations pendant leur première année d'élevage dans les mêmes conditions. Les différences de masse initiale des alevins correspondaient aux différences de taille des oeufs entre les deux groupes, mais il y avait également des différences génétiques entre leurs taux initiaux de croissance. Les différences de taille entre les populations ont diminué avec le temps et les corrélations de rang entre la masse moyenne d'une famille et la masse initiale des oeufs et la masse des alevins diminuaient de valeur à mesure qu'augmentait l'intervalle de temps, jusqu'à 9 mois. Les effets de l'origine sur la tolérance à l'hypersalinité n'étaient pas encore apparents à 4, 6 et 10 mois d'élevage (à partir de l'absorption du vitellus), mais l'origine familiale semble avoir de l'effet comme l'indiquent les analyses de variance et l'existence de groupes de familles qui semblent avoir des optimums saisonniers relatifs de tolérance différents. À ce jour, la recherche de caractéristiques juvéniles dans des conditions environnementales communes a révélé moins de divergences génétiques entre les deux populations néo-zélandaises que ne le suggère l'examen des caractéristiques phénotypiques mesurées chez les adultes sauvages au cours de travaux antérieurs.

[Traduit par la Rédaction]

Introduction

Adaptive variation among populations is central to the management and conservation of salmonid fishes such as Pacific salmon, *Oncorhynchus* spp., and Atlantic salmon, *Salmo salar* (Taylor 1991). Improved understanding of population-specific variation may be critical in efforts to maintain threatened populations, predict responses of populations to environmental change, and re-establish populations after extirpation. Within their natural range, most wild populations of Pacific salmonids are believed to have evolved in their respective river systems following the last glaciation event (ca. 10 000 years BP) or longer. Consequently, the initial processes (such as local adaptation, genetic drift, and phenotypic plasticity) by which populations diverge in particular traits, and the time intervals required before measurable differences emerge in the wild, remain unclear.

Translocations of natural populations to new environments provide an opportunity to study the mechanisms and patterns of phenotypic population divergence (cf. Endler 1986; Rose and Lauder 1996) over shorter and better defined time frames than are generally encountered with natural populations. In the case of Pacific salmonids, the introduction of chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento River, California, to the South Island of

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New Zealand between 1901 and 1907 has provided such an opportunity for study. Within approximately 10 years of these introductions, a number of self-sustaining, anadromous populations became established (McDowall 1994).

Recently, variation in several adult life-history traits has been detected among a number of naturally spawning New Zealand populations. These traits include age at maturity, size at age, morphology, fecundity, egg size, and timing of return to fresh water and spawning grounds (Quinn and Bloomberg 1992; Quinn and Unwin 1993; Kinnison et al. 1998*a*, 1998*b*). In addition, embryo and alevin development has been compared between populations reared under shared environmental conditions (Kinnison et al. 1998*b*). However, considerable scope remains for determining the degree and nature (genetic change or phenotypic plasticity) of population divergence in the broad spectrum of juvenile and adult traits and elucidating the basis of adult variation observed to date.

Growth rate, size at age, and seawater adaptation are among the phenotypic traits commonly used to differentiate populations of salmonids, and these are influenced by genetic and environmental factors. Variation in growth rate is expressed in the substantial interpopulation variation in size at age of chinook salmon within their native range (Roni and Quinn 1995). The genetic basis of growth rate is well documented, owing to its importance to the aquaculture industry (e.g., coho salmon, *Oncorhynchus kisutch*, Hershberger et al. 1990; Atlantic salmon, Jonasson 1993). Growth rate, or some closely correlated attribute, also interacts with a number of life-history traits. For example, changes in growing conditions from year to year can influence mean smolt age within sockeye salmon (*Oncorhynchus nerka*) populations (e.g., Koenings and Burkett 1987).

Chinook salmon show highly variable patterns of freshwater residence and seaward migration (Healey 1991). This variation is found both among populations, as in the case of ocean- and stream-type populations (Gilbert 1913; Healey 1983), and within populations, such as in New Zealand, where individuals migrate to sea as either subyearlings or yearlings (referred to as ocean- and stream-type individuals in previous works; Quinn and Unwin 1993). Genetic control over juvenile life history type and seawater-adaptability schedule has been demonstrated for chinook salmon populations in their natural range (Clarke et al. 1992; Kreeger 1995).

