

# Genetic control over survival in Pacific salmon (*Oncorhynchus* spp.): experimental evidence between and within populations of New Zealand chinook salmon (*O. tshawytscha*)

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**Abstract:** The ability to survive to adulthood and return to natal sites is a fundamental characteristic of anadromous salmonids, and low survival is likely to have prevented establishment of new populations within and outside their native range. We hypothesised that there is family-level genetic variation in traits contributing to survival and that populations evolve to maximise survival in response to prevailing local conditions. To test these predictions, we compared postrelease survival for chinook salmon families from two populations established in New Zealand in the 1900s. Both populations, Glenariffe Stream and Hakataramea River, had similar survival when released after translocation to a drainage familiar to neither population. However, Glenariffe families had higher survival than Hakataramea families when both populations were released from Glenariffe Stream, indicating a survival advantage for the local fish. In addition, there were significant correlations between survival rates for paternal half-sib families of Glenariffe fish and between survival rates for families released from the two locations. Family-specific survival was positively correlated with weight at release, but there were underlying genetic correlations unexplained by size. Taken together, these results suggest considerable genetic influence over survival and return of salmon and that population-specific adaptation can occur within 30 generations of establishment.

**Résumé :** La capacité de survivre jusqu'à l'âge adulte et de retourner aux sites de naissance est une caractéristique fondamentale des salmonidés anadromes; c'est probablement la faible survie qui empêche l'établissement de nouvelles populations à l'extérieur de leur répartition géographique naturelle. Nous posons en hypothèse qu'il y a une variation génétique au niveau de la famille dans les caractères qui contribuent à la survie et que les populations évoluent de manière à maximiser leur survie en fonction des conditions locales dominantes. Pour éprouver ces prédictions, nous avons comparé la survie après la libération de familles de saumons quinnat de deux populations établies en Nouvelle-Zélande dans les années 1900. Les deux populations, celle du ruisseau Glenariffe et celle de la rivière Hakataramea, avaient des taux semblables de survie lorsqu'elles furent transportées et relâchées dans un bassin hydrographique inconnu des deux populations. Cependant, les familles de Glenariffe avaient une meilleure survie que les familles de Hakataramea lorsque les deux populations ont été relâchées depuis le ruisseau Glenariffe, ce qui indique un avantage de survie pour les poissons locaux. De plus, il y avait des corrélations significatives entre les taux de survie des familles de demi-frères et demi-soeurs paternels des poissons de Glenariffe et entre les taux de survie des familles libérées des deux sites. La survie spécifique à la famille est en corrélation positive avec la masse à la libération, mais il y a des corrélations génétiques sous-jacentes qui ne s'expliquent pas par la taille. Dans leur ensemble, nos résultats laissent croire qu'il y a une influence génétique considérable sur la survie et le retour des saumons et que des adaptations spécifiques aux populations peuvent se développer en moins de 30 générations après leur établissement.

[Traduit par la Rédaction]

## Introduction

One fundamental component of evolution is the differential probability of survival to reproductive age among individuals with different phenotypic traits. Such variation is

observed not only within populations but also between populations, as different regimes of selection are associated with trait values. In fishes, for example, vulnerability to predation has been linked to patterns of morphology (Reimchen 1994), life history (Endler 1995), and behaviour (Magurran et al.

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1992). Salmonid fishes provide good opportunities to study natural selection because their life histories consist of distinct phases with associated agents of selective mortality. For example, fertilised eggs deposited in the gravel may suffer from poor water circulation associated with fine sediment (Chapman 1988) or gravel scour during floods (Thorne and Ames 1987), and juveniles in fresh water are lost to predation (e.g., Ruggerone and Rogers 1992). Salmonids appear to have adapted to these mortality agents by evolving a wide variety of population-specific traits, including egg size (Quinn et al. 1995), migratory behaviour (Brannon 1972), and morphology and aggression (Swain and Holtby 1989).

In addition to the agents of mortality in fresh water, anadromous salmonids face complex and poorly understood agents of mortality at sea. Within species, populations with larger migrants ("smolts") tend to experience higher survival rates than populations with smaller smolts (Koenings et al. 1993), though there is considerable variation in this regard. Within populations, survivors in a given year tend to be the larger smolts in a wide variety of salmonid species (e.g., chum salmon (*Oncorhynchus keta*), Healey 1982; coho salmon (*Oncorhynchus kisutch*), Holtby et al. 1990).

As well as the effects of body size, two lines of evidence suggest survival to adulthood is influenced by genetic factors. First, some families have higher rates of survival than other families of the same population (e.g., coho salmon (*O. kisutch*), McIntyre et al. 1988; pink salmon (*Oncorhynchus gorbuscha*), Geiger et al. 1997). Second, transplanted populations often have lower rates of survival or contribution to fisheries than local populations (e.g., Reisenbichler 1988). Survival reflects a suite of traits including size, foraging ability, feed conversion, and predator avoidance, so the genetic factors affecting it are likely to be complex. The importance of survival in determining how many progeny from any given mating contribute to future generations suggests that it should be heritable and thus amenable to natural selection. However, the patterns of selection may be complex, as biotic and abiotic factors causing differential survival may vary from year to year (e.g., Geiger et al. 1997).

Salmon populations were established in their native range by postglacial colonisation, followed by the evolution of population-specific traits that facilitated survival in that environment. The question is, how rapidly can a trait as complex as survival evolve? The successful translocation of chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento River, California, to the South Island of New Zealand (McDowall 1990) presented a unique opportunity to study the evolution and genetic control of survival to adulthood for several reasons. First, this represents the most long-standing and best understood case in which self-sustaining, anadromous populations of Pacific salmon have been established outside their native range. Second, the populations were established from a common source between 1901 and 1907 (Quinn et al. 2001) and have since diverged in a variety of phenotypic traits (Quinn and Unwin 1993; Unwin et al. 2000; Quinn et al. 2001). Third, there is no directed fishing for chinook salmon at sea, so returning adults represent virtually all fish surviving natural mortality. This permits a much more accurate estimate of survival than would be possible in North America, where both immature and maturing chinook are taken in the commercial fishery. Fourth, New

Zealand chinook salmon populations are largely confined to the central east coast of the South Island, with their marine distribution apparently restricted to inshore waters along an 800-km coastline (Unwin and James 1998), so all populations inhabit rather more similar marine environments than their North American counterparts.

This study was designed to test the hypotheses that (i) New Zealand chinook salmon populations have diverged in traits that control survival, becoming adapted to their natal environment within a century of colonisation, and (ii) survival rates differ between families. We conducted experimental releases of tagged juvenile salmon from two populations, Glenariffe Stream and the Hakataramea River (Fig. 1), and two release locations (Glenariffe and Silverstream). Our null hypothesis was that survival (as measured by the rate of tag recovery for all returning adults) did not differ between populations or release locations. The predicted alternative, assuming adaptation to local conditions, was that Glenariffe fish would have higher survival rates when released from their home river. Environmental influences on survival could not be controlled, but releasing representatives of both populations at two locations and in two years allowed us to assess the extent to which survival rates depended on these two fixed factors. We then used return data for marked half-sib families to test the null hypothesis that survival would not vary among families. The predicted alternative was that some combination of smolt size and other family-specific attributes affected survival.

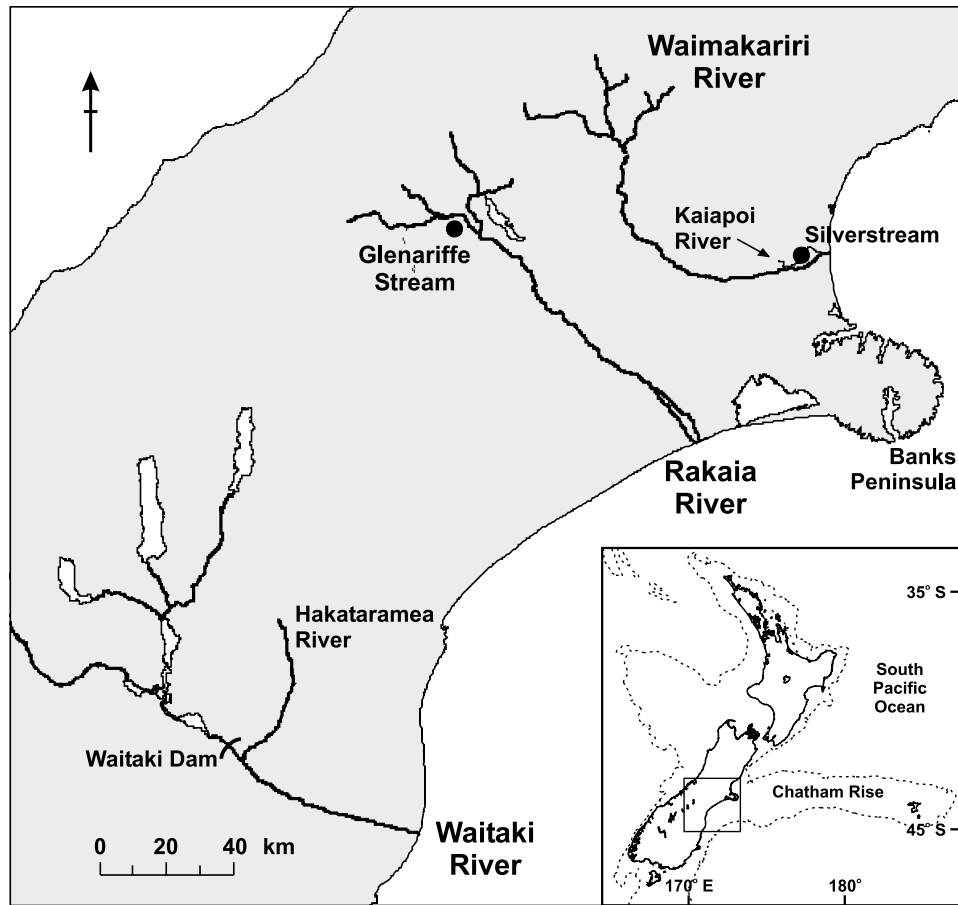
## Materials and methods

### Study populations and facilities

Glenariffe Stream is a stable, spring-fed stream joining the Rakaia River 100 km above the mouth at an altitude of 430 m (Fig. 1) and supports a mean annual spawning population of 1920 chinook (Unwin 1997). Spawning occurs from March to June (austral autumn), peaking in late April (Quinn and Unwin 1993). Wild juveniles leave the stream shortly after emergence from the redds (Unwin 1986) and rear in the mainstem Rakaia River for a few months or up to a year (Hopkins and Unwin 1987), entering the ocean in their first or second year of life (so-called ocean-type and stream-type chinook salmon, respectively). The Hakataramea River is a 60 km long rain-fed river joining the Waitaki River 60 km above the mouth at ~200 m elevation, 4 km below a dam blocking further upstream access to the Waitaki River (Fig. 1). As in Glenariffe Stream, Hakataramea River chinook salmon show a mixture of ocean- and stream-type juvenile life histories (Quinn and Unwin 1993).

Since 1980, naturally spawning stocks in Glenariffe Stream have been augmented by releases from a hatchery 200 m above the confluence with the Rakaia River (Unwin and Glova 1997). Yearling smolts released from this hatchery enter the upper Rakaia River and reach the South Pacific Ocean after a downstream migration thought to take only a few days (Unwin and Lucas 1993). The practice of releasing fall chinook as yearlings is unusual within their native range but became the norm in New Zealand following the widespread failure of earlier releases to achieve worthwhile returns (Unwin 1997). Hatchery yearlings are larger than their wild counterparts (Unwin and Lucas 1993) and tend to pro-

**Fig. 1.** The central South Island of New Zealand showing the source populations and release locations used in this study. The inset map shows the 1000-m isobath and the Chatham Rise to the east of the South Island.



duce higher returns of 2-year-old males (Unwin and Glova 1997) but appear similar to wild stocks in terms of annual variations in marine survival (Unwin 1997).

Experimental families from the Glenariffe (GA) and Hakataramea (Haka) populations were propagated in the Glenariffe Stream hatchery, which represented “home territory” for the GA fish. Representatives from these families were also reared in another hatchery on a third river system, the Silverstream Hatchery on the Kaiapoi River, a lowland tributary of the Waimakariri River, 13 km from the sea at an altitude of 17 m (Fig. 1). The Waimakariri River and its headwater tributaries support large chinook salmon populations, but the Kaiapoi River provides little natural spawning or juvenile rearing habitat and is populated only by fish of hatchery origin.