In 1994, we initiated a long-term investigation of life-history variation in New Zealand chinook salmon, which provided the previously mentioned comparisons of adult and juvenile traits (Kinnison et al. 1998*a*, 1998*b*). In this paper we compare sizes at age, growth rates, and salinity tolerance of juvenile chinook salmon from two study populations reared under common, controlled conditions. Our objectives were (*i*) to determine whether the populations differed in juvenile growth rate and seawater adaptability and (*ii*) to determine the scope of family variation in these traits within the populations. On a broader scale, we integrate these results into our growing record of the evolution of New Zealand chinook salmon traits and consider the overall pattern and rates of trait divergence in juveniles and wild adults from these populations.

Materials and methods

Study streams

Glenariffe stream (Fig. 1) is a stable, spring-fed tributary of the Rakaia River joining the main stem 100 km from the coast at an elevation of 430 m, and is one of four major chinook salmon spawning systems within the Rakaia catchment (Unwin 1986). The Hakataramea River (Fig. 1) is a rain-fed tributary of the lower Waitaki River, and was the site of the original New Zealand chinook introductions (McDowall 1994). It joins the Waitaki River 60 km from the coast at an elevation of 200 m, 7 km below a hydroelectric dam that is impassable to salmon migration. Both rivers have had spawning populations of 2–3000 individuals in recent years.

Establishment and rearing of families

Milt and eggs from the parent stock in both study streams were collected on 23–24 April 1994 for subsequent fertilization and rearing at Silverstream Hatchery (Fig. 1). Embryos and alevins were incubated and families culled (because of space limitations) as described by Kinnison et al. (1998*b*) to produce 30 full-sib families, nested within 15 half-sib families, for each population. Rearing initially occurred in sectioned stainless-steel hatchery troughs (5 m × 40 cm × 25 cm) fed by pumped ground water at 10–12°C and later in 30 replicate 3000-L circular tanks with ground-water turnover every 40 min.

Yolk absorption was completed on 20 July 1994, at which time fry were fed a commercially produced dry starter diet. Unless otherwise stated, all subsequent fry ages are measured from this date (89 d post fertilization). Family numbers were reduced on three occasions while in the troughs, from an initial count of 1900 fry per family at fertilization to 700 fry per section by 20 September 1994.

In mid-October (approximately 90 d after yolk absorption), all fry were transferred to outdoor tanks. To accommodate all families, two families (one marked externally by removal of the adipose fin) were randomly assigned to each tank. Fry were also marked to family level using coded-wire tags implanted in their snouts. Two families were accidentally mixed during transfer, reducing the number of full-sib families to 58 (29 per population) and the number of complete half-sib family pairs to 14 for subsequent data collection and analysis. In mid-February 1995 we reduced each family to 400 fish.

Measurement of growth and salinity tolerance

We estimated mean fry mass for each family from a bulk subsample of 50 anaesthetized individuals at 2-week intervals from August to October 1994 and at 4- to 5-week intervals from October 1994 to April 1995. The specific growth rate between weighings was calculated as described by Wootton (1990). We compared growth rates over periods delineated by major culls (10 August 1994 to 22 September 1994; 5 October 1994 to 13 February 1995; 28 February to 18 April 1995) using a repeated-measures design with nesting of the between-subjects factors (sire nested in population) and we plotted population growth rates between each of the collections. Masses (not transformed, as they did not differ significantly from normality) were compared between populations and among sire-related families by means of nested ANOVA models of family means within sires nested within populations, using 28 full-sib families nested within 14 half-sib families per population to provide a balanced design. Mean dam ovum masses (Kinnison et al. 1998*b*) and mean early (10 August 1994) fry masses were tested for correlation (Pearson's correlation) with family fry masses at later dates to examine the persistence of maternal egg size and initial fry size effects over time.

Seawater tolerance was assessed by recording survival time under high-salinity conditions (modified from Saunders and

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Fig. 1. Part of the central South Island of New Zealand, including the spawning tributaries of the two study populations and the Silverstream rearing facility.