#### **Establishment, culture, and release of experimental families**

In 1994 we established 72 experimental families by spawning salmon from the two study populations on consecutive days (22 and 23 April for GA and Haka, respectively). We collected gametes from all available fish at each location but subsequently used scale pattern analysis (Unwin and Lucas 1993) to select parents that were almost exclusively age-3 ocean-type fish, and of natural rather than hatchery origin, to minimise variation among families in factors other than population of origin. We used milt from each male to fertilise ova from two randomly selected females in a half-sib mating

design, creating 32 full-sib families nested within 16 half-sib families for the Haka population, and 40 full-sib families nested within 20 half-sib families for the GA population. All ova (~5000 per female) were taken from GA fish, but only 2000 ova were taken from each Haka female.

All families were individually incubated and reared at Silverstream Hatchery, using ambient (mean 12.1°C) ground water. As incubation progressed we reduced the number of families to 60, comprising 30 full-sib families within 15 half-sib families per population, primarily by culling both families from half-sib pairs for which one or both parents were of hatchery origin, or which were affected by unusually poor fertilisation or survival rates (see Kinnison et al. (1998a) and Quinn et al. (2000) for further details on the breeding and rearing protocols).

After hatching and completion of yolk absorption in early August, 700 fry from each family were set aside for further experiments, and the rest were transferred to circular tanks, each with a capacity of 3000 L. Each GA family (~4000 fry) was held in a single tank but Haka fry (~1000 per family) were pooled and divided evenly between two tanks (a necessary consequence of the limited number of tanks available). All fry were fed to satiation with a standard dry diet. In October 1994 (austral spring), 6 months after fertilisation, these fry were marked with sequential coded-wire tags (CWTs) to either population level (Haka) or family level (GA). Fry were also marked externally by excision of the adipose fin to

indicate the presence of the internal tag. The tagged fry were trucked to the Glenariffe Hatchery and pooled into a single large raceway for common rearing. On 19 July 1995 (after 9 months of additional rearing), they were released into the upper Rakaia River from Glenariffe Hatchery. A subsample of 600 fish (nominally 20 per family) was sacrificed one day before release for measurement of fork length and weight and recovery of CWTs, allowing mean weight at release to be determined for each GA family and for the Haka population. Final release numbers were 117 824 GA fish (averaging 3927 per family at an average weight of 59 g) and 23 655 Haka fish at an average weight of 60 g. We refer to these fish as the 1994 Glenariffe release (where 1994 refers to the brood year rather than the year of release).

We established a second release group, representing 58 of the original 60 families, by accumulating surplus fish from the 700 set aside from each family in August 1994 (see Kinnison et al. (1998b) for further details). Fish from both populations were coded-wire tagged to family level after excision of the adipose fin, pooled in an external raceway, and released from Silverstream on 31 July 1995 (13 709 fish, averaging 232 (range 90–366) per family). These fish were the “1994 Silverstream release”. Mean weight at release was 94 g for both populations but was not measured to family level because this would have required destructively sampling (for tag recovery) too many of the fish available for release. As a surrogate, we used mean weight (based on 50 fish per family) recorded on 14 May, 10 weeks before their release, in all calculations involving family-level comparisons of survival in relation to weight at release.

To protect against the possibility of a weak return from the 1994 brood year and to provide some degree of replication, we repeated the spawning programme in autumn 1995. We used a full-sib mating design to create 12 Haka and 13 GA families, following the same protocols for collecting gametes, incubating embryos, initial rearing at Silverstream, marking and tagging, and additional rearing at Glenariffe as for the 1994 brood year Glenariffe release group. On 29 July 1996, these fish were divided into two groups. The larger group (68 747 fish, averaging 2742 per family) remained at Glenariffe Hatchery, and the smaller group (15 753 fish, averaging 630 per family) was transferred back to Silverstream Hatchery. These two groups (the 1995 Glenariffe release and the 1995 Silverstream release) were released on 20 and 16 August 1996, respectively. We estimated the number of fish from each family released at each location by dividing the number of fish originally tagged in proportion to the total number of fish in each release group. Mean release weights at both locations, based on a sample of 500 fish sacrificed for tag recovery when the fish were divided into two groups, were 101 g (Haka) and 114 g (GA).

### Tag recovery

Adult chinook from the Glenariffe and Silverstream release groups returned to fresh water at maturity in autumn 1996 to 1999, representing 2-, 3-, and 4-year-old fish from both the 1994 and 1995 broods. These fish were intercepted at the Glenariffe Stream and Silverstream counting fences and were also taken in the sports fishery as they ascended the Rakaia, Waimakariri, and other east coast rivers. The

angler catch rate for both the Rakaia and Waimakariri rivers is typically 30–40% and varies little among years (Ross Millichamp, North Canterbury Fish and Game Council, Christchurch, New Zealand, personal communication), although tag recoveries from the sports fishery are typically underreported by about 50% (M.J. Unwin, unpublished data). We did not adjust the data to allow for unreported tags, so our survival estimates are conservative. However, they would be biased with respect to population of origin only if the probability of angler capture varied between populations. For the purposes of this study, we ignored this possibility. Tagged salmon taken incidentally at sea as a bycatch in commercial fisheries for other species accounted for 1.5% of the recoveries and were included in our survival estimates.

Heads from all salmon with a missing adipose fin were sent to the laboratory for tag recovery and identification. Because the 1995 Glenariffe and Silverstream release groups were established after the fish had been tagged, tag data did not uniquely establish the release location for each fish. We resolved this ambiguity by assuming (i) that all fish returning to either Glenariffe Stream or the Kaiapoi River were homing to their release site and (ii) that fish taken by anglers in all rivers except the lower Waimakariri River were of Glenariffe origin. This second assumption is consistent with very low straying rates for previous Silverstream releases (50 strays from 2916 returns (1.7%) over 20 years) compared with the higher straying rates (12%) of chinook released from Glenariffe Stream and also with the tendency for strays of GA origin to enter rivers to the north of the Rakaia (Unwin and Quinn 1993). Fish taken by anglers in the lower Waimakariri River below the Kaiapoi confluence (2% of the total recoveries) could have originated from either release site and were not used for calculating site-specific survival rates.