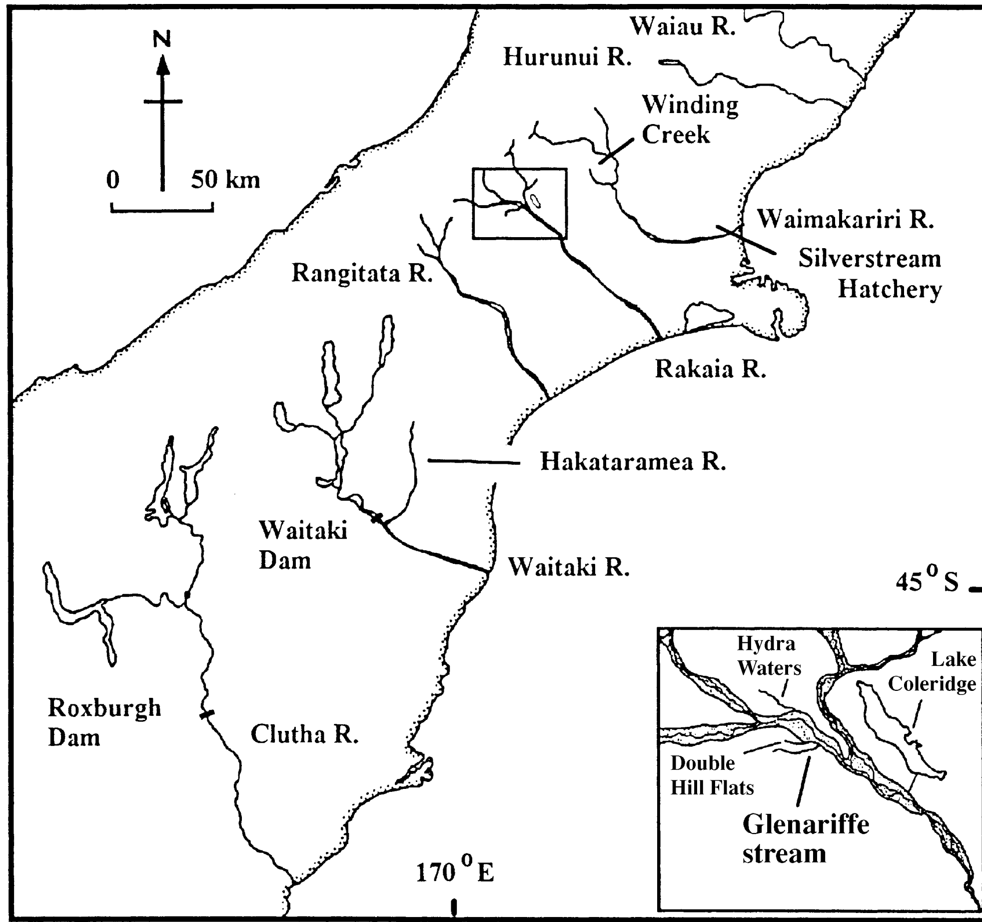

Table 1. Sample sizes, mean fork length (mm), mean survival time (min), and ANOVA models used to analyze hypersalinity challenges on two New Zealand populations at 4, 6, and 10 months.

	4 months	6 months	10 months
No. of families per population	20	28	15
No. of individuals per family	9–10	2	5
Fork length	96.3 (0.3)	128 (0.6)	168 (0.6)
Trial conditions (salinity, temp.)	43 ppt, 12°C	47 ppt, 13°C	45 ppt, 13°C
Survival time (Hakataramea stream)	408 (7)	510 (11)	1910 (262)
Survival time (Glenariffe River)	403 (7)	493 (13)	2393 (445)
ANOVA model used?			
(1) $Y = \mu + O + T + S\ (O) + D\ (S\ (O)) + L + E$	Yes	—	—
(2) $Y = \mu + O + T + OT + E$ (on family means)	—	Yes	Yes
(3) $Y = \mu + O + D\ (O) + E$ (test of family effect)	—	—	Yes
(4) $Y = \mu + T + D\ (T) + E$ (test of family effect)	—	Yes	—
(5) $Y = \mu + D + L + DL + E$ (test of length effect)	—	—	Yes

Note: Model notation is as follows: Y, individual survival time; μ, grand mean; O, origin; T, tank or test chamber; L, fork length; S, sire; D, dam; E, error. Numbers in parentheses are standard errors.

Henderson 1970). We conducted this challenge three times, at approximately 4 months (30 November 1994), 6 months (20 January 1995), and 10 months (4 May 1995) of age. Individuals were transferred to a freshwater holding tank and allowed to acclimate for 24 h. At the end of this period they were distributed among up to three test chambers containing hypersaline water (seawater from a nearby coastal site augmented by artificial aquarium sea salts). Salinity levels for each challenge (Table 1) were established by means of preliminary experiments to determine the approximate level at which most mortality would occur within a workable time frame (24 h for the 4- and 6-month tests and 72 h for the 10-month test). Oxygen levels were maintained at 7.5–8.0 ppm. Individuals were removed when cessation of opercular activity and failure to react when handled indicated death; fork length (FL (mm)) and

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Table 2. Mean masses and specific growth rates for chinook salmon from two New Zealand populations from 10 August 1994 to 18 April 1995.

		Mean		*p*	
		Hakataramea River	Glenariffe stream	Origin	Sire
Mass (g)					
1994					
	10 Aug.	1.21 (0.03)	1.01 (0.03)	0.001	0.006
	24 Aug.	1.80 (0.04)	1.54 (0.04)	0.001	0.003
	7 Sept.	2.54 (0.06)	2.22 (0.06)	0.004	0.10
	22 Sept.	3.46 (0.09)	3.07 (0.09)	0.03	0.02
	5 Oct.	5.03 (0.15)	4.54 (0.13)	0.053	0.10
	3 Nov.	9.74 (0.24)	9.20 (0.24)	0.25	0.06
	29 Nov.	13.0 (0.29)	12.2 (0.26)	0.19	0.04
1995					
	12 Jan.	22.1 (0.48)	22.3 (0.55)	0.64	0.27
	13 Feb.	23.3 (0.55)	23.8 (0.64)	0.51	0.26
	28 Feb.	32.2 (0.74)	32.5 (0.84)	0.70	0.52
	20 Mar.	42.1 (0.84)	41.7 (1.02)	0.98	0.12
	18 Apr.	57.0 (0.74)	58.7 (1.19)	0.21	0.16
Growth rate (%/d)	10 Aug. – 22 Sept. 1994	2.41 (0.04)	2.58 (0.05)	0.04	0.02
	5 Oct. 1994 – 13 Feb. 1995	1.17 (0.02)	1.26 (0.02)	0.01	0.08
	28 Feb. – 18 Apr. 1995	1.18 (0.03)	1.22 (0.03)	0.30	0.95

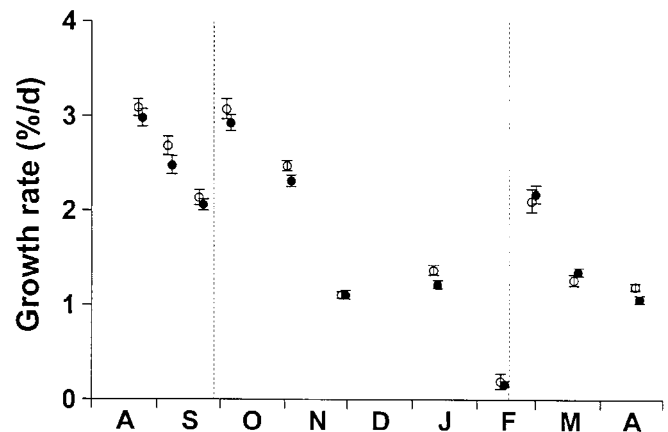
Note: Significance tests (*p* values) for nested ANOVAs, with sires nested within populations, are also shown. Numbers in parentheses are standard errors.

survival time (ST) were recorded, and the snout was retained for subsequent tag reading and family identification.