### Data analysis

For pairwise comparisons between populations, release sites, and brood years, we calculated survival at population level (all families combined) as the ratio of tags recovered ( $n$ ) to tags released ( $N$ ), with confidence intervals based on the binomial distribution (Schnute 1992). Significance tests for comparisons between release groups were based on the  $z$  statistic. We also performed these comparisons using family-level survival data to provide a natural measure of within-population variability via the analysis of variance (ANOVA) model

$$(1) \quad S_{ijkm} = \mu + O_j + Y_k + L_m + \text{interaction terms} + \epsilon_{ijkm}$$

where  $O$ ,  $Y$ , and  $L$  denote population of origin, year of release, and release location;  $S_{ijkm}$  denotes survival for family  $i$ ; and  $\mu$  and  $\epsilon$  represent mean and error terms, respectively. Family-specific survival rates were positively skewed, so we used a square-root transformation to improve normality, choosing this in preference to the more usual log-transformation (cf. Unwin 1997) because some families had zero survival at one or both release locations. Family-level survival estimates were not available for Haka fish in the 1994 Glenariffe release but the fish were released in two groups with separate tags, so we used survival data for those groups, which were

reared in separate ponds before being tagged and thus represented independent replicates (cf. Schnute 1992), as surrogates. This model was used to combine both brood years and release locations in the same analysis.

Mean weight at release did not vary greatly between populations but differed between release locations and brood years. The lack of family-specific weight data on the day of release for some groups precluded an adjustment based on analysis of covariance, so we used the relationship between survival and mean release weight ( $W$ ) for chinook salmon released from Glenariffe Hatchery between 1978 and 1990 (Unwin 1997) to adjust for differences in survival associated with variation in size. This result ( $\log S \propto 1.34 \times \log W$ ) suggests a 2.5-fold increase in survival for each 2-fold increase in weight. We used this relationship to standardise population level survival rates to a common release weight, facilitating comparisons between release locations and brood years.

To characterise genetic influences on survival for the 1994 brood, we formulated our analysis in terms of probability of survival for the progeny of each family. We represented the  $N$  tagged fish in each family as a series of independent binomial trials, with the  $n$  tagged fish recovered as adults having a survival of 1 and the remaining  $N - n$  having a survival of 0, via the model

$$(2) \quad S_{ijk} = \mu + \text{sire}_i + \text{dam}_{j(i)} + \varepsilon_{ijk}$$

where sire and dam are treated as random effects. This formulation of the data implicitly allows for variation in the number of fish originally marked within each family. We estimated this model for the Glenariffe release (30 dams within 15 sires, all of Glenariffe origin) and the Silverstream release (58 dams within 29 sires), both with and without mean release weight ( $W$ ) for each family as a covariate, to identify the extent to which genetic effects were associated with family-specific variation in release weight. We used restricted maximum likelihood (REML) procedures, as implemented in Genstat 5 (release 4.1; Genstat 5 Committee 1998), to estimate model 2 (eq. 2) with stepwise inclusion of sire, dam, and sire + dam effects, interpreting the incremental reduction in deviance ( $-2 \times \log$ -likelihood) as a  $\chi^2$  statistic with 1 df to evaluate the significance of each additional parameter. These analyses also estimated sire and dam variance components (and their associated sampling errors) for estimation of narrow-sense sire heritability ( $h^2$ ) on the observed scale (Becker 1984; Lynch and Walsh 1998). Because heritabilities for characters represented by binomial data tend to be severely underestimated when frequencies (i.e., survival rates) differ significantly from 50%, we also converted these values into estimates of heritability on the underlying "liability scale" (Lynch and Walsh (1998), equation 25.8b). Standard errors for these estimates were based on the corresponding errors for the variance components.

We used a similar model to estimate family-level effects for the 1995 brood, with the addition of release location and population of origin, so as to allow for any effects related to population of origin (which was excluded from the 1994 analysis because family-specific data were not available at both release locations). However, with only full-sib families we were unable to differentiate between sire and dam effects. The model used was

$$(3) \quad S_{ijkm} = \mu + O_i + \text{family}_{j(i)} + W_j \\ + L_k + O_i \cdot L_k + \varepsilon_{ijkm}$$

using the same notation as model 1 (eq. 1) with the addition of family mean weight ( $W$ ) as a covariate. We estimated this model for both release locations (Glenariffe and Silverstream) combined and also for each location separately after deleting all terms in  $L$ , using Wald tests (which approximate a  $\chi^2$  test, Genstat 5 Committee 1998) to determine the significance of fixed effects associated with population of origin and release location.

## Results

### Tag recoveries

A total of 1015 tags from 1994 and 1995 brood year chinook were recovered, of which 992 (97.7%) could be positively identified with respect to release location. Mean survival rates were 0.47 and 0.34% for the two brood years, respectively. Over 80% of the fish were recovered at the Glenariffe and Silverstream hatcheries; anglers took most of the rest. On the assumption that about half of the tagged chinook caught by anglers were reported, our data underestimated survival by between 0.05 and 0.1%. The number of tags recovered per family varied from an average of 15 (range 2 to 32) for the 1994 Glenariffe releases to 5 (range 0 to 14) for releases from Silverstream. Estimates of family-specific survival are therefore subject to considerable uncertainty, particularly for the 1994 Silverstream releases where (on average) each additional recovered tag represented an incremental change in survival of 0.4%.

As a check against the possibility that our population-specific estimates of survival might have been confounded by differential straying rates, we used tag returns for the 1994 Glenariffe release to compare straying rates for fish of GA and Haka origin. We detected no significant difference ( $\chi^2 = 0.59$ ,  $p > 0.25$ ), with straying rates of 11.9% (47 out of 395 recoveries), and 8.4% (4 out of 48 recoveries) for GA and Haka fish, respectively. Straying rates for the 1994 Silverstream release were too low to permit a statistically meaningful comparison (GA: 1 out of 130 recoveries; Haka: 2 out of 146 recoveries) but also suggested no marked difference between the two populations. We therefore assumed that any interpopulation differences in straying rates were too small to significantly bias our survival estimates.