Test protocols varied slightly between challenges, owing to space limitations and availability of facilities as fish grew. The 4-month test, designed to provide individual-, family-, and population-level data, used 10 individuals per family to form a combined test group that was then distributed between three 160-L tanks. The 6-month test involved two fish per family, with different subsets of families (equal numbers per population) assigned to two tanks. This challenge was intended to provide primarily a population-level comparison. The 10-month test used a single 1350-L test chamber partitioned into two halves by a mesh screen, and involved five individuals from 15 nonrelated families within each population (fewer families and fish per family than in the 4-month test, owing to space limitations). Again subsets of families from both populations were distributed nearly equally between chambers (each population was split into seven and eight families).

ANOVA models also differed between the challenges, reflecting subtleties of the experimental designs (such as those imposed by placing different families in different tanks in the 6- and 10-month challenges), but the combined analysis for each challenge addressed the effects of dam (family effect), origin, and test chamber (Table 1). The effect of size (FL) was also addressed in the 4- and 10-month challenges. The 4 month test data were used to investigate the quantitative genetic nature of hypersalinity tolerance by including a sire effect (random) in the nested model (Table 1, model 1). Twenty families per population, in which both members of the half-sib pair were present in each test chamber, were used in the ANOVA to avoid empty cells in the design, and restricted maximum likelihood was used to estimate variance components. Quantitative genetic analysis was performed with and without adjustment for a length effect in model 1. For the 10-month test, ST was log-normally distributed, so raw data were log-transformed to homogenize error variance and normalize the data.

Fig. 2. Growth rates (mean ±1 SE) for Glenariffe stream (○) and Hakataramea River (●) chinook salmon fry, August 1994 – April 1995. The vertical broken lines correspond to dates when rearing densities were reduced via culling or other husbandry-related activities (see the text).



Results

Size and growth

Glenariffe stream fry were initially smaller than Hakataramea River fry (1.01 vs. 1.21 g; $p < 0.001$), and remained so for the five collections during the period of trough rearing from 3 to 10 weeks of age (10 August to 5 October; $p \leq 0.053$ in all cases; Table 2). Thereafter, mean mass did not differ between populations ($p \geq 0.19$ in all cases), averaging 58.7 g (Glenariffe stream) and 57.0 g (Hakataramea River)

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Fig. 3. Correlations between post-hatch fry mass (10 August 1994) and egg–alevin–fry masses for 58 families of chinook salmon recorded on 17 occasions from April 1994 to April 1995.

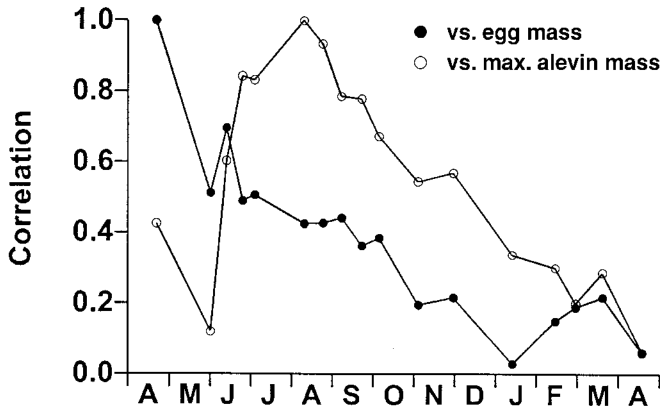
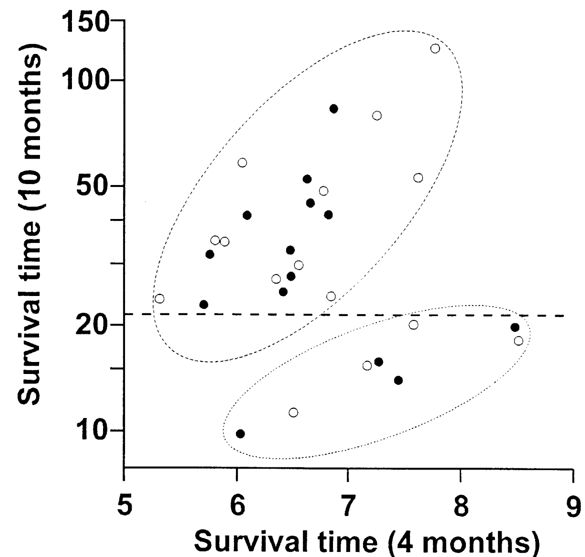


Fig. 4. Mean survival time (h) for 29 families of chinook salmon from Glenariffe stream (○) and the Hakataramea River (●) subjected to a hypersalinity challenge at 4 and 10 months. Ellipses indicate the two disjunct groups.



at the final collection on April 18. Repeated-measures ANOVA of specific growth rates, calculated over each of the three periods defined by the culls, indicated that populations differed in growth rate ($p = 0.001$) and that within half-sib families growth rate differed among periods ($p < 0.001$). Glenariffe fry grew faster from August to October ($p = 0.04$) and from October to February ($p = 0.01$), but not over the final 2 months of the study (Table 2, Fig. 2). Sire effects on growth rate and mass were detected for a number of sampling periods, based on nested ANOVAs (Table 2).

Growth of both populations slowed as rearing conditions became more crowded, with a jump in growth rates immediately following an early trough cull and again after the February cull (Fig. 2). Since the Hakataramea fish were initially larger, on average, and space allotted to all groups was largely identical, density effects may have resulted in the slower growth of the Hakataramea fish. However, a two-way ANOVA of population and growth period performed on subsets of families matched for means and variances of masses at the beginning of each period (ANOVA of beginning masses after subsets were chosen: $p = 0.97$) showed that the Glenariffe fry still grew significantly faster ($p = 0.04$).

Mean initial fry mass varied between families and was moderately correlated with mass of the eggs ($r = 0.43$), but individual family rankings (and associated rank correlations) were not maintained over the duration of the study (Fig. 3). Mean family masses for collections made within 30 d of each other were highly correlated ($r > 0.80$ in all cases), but these correlations degraded over longer intervals, to the extent that mass at the end of the study was uncorrelated with either egg mass ($r = 0.045$, $p = 0.74$) or initial fry mass ($r = 0.17$, $p = 0.19$). Growth rates showed a similar trend, with only a weak correlation within families between the first and third intervals shown in Fig. 2 ($r = 0.21$, $p = 0.11$).

Hypersalinity tolerance

Mean ST did not differ between the two study populations in any of the challenges ($p \geq 0.19$; Table 1, models 1 and 2). Mean ST for each family ranged from 5 h 19 min to 8 h 29 min at 4 months, and from 9 h 44 min to 118 h at 10 months, and there was significant variation among families in all trials ($p \leq 0.03$: dam effects in models 1, 3, and 4 in Table 1), based on nested analyses. FL of the tested fish did not differ between populations at any of the trials ($p \geq 0.39$), but did differ among families ($p < 0.05$) in nested ANOVAs. FL had an effect on ST (4 months, $p = 0.06$, Table 1, model 1; 10 months, $p < 0.01$, Table 1, model 5), but significant family effects still remained (4 months, $p = 0.07$; 10 months, $p < 0.001$), indicating that size did not account for all family variation in ST. A tank effect on ST was encountered in the 4-month challenge ($p < 0.001$; Table 1, model 1) and the 6-month challenge ($p = 0.03$; Table 1, model 2), probably as a result of slight differences in conditions (e.g., salinity, temperature, or oxygenation) among chambers. This is supported by the lack of a significant test-chamber effect in the 10-month challenge, where water could be exchanged between chambers.

Though family effects were detected for all challenges, sire effects were not significant in the 4-month challenge. Since origin effects were not found, and sample sizes were limited, heritabilities were estimated from model 1 (with and without the length covariate), combining the two populations. Significant additive genetic variation was not detected ($p = 0.274$) for models with or without length as a covariate. Consistent with this, heritability estimates were small with large standard errors (unadjusted for length: $h^2 = 0.160$, SE = 0.177; adjusted for length: $h^2 = 0.133$, SE = 0.179).