### Survival as a function of population and release location

Our initial analysis, including all salmon with tags indicating population of origin, showed that GA salmon had a significantly higher survival rate than Haka fish when released from Glenariffe but that survival rates for the two populations were similar when released from Silverstream (Table 1). Released from Glenariffe, the survival rate for GA fish was 1.7 times higher than for Haka fish in 1994 and 2.9 times higher in 1995. For the two brood years combined, mean survival rates were 0.33% for GA and 0.15% for Haka salmon. Released from Silverstream, Haka fish had a higher survival rate in 1994 and a lower survival rate in 1995 but in neither year was the difference between the two study populations significant (Table 1;  $p > 0.1$  in both cases). Mean sur-

**Table 1.** Estimated survival rates  $\pm 1$  standard error for 1994 and 1995 brood year chinook salmon of Glenariffe and Hakataramea origin released from the Glenariffe and Silverstream hatcheries, based on coded-wire tag recoveries.

Release location	Brood year	Population of origin	Mean weight (g)	Total released	Total returns	Survival, %	<i>p</i>
Glenariffe	1994	Glenariffe	59.1	117 824 (30)	402	0.34 $\pm$ 0.02	<0.001
		Hakataramea	60.2	23 655 (2)	48	0.20 $\pm$ 0.03	
	1995	Glenariffe	113.9	29 113 (13)	92	0.32 $\pm$ 0.03	<0.001
		Hakataramea	101.1	39 634 (12)	42	0.11 $\pm$ 0.02	
Silverstream	1994	Glenariffe	94.2	6 892 (29)	130	1.89 $\pm$ 0.16	0.19
		Hakataramea		6 617 (29)	147	2.22 $\pm$ 0.18	
	1995	Glenariffe	113.9	6 671 (13)	65	0.97 $\pm$ 0.12	0.10
		Hakataramea	101.1	9 082 (12)	66	0.73 $\pm$ 0.09	

**Note:** Numbers in parentheses, after the release totals, indicate the numbers of families or groups of families (1994 Hakataramea population) given discrete tags.

vival for the two brood years combined was 1.43% for GA and 1.47% for Haka fish.

More detailed analysis of the population-level difference, using model 1 with family-specific data, showed no significant two- or three-factor interactions ( $p > 0.17$  in all cases) but significant effects associated with release location ( $p << 0.001$ ) and brood year ( $p = 0.02$ ). When analysed separately for each release location, there was no significant interaction between brood year and population of origin at either location ( $p > 0.25$ ), indicating that population-level variation was consistent across brood years. For releases from Glenariffe, survival differed between populations ( $p = 0.01$ ) but not between brood years ( $p = 0.23$ ), whereas for releases from Silverstream, there was a strong brood year effect ( $p = 0.004$ ) but no population effect ( $p = 0.96$ ). Mean survival rates (transformed cell means  $\pm 1$  standard error (SE)) were  $0.29 \pm 0.03\%$  for GA vs.  $0.13 \pm 0.04\%$  for Haka families released from Glenariffe and  $1.18 \pm 0.19\%$  for GA vs.  $1.19 \pm 0.20\%$  for Haka families released from Silverstream. These results are consistent with those in Table 1, any differences being attributable to the effect of variation in the number of fish tagged within each family or release group (which influences the totals for  $N$  and  $n$  and the  $z$  statistics used to derive Table 1 but not the percentage survival figures used in the ANOVA).

The differences between the two study populations were not accounted for by differences in mean weight at release. For the 1994 releases, mean weights differed by little more than 1 g at either release location and at Glenariffe Stream should have favoured Haka fish (which were 1.1 g heavier). The more substantial differences in weight in 1995 were still insufficient to account for the observed differences in survival for releases from Glenariffe. When adjusted to a common release weight of 107 g (the mean for both populations), estimated survival rates for GA and Haka salmon were 0.31 and 0.12%, respectively, from Glenariffe Stream and 0.97 and 0.74%, respectively, from Silverstream.

Survival rates of chinook released from Silverstream were roughly 4-fold higher than for those released from Glenariffe Stream. Mean survival rates ( $\pm 1$  SE) for the two release locations were 1.63% (1.49, 1.78) and 0.26% (0.12, 0.44), respectively, for the 1994 brood, and 0.81% (0.667, 0.97) and 0.17% (0.11, 0.25) for the 1995 brood. Adjusted to common release weights (60 g in 1994 and 107 g in 1995), survival rates for families released from Silverstream were approxi-

mately 6-fold higher than for releases from Glenariffe Stream in 1994 and 4-fold higher in 1995.

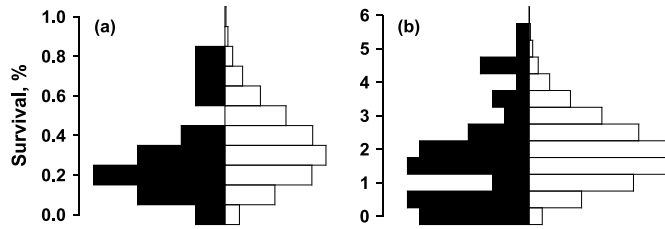
#### Family-level variation in survival

Survival varied considerably among families. For the 1994 brood, survival ranged from 0.04 to 0.89% for releases from Glenariffe Stream and from 0.0 to 5.8% for releases from Silverstream. Corresponding figures for the 1995 brood were 0.0 to 0.58% (Glenariffe releases) and 0.15 to 2.02% (Silverstream releases). As noted earlier, survival rates were positively skewed but tended to be more leptokurtic (with a higher proportion of extreme values) than would be expected had they been distributed randomly, in accordance with the Poisson (or gamma) distribution (Fig. 2). Within each brood year, family-specific survival rates were correlated between the two release locations (1994,  $r^2 = 0.19$ ,  $p = 0.02$ ; 1995,  $r^2 = 0.22$ ,  $p = 0.02$ ; Fig. 3). Family-specific survival was correlated with weight at release for the 1995 releases (Glenariffe,  $r^2 = 0.36$ ,  $N = 25$ ,  $p = 0.001$ ; Silverstream,  $r^2 = 0.20$ ,  $N = 25$ ,  $p = 0.03$ ) but not for the 1994 releases from either site (Glenariffe,  $r^2 = 0.09$ ,  $N = 30$ ,  $p = 0.1$ ; Silverstream,  $r^2 = 0.04$ ,  $N = 58$ ,  $p = 0.15$ ; Fig. 4).

Sire or dam effects on survival were apparent for all 1994 brood release groups, but the nature of these effects varied strikingly between release locations (Table 2). For releases from Glenariffe Stream, sire effects were highly significant ( $\chi^2 \geq 68.8$ ,  $df = 1$ ,  $p << 0.001$ ), whereas dam effects were not detectable ( $p \geq 0.11$ ; Fig. 5a). By contrast, dam effects were significant at Silverstream ( $\chi^2 \geq 33.2$ ,  $df = 1$ ,  $p << 0.001$ ), whereas no sire effect was detected ( $p \geq 0.79$ ; Fig. 5b). These results were unchanged when mean family weight at release was included as a covariate, confirming that the observed effects were independent of any family-specific variation in weight. In accordance with the observed sire effects, sire heritability was small ( $h^2 \approx 0.004$  on the observed scale,  $h^2 \approx 0.12$  on liability scale) but significantly greater than zero for the 1994 Glenariffe releases but did not differ significantly from zero for the Silverstream releases. As with the significance tests listed in Table 2, these heritability estimates were essentially unaffected when the model was adjusted to allow for interfamily variation in release weight.

For the 1995 brood year, the results of model 3 for both release sites combined also showed significant interfamily variation (Table 2) and a strong effect associated with release location ( $p << 0.001$ ). When analysed separately for

**Fig. 2.** Observed distribution of family-specific survival rates (%) for chinook salmon (*Oncorhynchus tshawytscha*) released from (a) Glenariffe Stream ( $N = 32$ ) and (b) Silverstream ( $N = 58$ ) in 1994, together with the expected frequencies for a Poisson distribution with the same mean survival. Observed, solid bars; expected, open bars.



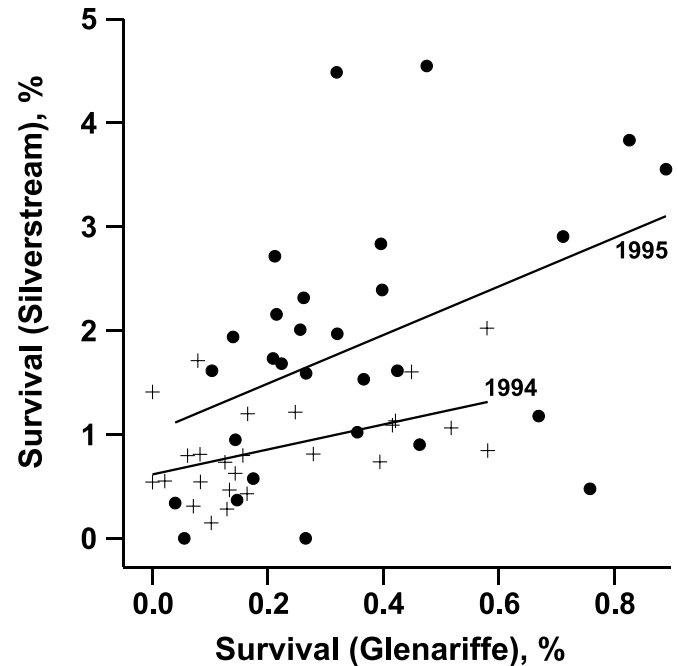
each release location, interfamily effects were apparent for the Glenariffe Stream releases but not for the Silverstream releases (Table 2). Likewise, population of origin effects were marginally significant at Glenariffe ( $p \approx 0.05$ ) but not at Silverstream ( $p \approx 0.99$ ).

## Discussion

Our results provided strong experimental evidence that variation in survival of chinook salmon was associated with genetic variation at both family and population level. First, in two consecutive release years, GA salmon had higher survival than Haka fish only when released from their native stream. This supports the hypothesis that GA fish have adapted in ways that increase their survival in Glenariffe Stream, the Rakaia River, and the local marine environment relative to salmon from another river. Although the differences in survival between GA and Haka fish were small in absolute terms (a few parts in  $10^{-3}$ ), they represented a 1.5- to 3-fold difference in survival rate and hence in the mean number of recruits per spawner. Second, the presence of a strong sire effect on survival rates for half-sib families released from Glenariffe Stream, beyond any effects associated with weight at release, and an equally marked dam effect for releases from Silverstream supported the hypothesis that survival is controlled by family-specific traits as well as by size. The correlation of family-specific survival rates also indicated underlying genetic control, despite the environmental effect revealed by the higher survival of fish released from Silverstream.

This study was part of a large research programme on New Zealand chinook salmon with the primary goal of determining whether they have evolved into genetically distinct populations since their establishment in the early 1900s (Quinn and Unwin 1993; Quinn et al. 2001). The apparent “home-court” advantage of GA over Haka fish at Glenariffe Stream but their similar performance on “neutral territory” suggests that some degree of interpopulation genetic differentiation has occurred in less than 100 years (~30 generations). We also have evidence of genetically controlled differences in juvenile growth rate (Kinnison et al. 1998a; Unwin et al. 2000), the timing of adult return migration and spawning (Quinn et al. 2000), and reproductive allocation in females (Kinnison et al. 2001). Logistic considerations prevented us from performing a more complete experimental test of our primary hypothesis by releasing tagged fish from both study

**Fig. 3.** Family-specific survival rates (%) for 53 families of chinook salmon (*Oncorhynchus tshawytscha*) released from Glenariffe Stream and Silverstream in 1994 (+) and 1995 (●).