Based on 29 families tested in both November and May, ST at 4 months (ST_4) was uncorrelated with ST at 10 months (ST_{10}; $r = 0.052$, $p = 0.78$). However, closer examination suggested that this result was confounded by the presence of two disjunct groups of families, independent of the two experimental populations, for which the relation between ST_4 and ST_{10} differed (Fig. 4). One group comprised 21 families for which ST_{10} exceeded 21 h (mean = 44.2 h), and represented families for which ST_{10} was generally average or above average, and was also correlated ($r = 0.62$, $p = 0.003$) with ST_4. The second group comprised eight families

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for which ST_{10} was less than 21 h (mean = 15.6 h), and in which their relative ST_{10} was poor compared with their relative ST_4. In particular, this group included the only two families for which ST_4 exceeded 8 h and six of the nine families for which ST_4 exceeded 7 h. A positive correlation of ST_4 and ST_{10} occurred in this group as well ($r = 0.83$, $p = 0.01$). Statistical support for the presence of these groups was provided by testing the fit of a double normal distribution and a single normal distribution to the ratios of log (ST_{10}) to ST_4. The data significantly deviated from a single normal distribution ($p = 0.016$) but not from a double normal distribution ($p = 0.299$), consistent with the presence of two modes.

Discussion

The existence of growth-rate differences between the chinook salmon populations under common rearing, even after initial fry-size differences are taken into account, indicates genetic divergence. The magnitude of the difference was consistent with the short period of isolation of the study populations and their geographic proximity; nevertheless, it suggests that populations in the two rivers have diverged measurably over the 90 years (28 generations, based on an average age of 3.2 years at maturity) since their Sacramento River ancestors were introduced to New Zealand. The existence of a genetic difference in a phenotypic trait adds credence to the possibility, suggested by Quinn and Bloomberg (1992), Quinn and Unwin (1993), and Kinnison et al. (1998*a*, 1998*b*), that interpopulation variation in other phenotypic traits measured on adult New Zealand chinook may likewise have a genetic basis.

Point estimates of the rate of divergence of the two populations in early fry growth rates amount to 0.009 (last stanza) to 0.030 (second stanza) haldanes (Gingerich 1993). This is comparable to rates computed for divergent traits measured on wild adults (egg mass 0.036–0.046, GSI 0.020–0.024, fin-morphology factor 0.006–0.035; from Kinnison et al. 1998*a*, 1998*b*). These rates represent averages over time, therefore actual rates may have been higher or lower over different periods during the 90-year interval. With the exception of fecundity, all phenotypic traits compared thus far between Hakataramea and Glenariffe adult salmon (egg mass, GSI, size at age, and mass at length), as well as morphology (a composite of many traits), have shown divergence (Kinnison et al. 1998*a*, 1998*b*). By contrast, only one juvenile trait (early growth) out of four compared under shared rearing conditions (egg development, alevin development, juvenile growth, and salinity tolerance) has suggested significant divergence. Although these traits may not be independent, the range of juvenile traits compared does not show as much divergence as is suggested by traits measured on wild adults. While this trend may be influenced by the particular subset of traits examined, and the particular attributes of the study populations, it may also represent a true difference in the divergence rates of juvenile and adult traits, or the influence of environmental variation in producing phenotypic population differences.

The initial discrepancy in fry sizes between the two study populations was related to differences in egg size; female chinook from the Waitaki–Hakataramea river system produced larger eggs than those from the Rakaia–Glenariffe river system (Quinn and Bloomberg 1992; Kinnison et al. 1998*b*). Larger eggs produce alevins with more yolk, resulting in larger fry at yolk absorption (Thorpe et al. 1984; Beacham and Murray 1990). The correlation between egg size and fry size degraded with time under common rearing conditions, consistent with the results of other studies (e.g., Fowler 1972). The rate of degradation detected (Fig. 3) for these hatchery fish resulted in less than 10% of the variation in fry size being related to egg or alevin size after 3–6 months. Thus, although fry size appears to have a considerable maternal component (essentially an environmental component of yolk amount) that may affect early fry size differences in the wild, over time other influences (genetic and environmental) may overcome or interact with initial egg size and disrupt the correlation. This has important implications for variation in traits expressed later in the life of these fish, as early size (i.e., maternal effect) is not expected to have a growth-related effect that would extend far into later life (indeed, Hakataramea adults tend to be larger at maturity than Glenariffe adults in the wild; Kinnison et al. 1998*a*).