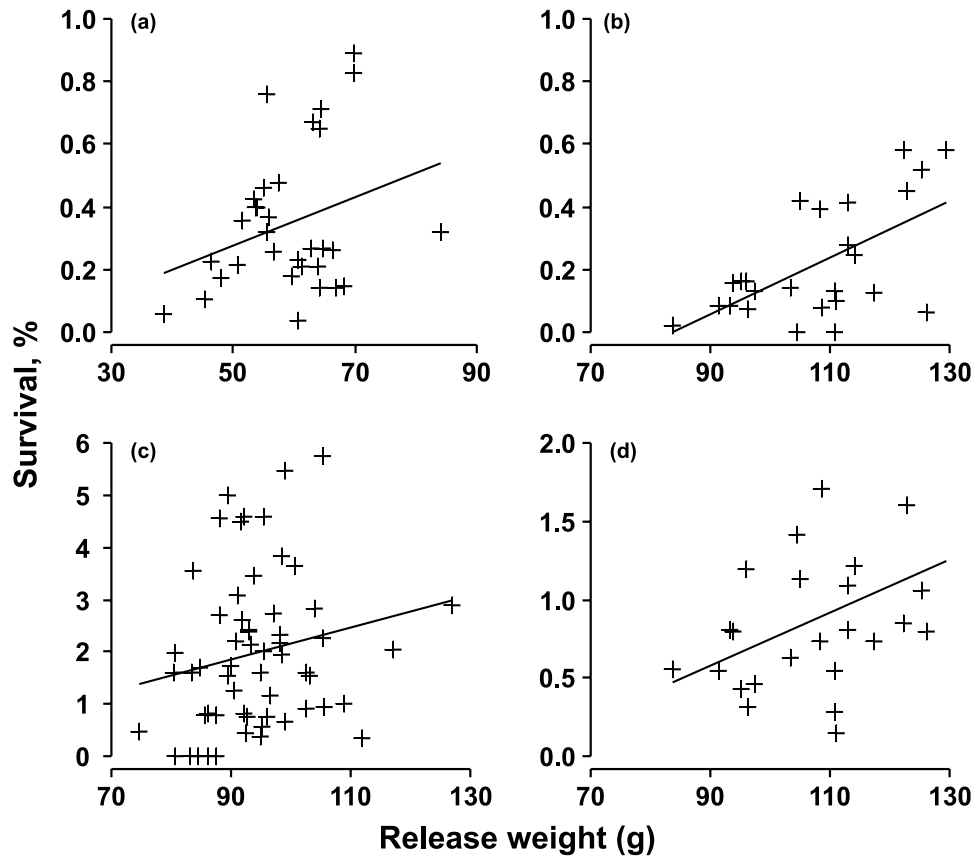


populations into the Hakataramea River, but our results invite the prediction that Haka fish would have outperformed those of GA at that location.

There is no way of knowing what properties or traits the GA-origin fish possessed that conferred the higher survival rate (relative to Haka River fish) when released from the upper Rakaia River but were nullified when released from Silverstream, in the lower reaches of the Waimakariri River. Size affected survival at the family level but did not explain the population effects. Factors influencing marine survival and mortality of salmon are poorly understood, especially in a non-native environment such as the South Pacific Ocean, but behaviour may have played a role. There is considerable evidence for genetic control over behaviour in fishes (Trexler 1990) and in salmonids in particular, including such traits that might influence survival as aggression (Rosenau and McPhail 1987; Swain and Holtby 1989), schooling (Swain and Holtby 1989), and predator avoidance (Johnsson and Abrahams 1991).

The conclusion that survival was influenced by genetic factors was supported by the tendency for survival rates for individual families to be correlated at both release sites and for offspring sired by the same males to have similar survival rates. Family-specific survival rates were positively correlated with mean weight at release. This is consistent with other studies showing that larger individuals in a given cohort are more likely to survive than smaller ones (e.g., Healey 1982; Holtby et al. 1990; Henderson and Cass 1991), though the earlier studies did not have family-specific data. The relationship between weight (a trait under genetic influence) and survival in itself thus represents an indirect but clear genetic influence on survival. However, analysis of sire and dam effects indicated that weight at release was insufficient to account for the observed differences in survival among families.

**Fig. 4.** Family-specific survival (%) vs. mean weight at release (g) for chinook salmon (*Oncorhynchus tshawytscha*) released as yearlings from Glenariffe Stream in 1994 (a) and 1995 (b) and Silverstream in 1994 (c) and 1995 (d).



**Table 2.** Significance of sire, dam, or family effects on marine survival of 1994 and 1995 brood year chinook salmon released from Glenariffe and Silverstream, based on restricted maximum likelihood analysis of linear mixed models (performed separately for each brood year), together with sire heritability estimates for the 1994 brood ( $h^2 \pm 1$  standard error) on both the observed and liability scales.

Brood year	Release location	Sample size $N$ , sires (dams)	Effect	Weight as covariate	$p$	$h^2$	
						Observed scale	Liability scale
1994	Glenariffe	117 824, 30 (15)	Sire	No	<0.001	0.004±0.002	0.12±0.06
			Sire	Yes	<0.001	0.004±0.002	0.12±0.06
			Dam	No	0.11		
			Dam	Yes	0.21		
1994	Silverstream	13 509, 58 (29)	Sire	No	0.79	0.008±0.013	0.07±0.10
			Sire	Yes	0.92	0.002±0.010	0.02±0.08
			Dam	No	<0.001		
			Dam	Yes	<0.001		
1995	Combined	84 500, 25 (25)	Family	Yes	0.002		
	Glenariffe	68 747, 25 (25)	Family	Yes	0.003		
	Silverstream	15 753, 25 (25)	Family	Yes	0.70		

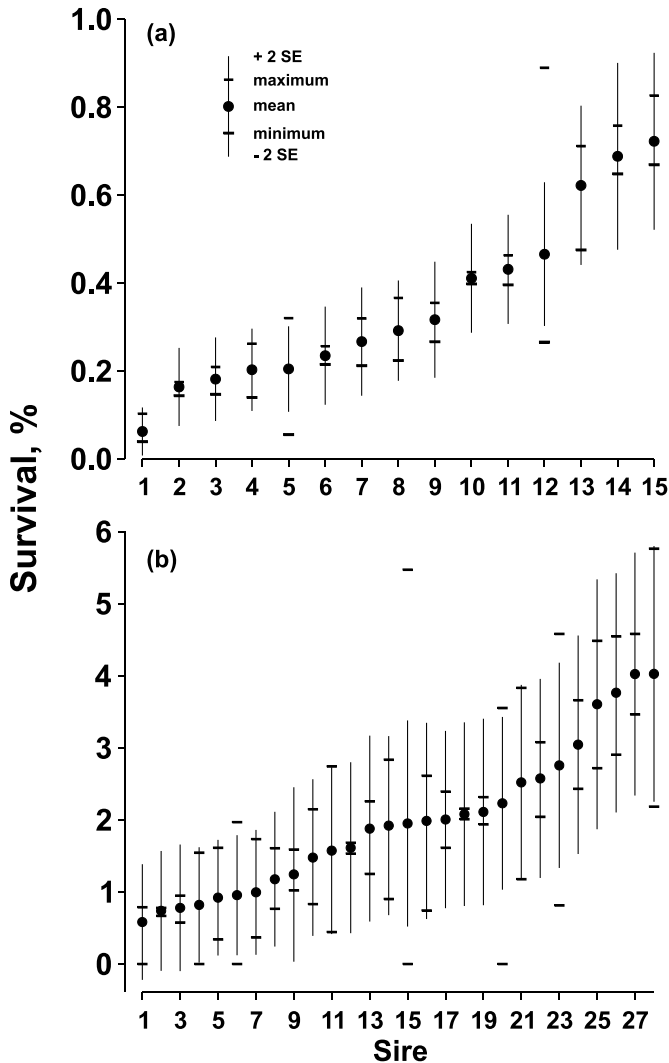
**Note:** Models that included weight at release as a covariate are indicated.

Salinity tolerance is correlated with size in salmon smolts, and this might contribute to the variation in survival among families. We compared survival rates for the 1994 brood year fish from this experiment with the results of salinity-tolerance experiments (described in detail in Kinnison et al. 1998a) conducted on the same families on two occasions, November 1994 and May 1995. Salinity tolerance was correlated with body size (Kinnison et al. 1998a) but survival showed little consistent relationship to salinity tolerance at

either challenge date. For families released from Glenariffe, survival was weakly correlated with salinity tolerance when measured in November 1994 ( $r = 0.37$ ,  $p = 0.055$ ) but not when measured in May 1995 ( $r = 0.17$ ,  $p = 0.54$ ). For the Silverstream releases, survival was uncorrelated with salinity tolerance at either experimental period.

Although genetic control over survival was significant, estimated sire heritabilities ( $h^2 \leq 0.12$  on the liability scale) were not particularly high compared with values approach-

**Fig. 5.** Marine survival (%) for half-sib families of 1994 brood year chinook salmon (*Oncorhynchus tshawytscha*) released from (a) Glenariffe Stream (30 families) and (b) Silverstream (58 families). Sires have been ordered to emphasise variation between families within sires (–) relative to variation between sires (●). Error bars are based on returns for each sire averaged across both families. Note the low within-sire variation at Glenariffe compared with the high variation at Silverstream. SE, standard error.



ing 1.0 for the timing of adult return and maturation (Quinn et al. 2000) and values of about 0.7 for egg size, fecundity, and ovary mass (Kinnison et al. 2001) calculated for the same families. Timing and egg production are more discrete traits, whereas survival is the resultant of a number of traits, which may strike a different balance within and between families. Traits more closely related to fitness may have lower heritability than traits less correlated with fitness in laboratory (Roff and Mousseau 1987) and wild populations (Kruuk et al. 2000; Merila and Sheldon 2000). Lower calculated heritability may result from little additive genetic variation or considerable residual (environmental or dominance) variation. This latter hypothesis is supported by the work of Merila and Sheldon (2000) and Kruuk et al. (2000) using the coefficient of additive genetic variation rather than heritability. Survival in the ocean is likely to have great environmental

variation so this seems a plausible explanation for the low heritability in our data.

One indication of environmental control over survival was the markedly higher survival for sibling chinook from both study populations when released from Silverstream compared with Glenariffe. Mean release weights at the two locations were either the same (in 1995) or not large enough to account for the difference in survival (1994). Our results do not allow us to differentiate between freshwater and marine influences on survival, both of which may have contributed to the observed differences between the two release locations. Within the freshwater environment, the longer downstream migration path to the sea from Glenariffe Stream, relative to Silverstream (100 vs. 13 km), may have contributed to higher mortality rates before seawater entry. Yearling hatchery chinook released from Glenariffe Stream appear to reach the mouth of the Rakaia River within a few days (Unwin and Lucas 1993), so it is unlikely that differential mortality during this period was the primary reason for the observed differences between the two release locations. However, it is also possible that at the adult end of the life cycle, differences in the cost of upriver migration may affect survival between release sites and populations. Chinook released from Silverstream undertake a much shorter freshwater return migration than their Glenariffe counterparts, which also must gain an altitude of 430 m. These differences impose significant costs on energy reserves and reproductive investment (Kinnison et al. 2001) and could potentially affect survival.

Within the marine environment off the east coast of the South Island, numerous factors (e.g. predators, prey abundance, or ocean currents) potentially affecting survival could differ between the mouths of the two rivers or the larger regions occupied by the salmon as they grow to maturity. The migratory movements of New Zealand salmon at sea are poorly known, although there is some evidence that individual populations have a relatively localised marine distribution, particularly when compared with North American populations (Unwin and James 1998). Coded-wire tag recoveries show that salmon of Rakaia origin commonly stray to rivers north of Banks Peninsula (Unwin and Quinn 1993) but (as noted earlier) that salmon released into the Waimakariri River are only rarely recovered south of this point, suggesting that their respective marine distributions overlap but do not coincide. Differences in the marine environment off these two rivers may be further accentuated by the presence of the Chatham Rise, a prominent undersea ridge east of Banks Peninsula associated with marked north–south gradients in water temperature and salinity (Unwin and James (1998) and references therein). Survival rates for fish released from Glenariffe and Silverstream over the last two decades have tended to be no more than weakly correlated (M.J. Unwin, unpublished data), with higher survival rates for Glenariffe releases during the early to mid-1980s but higher survival for Silverstream releases in the late 1980s and early 1990s.

The implications of this study are that not only does marine survival have a substantial genetic component (through smolt size and less obvious additional mechanisms) among families, but also that population-specific differences can evolve in the comparatively short time frame of about 30 generations. This rapid evolution is particularly striking given the fact that the

New Zealand rivers all discharge into the South Pacific Ocean over a limited (~200 km) length of coastline and that the major salmon-producing rivers (including those in this study) have broadly similar physical characteristics. All lack major estuaries, are comparatively short and steep, flow through broad, gravel-rich braided channels, lack significant tributaries in the middle and lower reaches, and tend to flood in an erratic but synchronous pattern among rivers. We infer that despite these similarities, environmental conditions experienced by their chinook salmon are sufficiently different, and the traits sufficiently heritable, to give rise to locally adapted populations in this brief period of time. This not only presents a window into the rapid evolution of Pacific salmon, but also may provide encouragement to efforts to restore extirpated populations within their native range. Although such efforts will be fraught with difficulties, it is important to know that salmon display considerable scope for evolution.

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