Under natural conditions, peak spawning occurs at nearly the same time of year (late April) in both study populations. However, on the basis of stream-temperature data collected from 1994 to 1996, fry emergence in Glenariffe stream may occur 4–6 weeks later than in the Hakataramea River (Kinnison et al. 1998*b*). Growth rate responds very quickly to selection (Gjedrem 1983), whereas embryonic development rates are more often conserved among populations within species (Murray and McPhail 1988; Kinnison et al. 1998*b*), despite some evidence of interpopulation differences (Tallman 1986; Konecki et al. 1995). The faster growth of Glenariffe fry may therefore represent a compensatory adaptation to the smaller mean egg size, and to later emergence resulting from lower water temperatures. However, it would be difficult to determine whether selection is acting directly on growth rate or indirectly through selection on genetically correlated traits, and random genetic effects cannot be excluded.

Most fry showed clear external signs of smolting at 4 months, including silvering of the skin and disappearance of parr marks (Folmar and Dickhoff 1980), and all appeared to be fully smolted at 6 and 10 months. Hypersalinity tolerance did not differ between populations at any age tested, indicating an absence of seasonal as well as absolute differences. The ability to tolerate and adapt to seawater appears to be conserved within salmon species. For example, salinity tolerance is retained even among landlocked populations such as kokanee (*O. nerka*) in North America (Foote et al. 1992) and transplanted freshwater resident sockeye in New Zealand (Franklin et al. 1992). Our use of artificially high salinity levels, and the large size of our experimental fish relative to wild fish of comparable age, limit direct conclusions about seasonal seawater survival in the respective wild populations. Also, our testing frequency (one test each in spring, summer, and fall) may not have been sensitive to differences in the ontogeny of changes in salinity tolerance before or after our test dates.

The braided Rakaia and Waitaki main stems are relatively comparable to each other, compared with the range of chinook habitats encountered in North America, with respect to

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length, gradient, channel morphology, and the lack of a significant estuary. However, scale-pattern analysis (Unwin and Lucas 1993) suggested that Waitaki chinook experience a shorter period of freshwater growth and are slightly smaller at seawater entry than Rakaia chinook (National Institute of Water and Atmospheric Research, unpublished data). This size difference, which is consistent with the growth-rate differences we observed, could result in some difference in seawater adaptability between the two study populations even in the absence of any direct genetic effects on salinity tolerance.

The existence of family effects at each challenge, even after adjustment for body size (in November and May) and rearing under common conditions, is consistent with the results of other investigations (e.g., Murray et al. 1993) and suggests a potential heritable influence on hypersalinity tolerance. However, the absence of significant sire effects and additive genetic variation for the 4-month challenge did not corroborate this, but the small number of families in this analysis (relative to some quantitative genetic programs) may have limited the power of our analysis (Klein et al. 1973; Gjedrem 1983). The tendency for families to fall into one of two distinct groupings, based on relative survival time at 4 and 10 months, is further evidence of family-level effects. The existence of these groups suggests that families may differ with respect to the timing of their optimum smolting "window" relative to other families, and that families with high salinity tolerance at 4 months do not necessarily retain (or redevelop) a similarly high rank at 10 months. Under more natural conditions this tendency may reflect family variation in juvenile life history. Such variation may contribute to the population differences in proportions of subyearling (ocean type) and yearling (stream type) migrants observed among New Zealand populations (Quinn and Unwin 1993).

We would not expect the genetic differences in juvenile growth rate and size observed in this study to account for the substantial differences in adult traits of wild chinook of Glenariffe stream and Hakataramea River origin (Kinnison et al. 1998*a*, 1998*b*), particularly given the observed degradation of size correlations over time. However, the extent to which these traits are interrelated in chinook salmon is unknown. New Zealand chinook salmon populations differ phenotypically in a number of traits, but comparisons of juvenile life history traits (Kinnison 1998*b*; this study) under common rearing conditions appear to be less pervasive than the range of differences found in comparisons of adult traits in the wild. Further work is therefore needed to assess the environmental and genetic components of the divergence in adult phenotypic traits that is apparent among these recently established populations, and to determine the extent of underlying associations among life-history traits.

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